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New materials of the steppe mammoth, *Mammuthus trogontherii*, with discussion on the origin and evolutionary patterns of mammoths

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Recently found materials indicate that the steppe mammoth, *Mammuthus trogontherii*, survived in northern China into the late Pleistocene. East Asia is the key area of mammoth evolution after the initial radiation of early forms out of Africa and into Eurasia at the beginning of the late Pliocene (c. 3.5–3.0 Ma). *M. rumanus*, *M. meridionalis*, *M. trogontherii*, and *M. primigenius* probably formed a continuous and transitional evolutionary lineage within the pan-Eurasian mammoth radiation in East Asia. Each speciation event of the Eurasian mammoths was followed by a rapid and large-scale dispersal event: out of East Asia. Allopatric speciation is the main speciation pattern of *Mammuthus*. The climatic vacillation was severe and frequent in East Asia from the early part of early Pleistocene (c. 2.6 Ma) onward, which probably brought about successive speciation in East Asia and the subsequent dispersal of the mammoths.

***Mammuthus trogontherii*, *Mammuthus sungari*, MSE, allopatric speciation, out of East Asia, climate**

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During the last decade, European scholars have made considerable progress in the study of the origin and evolution of mammoths. Owing to the successive discoveries of a series of important fossils, the application of a variety of dating technologies, the gradual unification of terminology and measuring method, the pattern and process of mammoth evolution in Eurasia have generally taken shape. The research of Chinese mammoth fossils lags relatively behind. The taxonomy and biostratigraphy of Chinese Elephantidae fossils have been in a long-term state of chaos, due to the scarcity of remains, weak chronostratigraphy, and poor understanding of foreign fossils plus slow communication with foreign colleagues.

In recent years, some achievements have been gained on the research of Chinese mammoth remains, and the Pliocene-Pleistocene biostratigraphic framework based on

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mammoth fossils of northern China has been established. On the basis of the newly discovered mammoth remains and combined with literature and restudy of the specimens previously reported, this paper further enriches the stratigraphic distribution of mammoth fossils from Eurasia, especially China, and explores the origin and evolutionary model for large terrestrial mammals represented by the mammoth.

1 Taxonomy of new materials and status of *M. sungari* Chow et Chang, 1959

1.1 Material from Weihe River terrace of Gaoling County, Shaanxi Province

Elephantidae Gray, 1821
Elephantinae Gray, 1821
***Mammuthus* Brookes, 1828**
***Mammuthus trogontherii* Pohlig, 1885**

Material: The mesial part of a third right upper molar (Figure 1).

Specimen No.: SMD: 8.

Locality: The northern bank of the Wei River, Shangmadu, Gaoling County, Xi'an City, Shaanxi Province, China, with an altitude of 400 m (34°32′N, 109°04′E).

Horizon: Unclear.

Storage: Shaanxi Provincial Institute of Archaeology.

Geological age: Late Pleistocene.

Dating results: 33.858–24.857 ka BP (Table 1).

Dating laboratory: Radiogenic Isotope Laboratory, Centre for Microscopy and Microanalysis, University of Queensland, Australia.

Sample selection and analytical methods: We use TIMS (thermal ionization mass spectrometric) U-series technique to date dental samples. At first we manually cleaned teeth by polishing any weathered surfaces, and then got about 0.06 g fresh specimen for each sample. The specimens were ultrasonically cleaned in Milli-Q water, dried, and then each of the specimens was spiked with 0.03–0.05 g ^{229}Th-^{233}U-^{236}U mixed tracer (0.03–0.05 g), and totally dissolved in 15.8 mol/L HNO_3. Further chemical treatment and TIMS U-series analytical procedures followed those described in refs. [1, 2].

Discussion (see Table 2 for measurements): This specimen is the mesial part of a moderately worn right M3 of large dimension. With medium thickness, plates are covered with thick and uneven cement. In lateral view, this molar is nearly triangular-shaped without preserved roots while abrasion surface is apparently convex. The cervical line is distinctly visible. Midline of crown obviously curves toward the lingual side. Plates are weakly convergent towards the lingual side in occlusal view. There are only 15 preserved plates leading to uncertainty of the number of original plates, but the reconstruction of the missing distal part of the crown suggests a total plate number of about 18–20 (personal communication with van Essen Hans, 2007).

