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and are excluded [see supplementary materials, Part 2 (37)]. For each study area, spatially replicate samples were pooled into habitat-level datasets on the basis of sedimentary grain size, seafloor features (bedforms, vegetation, mass properties), and salinity. These habitats are comparable in scale and distinctiveness to sedimentary facies in the stratigraphic record, and were defined independently of faunal data. Habitats are grouped into four broad environments: salt marsh and tidal creek; intertidal flats and channels; coastal embayment (lagoons, estuaries, rias, and other semi-enclosed coastal bays where water energy, salinity, and/or oxygen level are reduced); and shelf (includes shoreface sands above fairweather wavebase, and an array of shallow and deep-water muds, muddy sands, and actively-building and relict shell gravels).

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19. Only 21% of ≤ 1 mm mesh comparisons show a significant correlation by a Sequential Bonferroni test [per W. R. Rice, *Evolution* **43**, 223 (1989)], whereas 84% of > 1 mm coarse-mesh comparisons are significantly correlated after correction. If the threshold mesh is set at ≥ 2 mm, then 100% of datasets show a significant correlation, including after correction.
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26. Fine-mesh death assemblages have slightly lower representation of live species ($87 \pm 6\%$ found dead; 38 data sets with > 100 dead individuals), and lower agreement in species dominance ($68 \pm 6\%$ of dead individuals are from species censused alive). An earlier synthesis using a methodologically variable set of live-dead studies also yielded lower estimates than the present analysis [S. M. Kidwell, in *1998 Belle Baruch Conference on Organism-Sediment Interactions*, J. Y. Aller, S. Woodin, R. C. Aller, Eds. (Univ. of South Carolina Press, Columbia, in press); see supplemental materials for list of studies used (37)].
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29. In general, strong rank-order agreement between a time-averaged death assemblage and a single-cen-

sus of live fauna suggests that either (i) rank-order of the standing live fauna does not change significantly over the duration of time-averaged input, or (ii) community composition does change, but the death assemblage is numerically dominated by the most recent cohort(s) of dead input. The latter scenario is ecologically more likely, and is also consistent with strongly right-skewed frequency distributions of shell age-since-death [e.g., K. H. Meldahl, G. A. Goodfriend, K. W. Flessa, *Paleobiology* **24**, 287 (1998)]. This scenario implies that, although species richness values may well reflect input from the entire duration of time-averaging [e.g., conclusions of (1-3, 10, 12, 14-16, 22)], dominance information might reflect only a final short segment of total elapsed time and thus have higher time-resolution.

30. Additional bias does accrue with lithification and subaerial emergence of marine sedimentary records, even where aragonitic shells persist, but species pres-

ervation is still very high. For example, J. W. Valentine [*Paleobiology* **15**, 83 (1989)] found that 77% of species living today in the Californian Province are preserved in Pleistocene terrace deposits.

31. Supplementary materials are available at www.sciencemag.org/cgi/content/full/294/5544/1091/DC1.
32. I thank original authors for discussion and permission to reanalyze their raw data, L.V. Hedges and C. W. Osenberg for meta-analytic statistical advice via the U.S. National Center for Ecological Analysis and Synthesis, M. Foote and D. Jablonski for early reviews, and the many individuals who assisted my search for datasets, especially associates of the U.S. National Museum of Natural History (Smithsonian Institution), Natural History Museum (London), Texas Bureau of Economic Geology, and California Academy of Sciences.

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The Origin and Evolution of the Woolly Mammoth

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The mammoth lineage provides an example of rapid adaptive evolution in response to the changing environments of the Pleistocene. Using well-dated samples from across the mammoth's Eurasian range, we document geographical and chronological variation in adaptive morphology. This work illustrates an incremental (if mosaic) evolutionary sequence but also reveals a complex interplay of local morphological innovation, migration, and extirpation in the origin and evolution of a mammalian species. In particular, northeastern Siberia is identified as an area of successive allopatric innovations that apparently spread to Europe, where they contributed to a complex pattern of stasis, replacement, and transformation.

Testing among models of species-level evolution in the fossil record ideally requires abundant samples that are finely stratified, accurately dated, and correlated across a broad geographical area (1). Most previous studies of fossil mammals have lacked the resolution to identify lineage splitting in contrast to phyletic change, nor have they offered sufficient geographical spread to distinguish in situ transformation from immigration (2, 3). Among large mammals, the mammoth lineage has one of the most complete records as well as pronounced adaptive morphological evolution through a time of well-studied environmental change. It also allows us to address the issue of geographical variation by sampling correlated sequences in both the European and Siberian parts of the mammoth's Eurasian range.

European mammoths (*Mammuthus*) have conventionally been divided into three chronospecies: the Early Pleistocene *M. meridi-*

onalis [recorded about 2.6 to 0.7 million years ago (Ma)], the early Middle Pleistocene *M. trogontherii* (~0.7 to 0.5 Ma), and the woolly mammoth *M. primigenius* of the late Middle and Late Pleistocene (~0.35 to 0.01 Ma). Important changes through this sequence include shortening and heightening of the cranium and mandible, increase in the height of the molar crown (hypsodonty), increase in the number of enamel bands (plates) in the molars, and thinning of the enamel (4-6) (Fig. 1). The dental changes resulted in increased resistance to abrasion, which is believed to correlate with a shift from woodland browsing to grazing in the open grassy habitats of the Pleistocene.

Critical to our study is the selection of samples that are chronologically restricted and independently dated (7). Dating methods for source deposits include radiometry (e.g., K/Ar or ¹⁴C), electron spin resonance/thermoluminescence, paleomagnetism, amino acid epimerization, first- and last-appearance datum of marine microfossils, and associated mammalian fauna. Samples from ~500,000 years ago (500 ka) onward can be tentatively correlated with marine isotope stages (MIS) (8).

The variable most frequently used in tracing elephantid evolution is lamellar frequency of

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the molar teeth (LF), defined as the number of enamel plates in a 10-cm length of crown (4). Fourteen European samples are plotted in Fig. 2, spanning ~2.6 Ma to 25 ka, and show a largely directional trend: Rank correlation against time is highly significant ($P < 0.001$) (9). This is of adaptive significance, as lamellar spacing is critical to elephant dental function (4). However, the apparently gradualistic sequence is somewhat misleading, because LF can be raised not only by an evolutionary increase in the number of plates in the crown, but also by a simple reduction in size: Isometrically smaller teeth with identical plate counts have more closely spaced plates (10). Because mammoth size varied through the Pleistocene (6, 10), this could be responsible in part for the LF trend.

We have therefore plotted the raw number of plates (P) in complete third molars (Fig. 3A) (11). A second, independent variable, the hypsodonty index (HI), is plotted for third upper molars in Fig. 3B (12); this character is linked to important concomitant changes in skull architecture (deepening of cranium and mandible). The earliest known mammoths, *M. subplanifrons* from southern and eastern Africa (~4 Ma), with very low plate number ($P = 7$ to 9 only) and shallow crown ($HI = \sim 0.6$ to 0.9), are the most primitive sample.

The oldest European population is based on a combined sample from Britain (Red Crag), Italy (Montopoli), and Romania (Cernatesti), all around 2.6 Ma. Hypsodonty is already at typical *M. meridionalis* level, but plate number shows a transitional condition from the African progenitor, with only 9 to 11 plates in third molars.

Typical *M. meridionalis* morphology ($P = 12$ to 14, with outliers at 11 and 15, and mean $HI = \sim 1.2$) is achieved by ~2.4 to 2.2 Ma

(Khapry), and P remains in stasis for around a million years, through ~1.8 Ma (Upper Valdarno, the type area of the species) to Pietrafitta (~1.4 Ma).

Around 1.0 Ma, some samples show little change (13) or slight advancement in P to a range of 13 to 15 [e.g., St-Prest, France (Fig. 3)]. However, an east European sample from the Taman' Peninsula, Azov Sea, codified as the "advanced form" *M. meridionalis tamanensis* (14), shows enhanced variability in the direction of *M. trogontherii* and has been posited as a key "intermediate" between the two species. But although this sample as a whole is intermediate in both P and HI between the type *M. meridionalis* and *M. trogontherii*, it has a rather broad morphological range ($P = 14$ to 19, $HI = 1.3$ to 1.8), and the distribution of these characters is bimodal (Fig. 3) (15), unexpected for a simple anagenetic intermediate.