Abrasion surface of this molar bears typical morphological characters of *Mammuthus* as follows: elasmodont cheek teeth, the enamel layers of the mesial and distal sides parallel with each other; wear figure of some plates typically showing the tripartite structure of two lateral lamellar enamel loops with nearly the same size and rectangle-shaped and one central annular enamel loop (wear figure of *Palaeoloxodon* plates showing the lateral annular and central lamellar structures); the three enamel loops fusing into one single loop with advanced abrasion, with the mesial

Figure 1 *Mammuthus trogontherii* (Pohlig). (a) SMD: 8, Right M3, Occlusal view; (b) SMD: 8, Right M3, Labial view, Shangmadu, Gaoling County, Xi'an City, Shaanxi Province. (c) ZLNE001, Right M3, Occlusal view; (d) ZLNE001, Right M3, Lingual view, Zalainuoer, Manzhouli City, Inner Mongolia Autonomous Region.

Table 1 Original data of the TIMS U-series dating

Sample	U (ppm)	±2σ	^{232}Th (ppb)	±2σ	^{230}Th/^{232}Th	^{230}Th/^{238}U	±2σ	^{234}U/^{238}U	±2σ	Uncorr. ^{230}Th age (ka)	±2σ	Corr. ^{230}Th age (ka)	±2σ	Corr. initial ^{234}U/^{238}U	±2σ
SMD-1	0.5583	0.0004	0.4353	0.006	1452.052	0.37312	0.00385	1.3765	0.0022	33.874	0.410	33.858	0.410	1.4144	0.0024
SMD-2	0.7830	0.0006	0.5576	0.003	1201.165	0.28193	0.00185	1.3664	0.0030	24.872	0.192	24.857	0.192	1.3932	0.0032

Table 2 Comparative measurements for the upper third molars of the three species of *Mammuthus*

Species	Locality of sample	P	L_{max} (mm)	H_{max} (mm)	W (mm)	E (mm)	LF	HI	Source
M. meridionalis	Eurasia	11–14	228.8–317.1	100.2–141.8	85.6–126.4	2.6-4.1	3.7–6.1	93.8–152.7	[3]
		11–15							[4]
	Upper Valdarno, Italy	11–13	240.0–298.0		85.0–122.0		4.5–5.0		[5]
		12–14	220.0–335.0	104.0–147.0	80.0–123.5	2.5-3.8	4.18–6.41	113.0–147.0	[6]
M. trogontherii	Eurasia	14–21	213.0–358.0	118.0–218.0	57.0–107.5	1.5-3.0	6.0–8.2	145.3–304.9	[3]
		17–22							[4]
	China	x17x–x17$^{1/2}$x	264.0–313	160.0–163.0	89–91	⩾2.0	5.8–7.3		[7]
	Süssenborn, Germany	18–23	246.0–400.0	129.0–212.0	73.0-120.0	2.0-3.0	4.0–7.0	143.0–208.0	[5]
M. primigenius	Eurasia & N. America	20–27	226.0–285.0	135.0–188.5	68.0-113.0	1.3-2.0	6.5–11.1	164.6–211.8	[3]
Present specimen	SMD: 8 (Xi'an)	∞15+ (about 18–20)	222+	189+	115.0	3.0	6.1	164.3+	
	ZLNE001 (Zalainuoer)	x19x	280+	212	104	2.4	6.6	203.8	

and distal sides of the loop parallel with each other; the distally and/or mesially prominent, small and pointed structure (loxodont sinus) absent at the central part of plate.

In this specimen, it is the type of enamel fold that most of all indicates points to the direction of a mammoth. In *Palaeoloxodon* specimens, the enamel fold is more intense and at the same time more regular. Especially deep loops (amplitude more than twice the enamel thickness) occur both at the median line and from there at regular intervals in buccal and lingual direction. In mammoths, there seems to be a kind of "hesitation" in the enamel to commit to a direction of folding. In this specimen, for example, in certain places there is very little enamel folding, and in others it may be stronger, but it is never as sharp and regular as in *Palaeoloxodon*.

This specimen must be assigned to the genus *Mammuthus*. All the measurements of this molar, such as plate number (P), lamellar frequency (LF), enamel thickness (E), and width (W) and height (H) of crown, fall within the ranges of *M. trogontherii* (Table 2). The above characters preclude the possibility of referring the M3 to *M. primigenius* and *M. meridionalis*.

U-series dating results show that this specimen is probably the latest record of *M. trogontherii* anywhere in the world. Previously, the latest global record of *M. trogontherii* was from Marsworth, England with the date 200—150 ka [4, 8].

1.2 Material from Zalainuoer, Inner Mongolia

Elephantidae Gray, 1821
Elephantinae Gray, 1821
***Mammuthus* Brookes, 1828**
***Mammuthus trogontherii* Pohlig, 1885**

Material: The complete third right upper molar (Figure 1).

Specimen No.: ZLNE001.

Locality: Lingquan Strip Mine, Zalainuoer, Manzhouli City, Inner Mongolia Autonomous Region (49°20′N, 117°35′E).

Horizon: Bottom of the alluvium of the Zalainuoer old riverbed.

Storage: Zalainuoer History and Culture Museum.

Geological age: Late Pleistocene.

Absolute age: c. 33.7 ka BP (AMS ^{14}C) [9].

Discussion (measurements see Table 2): Similar to the above specimen, abrasion surface of this molar bears typical morphological characters of *Mammuthus*. The enamel layers of the mesial and distal sides are parallel with each other in medium or advanced wear. The labio-lingual length of the central enamel loop is nearly equal to those of the two lateral enamel loops (in *Palaeoloxodon*, the central part is rather wider mesio-distally than the lateral parts, showing an elongated rhombic shape). A prominent and obtuse mesial and/or distal median sinus is developed in the central part (in *Palaeoloxodon*, a small and acute loxodont sinus is visible in the same position). There are irregular folds of enamel layer in this specimen (viz., strong folds in places, little folding elsewhere). This specimen should be referred to the genus *Mammuthus* for all the measurements of the molar, especially plate number, fall within the range of this species.

As the type materials of *M. sungari* Chow et Chang, 1959 (mammoth skeletons unearthed from Zalainuoer, Inner Mongolia Autonomous Region), are well-known, *M. sungari* is till employed by Chinese scholars for local *Mammuthus*. However, we consider that the specific name is a synonym of *M. trogontherii* for the following reasons.

Firstly, when Zhou and Zhang [10] erected *M. sungari*, there were only referred specimens without a holotype, which violated paleontological nomenclatural rules. Meanwhile, the referred specimens, most of which were M1/m1, M2/m2 and P/p, were very few and lacked skull material or complete M3/m3, which are most significant for identifying mammoths at the specific level. The only M3 (V. 2053) was broken, without distinct characters.

Secondly, the formal diagnosis of *M. sungari* is very ambiguous and it could not be distinguished qualitatively or quantitatively from other species of *Mammuthus.*

Further, the typical materials of *M. sungari* assigned by

Chow and other researchers, after restudy, can be shown to be referred to *M. trogontherii* (such as one third left m3 from Ji'xian County, Heilongjiang Province [11]) or *M. primigenius* (such as the skeleton from Zhaoyuan County, Heilongjiang Province [12]) respectively according to morphological characters and measurements.

Lastly, the general acceptance of the specific name *M. sungari* by most of the Chinese scholars mainly depends on its gigantic stature and the more primitive morphological characters compared with *M. primigenius* specimens; these two points are just the main characters of *M. trogontherii.*

To date, three mounted skeletons have been considered to represent *M. sungari*, i.e., the skeletons of No.1, No.2 and No.3 from Zalainuoer. The first two are exhibited in Inner Mongolia Museum whereas the last one is conserved in the Zalainuoer History and Culture Museum. There is also a mounted mammoth skeleton from Zhaoyuan, Heilongjiang, preserved in Heilongjiang Provincial Museum. Compared with the mixed mounting of No.1 and No.2 skeletons, the 80% recovery of No.3 skeleton is more credible. The height of the mounted No.3 skeleton is 4.33 m, which is almost the same as the height of the large *M. trogontherii* skeleton from Europe.