At around 700 ka, two smaller samples, from Voigtstedt, Germany [*M. meridionalis voigtstedtensis* (16)], and West Runton, England (type Cromerian plus adjacent late Beestonian gravels), are of very similar age (17). They include molars at full *M. trogontherii* level ($P = 19$ to 22, $HI = 1.6$ to 1.9), but also specimens showing persistent "advanced *M. meridionalis*" morphology in one or more characters (Fig. 3) (18). P and HI are only partly congruent at Taman' and Voigtstedt: Some specimens are of "mosaic" morphology (low P, high HI), whereas a few others show "intermediate" values ($P = 16$, $HI = 1.5$) between typical *M. meridionalis* and *M. trogontherii* (Fig. 3).

By ~600 ka, only *M. trogontherii* occurred in Europe, as at Süssenborn, the type locality of the species. The sample from Mosbach (~500 ka, probably MIS 13) is equivalent to Süssenborn in plate number, but shows an increase in mean HI to ~2.0, bringing

it to the maximum level of the lineage, a further example of mosaic change.

Mammoth samples postdating the Anglian/Elsterian glaciation in Europe (~450 ka, probably MIS 12) have often been regarded as early forms of woolly mammoth *M. primigenius* on the basis of increased LF relative to *M. trogontherii* (19, 20). However, the change in this variable is misleading and masks underlying stasis. The rising LF trend (Fig. 2) from Mosbach (~500 ka) through Steinheim (~350 ka) to Ilford (~200 ka) is due entirely to compression of the molar plates resulting from the size reduction experienced by mammoths through this part of the sequence (6, 10). Plate number itself, the true indicator of evolutionary level, remained in stasis at the "*M. trogontherii*" level through the interval 600 to 200 ka (Fig. 3A). Other dated European samples that we have measured—such as Ariendorf, Germany (~300 to 150 ka), Tourville la Rivière, France (~230 ka), and several MIS 7 sites such as Stanton Harcourt, England, and Ehringsdorf, Germany (~200 ka)—corroborate the late persistence of *M. trogontherii* morphology (21).

Moreover, there is evidence that the end of this interval is marked by the simultaneous occurrence in Europe of mammoths of *M. trogontherii* and *M. primigenius* morphology. The sample from Marsworth, UK, of late MIS 7 or early MIS 6 age (~190 to 150 ka) was carefully collected from a single horizon. It shows a wide spread of P values with an apparently bimodal distribution, the two modes closely corresponding in morphology to the immediately preceding (*M. trogontherii*) and succeeding (*M. primigenius*) populations. A similar distribution of P values (18 to 24) is seen in a smaller sample from another site, Brundon (Suffolk, UK), of late MIS 7 age (22).

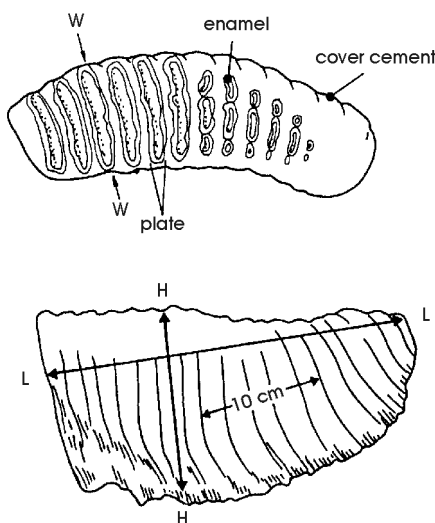


Fig. 1. Diagram of a mammoth molar, in occlusal and lateral views, showing measurements taken. W-W, width; L-L, length; H-H, height (4, 11, 12).