According to Wang Zhengyi of Zalainuoer History and Culture Museum (personal communication, 2008), the above M3 is from the same locality and horizon as No.3 mammoth skeleton. Being similar, they are likely the same species. The measurement of one complete third m3 (with complete plate number of 18 and enamel thickness of 3 mm) [13] also falls within the range of *M. trogontherii*. According to the present data, the three skeletons of mammoth, as well as the above M3, should be referred to *M. trogontherii.* The mammoth skeleton from Zhaoyuan, with the height of 3.33 m after mounting (c. 21.2 ka BP) [12], is similar in size to the remains from NE Siberia and Europe and should be referred to *M. primigenius.*

Remains previously assigned to *M. sungari* can be divided into two morphologies after restudy. The primitive type represents an advanced remnant group of *M. trogontherii*, probably the latest record of that species. A derived form represents *M. primigenius* migrated from NE Siberia. Relative to the Late Pleistocene *M. primigenius* from NE Siberia and Europe, the *M. trogontherii* from northern China had more primitive characters and gigantic stature, and the evolutionary level of the latter is nearly the same as *M. columbi* from North America. It is difficult to judge whether this group should be divided into spatial or temporal subspecies, or whether *M. trogontherii* and *M. primigenius* overlapped spatially or temporally in northern China, due to the scarcity of materials and the inadequate degree of study.

With climate fluctuations and environmental changes, the remnant group of Chinese *M. trogontherii* ranged in 35°–50°N during the late Pleistocene. There was a large-scale cooling event during 40–30 ka, pushing southward *M. primigenius* into the Jin'an area [14]. The time interval largely agrees with the latest record of Chinese *M. trogontherii*. Consequently, it is most probable that during this cooling event the latest *M. trogontherii* gave way to *M. primigenius*, which migrated from NE Siberia with the latitudinal shift in steppe environment.

2 Evolution and dispersal patterns of Eurasian mammoths

2.1 Origin and evolution of species of *Mammuthus*

The generalized mammoth genus *Mammuthus* originated during 5–4 Ma from Africa, where the early Pliocene species *M. subplanifrons* Osborn, 1928 and the late Pliocene-early Pleistocene species *M. africanavus* Arambourg, 1952 were named [3]. The former taxon incorporates the earliest known mammoth materials living in African tropical circumstances and may be the ancestor of all mammoths flourished in Eurasia and North America. *M. africanavus* is considered as the descendant of *M. subplanifrons* and an evolutionary "dead end" restricted to Africa [15].

So far, five continental mammoth species are generally accepted by different authors for Eurasia and North America: *M. rumanus* Stefanescu, 1924, *M. meridionalis* Nesti, 1825, *M. trogontherii* Pohlig, 1885, *M. primigenius* Blumenbach, 1799, and *M. columbi* Falconer, 1857. In addition, there are still some small-sized or pygmy mammoth types in the islands of Eurasia and North America, such as *M. protomammonteus* from Japan, *M. lamarmorae* from Sardinia, and *M. exilis* from Channel Islands, California. *M. protomammonteus* from Japan is a small-sized mammoth without dwarfism. This paper emphasizes the four kinds of Eurasian continental mammoth species.

The earliest Eurasian mammoth fossils are named *M. rumanus* because the holotype was found in the Dacic Basin, Romania. The first emergence of this species is almost at the same time in both Europe and China, i.e., mammalian biozone MN16a, correlated to palaeomagnetic data in the middle Gauss subchron, c. 3.5–3.0 Ma [4, 16]. The first appearance of *M. rumanus* in Eurasia follows the first important dispersal event of mammoth lineage: Out of Africa, as well as the shift of center of the mammoth evolutionary lineage. *M. rumanus* is known to have survived until the early part of early Pleistocene (c. 2.5 Ma) in Europe [4, 17], but somewhat earlier in China [7, 16]. Due to the scarcity of materials, it still needs further study concerning the locus and time of origin of *M. rumanus* in Eurasia.

The holotype of *M. meridionalis* was found in Upper Valdarno, Italy, situated in southern Europe. The distribution of *M. meridionalis* was limited in Eurasia and nearby islands. The temperate forest environment of Europe during most of the interval of 2.0–0.7 Ma [15] was advantageous to the survival and evolution of *M. meridionalis*. The earliest European *M. meridionalis* (*M. gromovi,* coined by Alexeeva and Garutt, 1965, for remains from the Khapry Faunal Complex in the south of European Russia) is now dated to early Pleistocene, early MN17, 2.6–2.2.2 Ma [18] or 2.4–2.2 Ma [8]. The emergence of *M. meridionalis* in West Europe was somewhat later than that in East Europe, such as at the Chilhac site in France with the age of 2.0 Ma [4, 8] and the Upper Valdarno, Italy with 2.0–1.77 Ma [19].

The most primitive *M. meridionalis* remains from China, originally identified as *Archidiskodon planifrons* by Wang [20], were found in Houhecun, Dali, Shaanxi, including relatively complete skull and postcranial material. According to the original plate and description of Wang [20], these materials are most similar to the typical specimens of *M. meridionalis* both from Europe and China. Specifically, the Houhecun mammoth is probably in a more primitive evolutionary stage than the Khapry mammoth. As the most important indicator of the evolutionary level of mammoth, the lowest complete plate number of M3 observed in Khapry fossils is 12 [4, 17] while that of the Houhecun remains is only 11 [20]. The age of the Houhecun fauna correlates to the Matuyama-Gauss palaeomagnetic transition [21], c. 2.6 Ma, which is a little earlier or equal to the age of Khapry remains.

There are remains of *M. rumanus*, the precursor of *M. meridionalis*, in the Youhe Formation subjacent to the Houhecun Formation. These two species, without obvious overlap, display continuity in temporal distribution and morphological characters [4, 7, 16]. On the contrary, there has not been any record of *M. rumanus* remains in the Khapry district. *M. meridionalis* most likely originated from northern China at c. 2.6 Ma and subsequently rapidly spread westward to Europe with *Equus* from North America. The major growth of global ice at about 2.6 Ma occurred, while the arctic icecap appeared and the Bering Landbridge formed [21].

Micro-mammal fossils and ostrich eggs from Houhecun also indicated a dry and cool grassland environment, whereas the Youhe fauna complex including *M. rumanus* suggested a moist and temperate forest environment [20]. It is probable that just the cooling event provided selection for the faunal change, also for the origin of *M. meridionalis* from an indigenous *M. rumanus* population. There were likely environmental differences for *M. meridionalis* between east and west. On the one hand, European *M. meridionalis* adapted to a temperate forest environment and was replaced by the eastern *M. trogontherii* at the early part of middle Pleistocene c. 0.7 Ma [4]. On the other hand, East Asian *M. meridionalis* had adapted to dry and cool grassland environment around 2.6 Ma. With climatic fluctuations in East Asia, mammoths gradually adapted to withstand cold and dry conditions and finally evolved to *M. primigenius*, which possessed long fur and survived in the tundra.

The first emergence of *M. meridionalis* and *Equus* in Eurasia is called the Elephant-*Equus* event. However, long-term ambiguity on the definition of "Elephant" caused controversy on defining the first appearance of "Elephants" in Eurasia as the beginning of the Quaternary. Generally, "Elephant" includes members of Elephantinae, such as the extinct genera of *Primelephas*, *Palaeoloxodon*, and *Mammuthus*, as well as the extant genera of *Elephas* and *Loxodonta*. The mammoth evolutionary lineage in Eurasia is one of continuous evolution, extensive distribution, and distinct characters. The first emergence of one new species in the lineage can be the basis of geological age division. However, there is temporal and regional asynchronization on biological and climatic events, while palaeomagnetic reversal events are globally simultaneous. Thus, it is preferable to avoid biological events as the basis of geological age division, and we adopt the international dividing standard based on palaeomagnetic reversal events passed by the International Commission on Stratigraphy (ICS) in May, 2009. According to this new dividing standard, the Pleistocene/Pliocene boundary locates at the Matuyama/Gauss reversal (c. 2.6 Ma).

The earliest global *M. trogontherii* remains were recovered *in situ* from Majuangou-3, Nihewan basin, China, with palaeomagnetic dating of 1.66 Ma, and North China is considered as the locus of origin of *M. trogontherii* [22, 23]. Among the steppe mammoth fossils recovered in China, one complete M3 from Pinglu, Shanxi [11] has only 17 complete plates while other measurements (such as Lamellar Frequency and Hypsodonty Index) also show more primitiveness than among the Majuangou materials [16]. The M3 from Pinglu most likely represents the earliest and most primitive steppe mammoth. Unfortunately, there is no exact locality and horizon record of this molar.