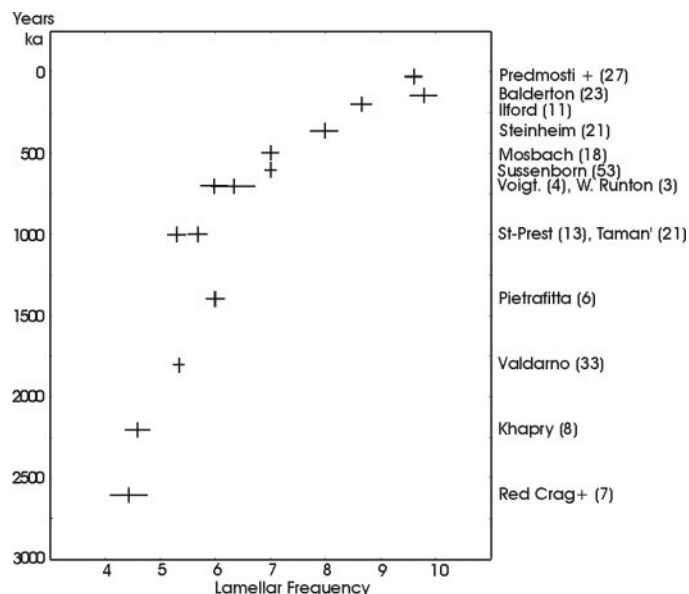


Fig. 2. Lamellar frequency of third upper molars in European mammoths, plotted against linear time. Mean ± 1 standard error shown. For West Runton, only "*trogontherii*" specimens, omitting the "*meridionalis*" molar at $P = 15$ (see Fig. 3A), are included. Sample sizes are in brackets.

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In keeping with this timing for the transition, several samples from MIS 6 (~190 to 130 ka) represent the earliest sole occurrence of *M. primigenius*, fully derived in all characters, in Europe (23). These include La Cotte, Jersey, Channel Islands (UK); Tattershall Thorpe, Lincolnshire, England; Zemst IIB, Flemish Valley, Belgium; and Balderton, Nottinghamshire, England, the latter plotted in Figs. 2 and 3. Similar mean values for all

variables persist in almost all European samples from the “last cold stage” (MIS 4-2) (Figs. 2 and 3). Many of these latest samples do, however, show a marked degree of intra-population morphological spread (Fig. 3), including specimens reminiscent of *M. trogontherii* in P values (24).

Our Siberian sequence shows morphological transitions similar to those in Europe, but persistently ahead of Europe in the timing of

successive morphologies. Our samples are all from northeastern Siberia, between the Lena and Kolyma River valleys; the earliest, from the Early Olyorian, spans 1.2 to 0.8 Ma. From this date or earlier, mammoths in northeastern Siberia were living in an herb- and grass-dominated environment under permafrost conditions (25). The Early Olyorian sample is approximately equivalent to the European Taman’ sample in age but is more derived in plate count, whereas in hypsodonty it corresponds only to the “advanced” mode at Taman’ (Fig. 3). Except in a smaller size of teeth, the Early Olyorian sample is barely distinguishable from *M. trogontherii*, which does not appear in Europe until ~700 ka.

By the Late Olyorian (~800 to 600 ka), mammoths in Siberia approached *M. primigenius* morphology in all characters, anticipating the European sequence by several hundred thousand years; by the Late Pleistocene (~150 to 10 ka), Siberian mammoths exceeded European values in mean plate number (although not in hypsodonty) (Fig. 3), with “relict” *M. trogontherii* morphology much rarer than in Europe.

In sum, the pattern of change in Europe, although incremental on a broad time scale, includes substantial intervals of stasis and—at the two intervals of important transition—bimodality, which suggests more complex populational or cladogenetic processes. In keeping with this pattern, the early development in northeastern Siberia of advanced mammoths similar to later European *M. trogontherii* suggests the origin of this morphology in northeastern Siberia (presumably from an eastern *M. meridionalis* population), followed by its later dispersal to the south and west, where it eventually superseded the indigenous *M. meridionalis* morphology. Previous authors have questioned the simple descent of *M. trogontherii* from *M. meridionalis* in Europe (26) or have suggested the occurrence of two forms of mammoth there in the interval ~1.0 to 0.8 Ma (13), but the source of the more advanced form was not known. It may be significant that the earliest detected *M. trogontherii* morphology in Europe is at the eastern fringes of the continent (Taman’), whereas penecontemporaneous samples in western Europe (e.g., St-Prest) remained at a primitive *M. meridionalis* level.