As discussed above, *M. trogontherii* in China survived to the late Pleistocene. The steppe mammoth experienced a large-scale dispersal from northern China during 1.5–1.2 Ma. Firstly, it spread northward to NE Siberia, and then entered North America via Bering Landbridge where it evolved to the large-sized local taxon *M. columbi*, which became extinct in the late Ice Age, c. 11 ka BP. Secondly, it migrated eastward to Japan and evolved as an insular species *M. protomammonteus*, which became extinct around 0.5 Ma [4, 24]. Lastly, it dispersed westward to Europe via the Middle East, and displaced the local *M. meridionalis* around 0.7 Ma [4, 8]. In Europe, the replacement of *M. meridionalis* by *M. trogontherii* was intertwined with a complex pattern of stasis, transformation, and hybridization [4, 8].

M. primigenius (wooly mammoth) adapted to dry and cold environment and originated from *M. trogontherii* in NE Siberia as early as 0.8 Ma [8]. The primitive *M. primigenius* spread westward to Europe, eastward to North America via the Bering Landbridge and southward to China and Japan. The insular group of *M. primigenius* survived as late as 3.7 ka [25]. Based on the present data, the first appearance of *M. primigenius* in North China and Northeast China was probably no earlier than 40 ka. The Chinese *M. primigenius*, with continental *M. primigenius* from Eurasia and North America together, became extinct at the end of the Ice Age, c. 11 ka BP.

2.2 Patterns of mammoth evolution

During the late Pliocene and Pleistocene, the mammoth lineage experienced eight Mammoth Speciation Events (MSE), resulting in the emergence of five continental species (*M. rumanus*, *M. meridionalis*, *M. trogontherii*, *M. primigenius* and *M. columbi*) and three insular species (*M. protomammonteus*, *M. lamarmorae* and *M. exilis*). The pattern and process are shown in Figure 2. It is probable that the transformation within *M. rumanus*, *M. meridionalis* and *M. trogontherii* occurred in northern China whereas the shift from *M. trogontherii* to *M. primigenius* took place in NE Siberia.

As the dominant speciation mode for mammoths, allopatric speciation can be further divided into peripatric speciation and vicariance speciation [26]. The appearance of *M. rumanus* (MSE1), *M. columbi* (MSE5), *M. protomammonteus* (MSE6), *M. lamarmorae* (MSE7) and *M. exilis* (MSE8) apparently belongs to the typical vicariance speciation (geographic speciation) whereas the emergence of *M.meridionalis* (MSE2), *M. trogontherii* (MSE3), and *M. primigenius* (MSE4) accords with peripatric speciation (see Figure 2). Recent work has tended to emphasize the power of local habitat variation, rather than mere isolation, in driving peripheral populations to speciation via adaptive natural or sexual selection [4, 27].

As discussed above, the geological distribution of every species of the genus *Mammuthus* indicates regional asynchronization (see Figure 3). During the process of mam-

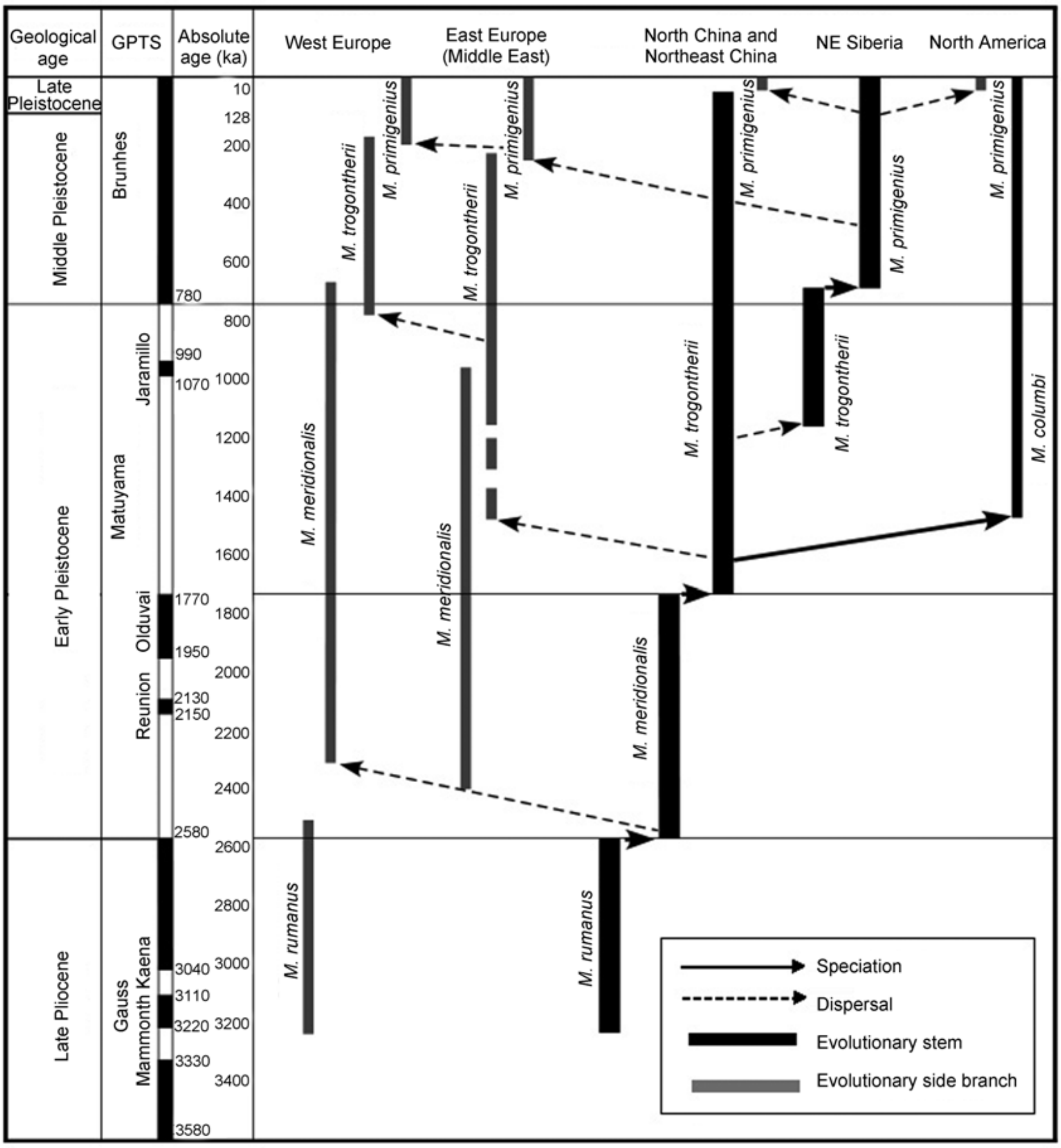

Figure 2 Stratigraphic distribution of Eurasian and North American *Mammuthus* (excluding insular species).