However, the complexity of variation in Europe between 1.0 and 0.5 Ma, with incremental morphological advancement and mosaic or intermediate specimens within the samples, suggests that Early Olyorian immigrants were not completely reproductively isolated from the contemporary European population, but received some genetic input from it through this period (27). This is consistent with the fact that *M. trogontherii* at West Runton and even Süssenborn are still slightly more “primitive” than the ancestral

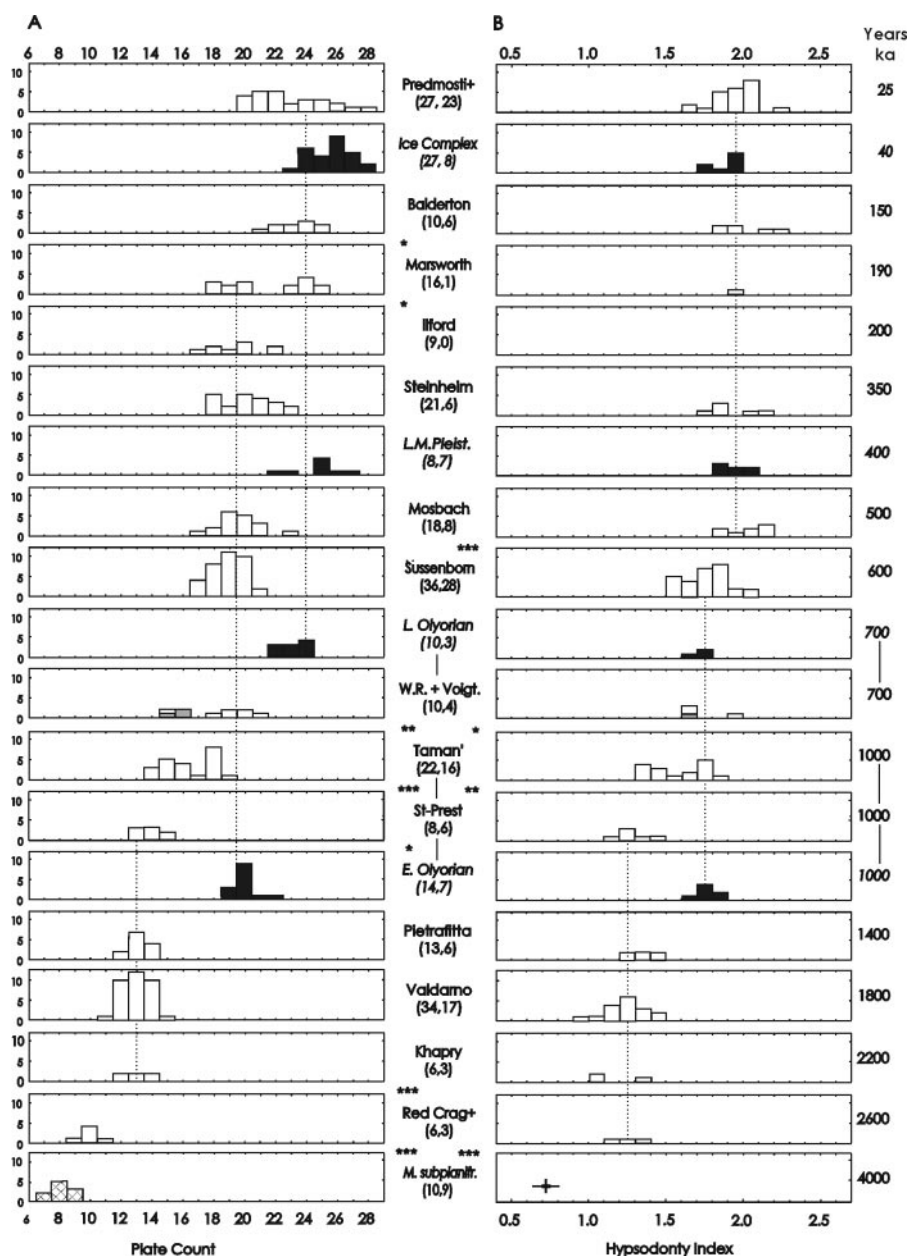


Fig. 3. (A) Plate count (P) of third upper plus lower molars; (B) hypsodonty index (HI) of third upper molars in the mammoth lineage. Open bars: European samples (shaded, Voigtstedt); filled bars and italic names/ages: northeastern Siberian samples; cross-hatched bars, African sample. Solid vertical lines connect sample names of equivalent age. Dotted lines traverse groups of samples (or subsamples, in the case of Taman’ HI and West Runton and Marsworth P) at similar evolutionary level. Asterisks indicate conventional significance levels (two-tailed *t* tests; **P* = 0.05, ***P* = 0.01, ****P* = 0.001) between successive, whole European samples only (i.e., bimodal samples are treated as a whole, and Siberian samples are ignored); P to the left of the central gutter, HI to the right. HI of *M. subplanifrons* is shown as mean ± 1 standard error and 1 standard deviation, from (4). Sample sizes (P, HI) in brackets are after site names.