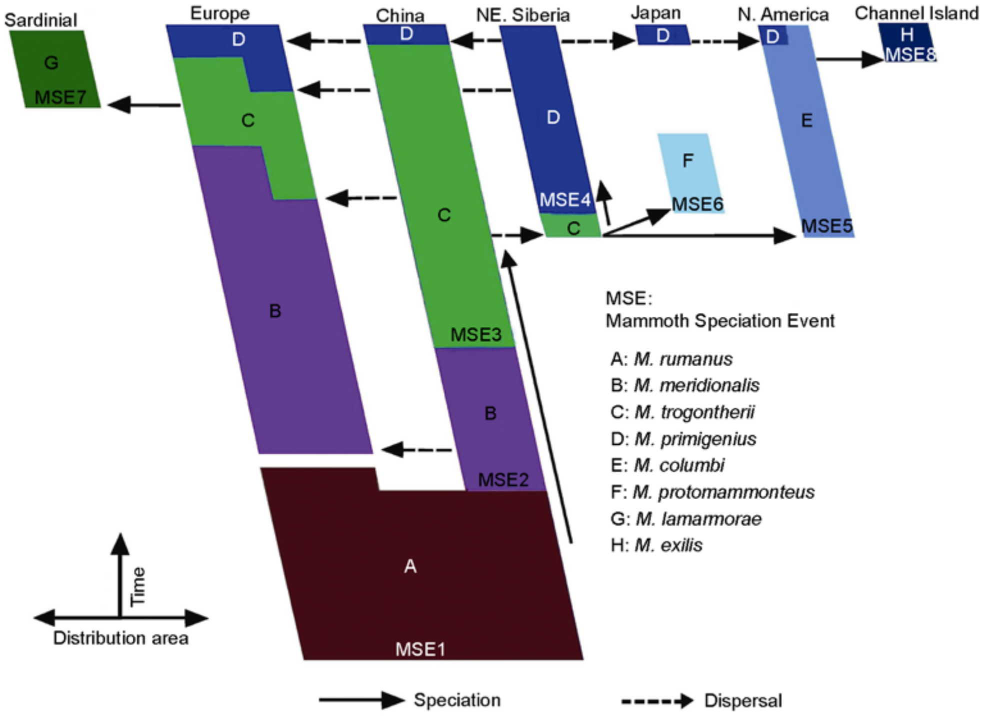

Figure 3 Model of Eurasian and North American mammoth evolution and dispersal at specific level.

moth evolution, there is large-scale dispersal after each speciation event. The dispersal route in the late Pliocene was from Africa to Eurasia (Out of Africa). Later in the Pleistocene, the mammoth evolution and dispersal center turned to East Asia including northern China and NE Siberia. The main dispersal routes of mammoths are from East Asia westward to Europe and eastward to North America (Out of East Asia).

The relationship between mammoths and humans deserves discussion. The coexistence of mammoth fossils and human remains or artifacts in many Paleolithic sites of Eurasia since the Pleistocene indicates that mammoths and humans inhabited the same biozone for a long time. For example, the coexistent interval of steppe mammoths and humans was at least 0.6 Ma in the Nihewan Basin of North China. The interval between the age of Majuangou site and Donggutuo site both including *M. trogontherii* fossils and artifacts was 1.7–1.1 Ma [16]. At the Majuangou site, one recovered rib of *M. trogontherii* with distinct chopping and scraping traces demonstrates mammoth-hunting by humans. There is synchronization between mammoth speciation and human evolution. The emergence of *Australopithecus afarensis*, *Homo rudolfensis*/*Homo habilis*, *Homo erectus,* and *Homo heidelbergensis* may correlate with the evolution of *M. rumanus* (3.5–3.0 Ma), *M. meridionalis* (2.6–2.5 Ma), *M. trogontherii* (1.8 Ma), and *M. primigenius* (0.8 Ma). On the other hand, the appearance of new species of mammoth, as many other terrestrial mega-mammals, closely follows palaeomagnetic reversal or global climatic events. Detailed study is required concerning the correlations within the above factors.

During the evolution and dispersal of the mammoth lineage, morphological variations of the skull, mandible, and molars reflected environmental selection and corresponding adaptation. For example, the evolutionary trends of molars could be recognized as increase of plate number and height of crown and decrease of cement thickness, strengthening the chewing ability. Mammoths from moist and warm tropical or subtropical forest environments of Africa adapted to dry and cool grassland environments of the mid-latitude or cold tundra at high latitude. Correspondingly, the food source was also broadened from arbor (fruit, bark and leaf) and shrub to herb; the former were rich in nutrition, easily edible and less wearing on molars while the latter were poor in nutrition, difficult to chew and more abrasive.

An increasing number of scholars recognizes that the evolutionary trend or rate of terrestrial mega-mammals mainly depends on the changes of climate and ecology. It is probable that mammoths and humans were able to spread out of Africa successively or simultaneously just because of the remarkable climatic and environmental changes after the late Pliocene. From the data of deep-sea records in the South China Sea [28] and loess deposit sequence [29], East Asia experienced frequent and dramatic climate fluctuations since the early part of early Pleistocene, c. 2.6 Ma. The uplift of Tibet is probably one important reason of the global climate deterioration [30]. Climatic fluctuations since the early part of early Pleistocene probably stimulated successive mammoth speciation and dispersal events out of East Asia.

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