Early Olyorian population in features such as mean plate number (Fig. 3A) and enamel thickness (28).

In the second part of the sequence, comprising the shift from *M. trogontherii* to *M. primigenius* (~500 to 200 ka), our reappraisal of the European sequence suggests that a transition formerly assumed to be “gradualistic” in fact entails stasis followed by apparent sympatry and then replacement, a conclusion strengthened by the absence of a transitional population in Europe. Previous suggestions of differently adapted mammoth populations in Europe from 200 to 100 ka (29, 30) have been based on remains from a variety of deposits, and so could not distinguish between cladogenesis (implied by sympatry) and rapid anagenesis between populations of slightly differing ages. Moreover, the fossil sequence in northeastern Siberia demonstrates, as early as the Late Olyorian (~800 to 600 ka) and certainly by the late Middle Pleistocene (~500 to 200 ka), mammoths essentially indistinguishable from later European *M. primigenius*. This invites the hypothesis that the transition between the two chronospecies occurred in Siberia, with *M. primigenius* morphology later spreading to Europe.

In this transition as in the earlier one, a modified hypothesis to strict allopatric replacement would be partial introgression from the European to the incoming Siberian population (27). The persistence of some *trogontherii*-like variation within Late Pleistocene European *M. primigenius* is likely to be the heritage of an incomplete genetic barrier between the two species in the Middle Pleistocene, which, in view of the apparent isolation of the two forms at Marsworth, implies complex and variable degrees of isolation within a metapopulation around the time of speciation. In accordance with our model, the rarity of relict *M. trogontherii* morphology in Late Pleistocene Siberia reflects its phyletic transformation into *M. primigenius* there, in contrast to Europe, where both forms may have contributed to later populations.

This study shows that substantial evolutionary transformation can be effected through a sequence of intermediate morphologies over several hundred thousand to a few million years—in this sense “gradual,” or better, incremental (31). It is also clear that different characters change at different times: “mosaic” evolution or, in phylogenetic terms, the order of building of the character complex. In Europe, P increases in several significant steps spread across the interval 2.6 to 0.15 Ma, whereas HI undergoes its major change in two bursts between 1.0 and 0.5 Ma (Fig. 3).

The incremental, directional change observed both in Europe and in Siberia might be accounted for by separate anagenesis, convergent between the two regions. However, from a cladistic perspective, it is more parsimonious to regard the shared dental and cranial features of

Olyorian and European mammoths as evidence of phylogenetic links in the origin both of *M. trogontherii* and of *M. primigenius*, and this is supported by the patterning among samples in time and space. The earlier origin of *M. trogontherii* and *M. primigenius* morphologies in Siberia, and the enhanced variation or bimodality in Europe around the times of transition, are consistent with a critical input from outside, whether by simple replacement or (more likely) by more complex metapopulation processes including hybridization. The pattern of stasis and change in Europe shares elements with a “punctuated equilibrium” pattern of evolution (1–3). However, species origins in this example are not as clear-cut as in classic allopatric models, but apparently proceeded through the differential development of partially isolated populations.

Finally, our data should allow testing of correlations between the pattern of evolutionary change and the shifting paleoenvironments of the Pleistocene. For the moment, we note that the early initiation and persistent advancement of grazing adaptations in Siberian mammoths, compared to those in Europe, was very likely linked to the earlier advent and greater severity and continuity of periglacial conditions in that region (32). Siberia thereby provided a continuing source of grazing-adapted mammoths, which we suggest acted as a repeated source of evolutionary advancement into periodically glaciated Europe.

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and is thus normalized for molar size. In partially worn or damaged teeth, HI was calculated only if plates in the “standard zone” of maximal crown height are preserved unworn (34).

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