



The origin of Eurasian Mammoth Faunas (*Mammuthus*–*Coelodonta* Faunal Complex)



Ralf-Dietrich Kahlke¹

Senckenberg Research Institute, Research Station of Quaternary Palaeontology, Am Jakobskirchhof 4, D-99423 Weimar, Germany

ARTICLE INFO

Article history:

Received 25 July 2012

Received in revised form

21 November 2012

Accepted 8 January 2013

Available online 26 March 2013

Keywords:

Mammoth Fauna

Mammuthus–*Coelodonta* Faunal Complex

Pleistocene

Eurasia

ABSTRACT

Pleistocene Mammoth Faunas were the most successful, cold-adapted large mammal assemblages in the history of the Earth. However, the causes for their emergence can not be attributed only to the global trend of climate cooling which occurred during the Neogene/Quaternary period. The formation of the Eurasian *Mammuthus*–*Coelodonta* Faunal Complex was a result of interacting tectonic, geographical, climatic, ecological and phylogenetic processes. The key environmental factors controlling the origin and evolution of Palaearctic cold-adapted large mammal faunas were successive aridification of major parts of Eurasia, rhythmic global climatic cooling with prolonged and intensified cold stages, and increasing continentality.

Between 2.6 Ma and around 700 ka BP, largely independent mammal faunas became established in continental Asian steppe regions as well as in the circumpolar tundra. Both faunal complexes were adapted to open environmental conditions but were largely separated from each other. The principal requirements in order for species to evolve into members of Mammoth Faunas are progressing adaptation to aridity, decreasing temperatures and rapid temperature fluctuations. Eurasian Mammoth Faunas were mainly composed of the descendants of either Central Asian steppe or Arctic tundra faunal elements. The majority of species of Central Asian origin emerged in regions north of the Himalayan–Tibetan uplift. Between 640 and 480 ka BP, saiga, musk-ox and reindeer occasionally spread far beyond the limits of their respective traditional areas, thus anticipating the subsequent merge of steppe and tundra originated species in Eurasian Mammoth Faunas.

During the pronounced cold period of MIS 12, tundra species regularly expanded south- and south-westward into a newly formed type of biome, the so-called tundra-steppe. In parallel, species originating from the Asian steppe dispersed into new habitats north and northwest of their ancestral distribution areas. This drastic faunal turnover led to the formation of the earliest pan-Eurasian Mammoth Fauna at around 460 ka BP. The sister taxa of several species involved in Mammoth Faunas underwent separate evolution in Central Asia, thus indicating ecological differences between the Asian core steppe and Eurasian tundra-steppe habitats. During temperate and humid stages of the late Middle to Late Pleistocene periods the transcontinental reach of the steppe-tundra biome collapsed. As a result, the majority of the characteristic mammal species were forced back to continental steppe or Arctic tundra refugia, only returning during subsequent cold stages when the formation of a new and more evolved Mammoth Fauna began. The maximum geographic extension of the Palaearctic *Mammuthus*–*Coelodonta* Faunal Complex occurred during the Late Pleistocene, when it covered an area of up to 190 degrees of longitude and 40 degrees of latitude.

© 2013 Elsevier Ltd. All rights reserved.

E-mail address: rdkahlke@senckenberg.de.

¹ This paper is dedicated to Alan Turner, a friend and colleague for over 26 years. The ideas contained in this paper were first presented at the Vth International Conference on mammoths and their relatives in Le Puy-en-Velay (France) in 2010. Alan attended this conference and was back on form following some sad years in his life. “To meet old friends”, he said. For many of us it proved to be our last meeting. His good company is a memory that we will treasure.

1. Introduction

Over a period of 15 million years, a global climatic cooling trend, which culminated in the spectacular glacial periods of the Quaternary, combined with drastic environmental changes to produce a profound effect on the origin of species and the development of their ecology, as well as on the formation and dispersal of faunal assemblages. Mammoths and their faunistic companions have long

been subjects of study as indicators for Northern hemispheric cold climatic conditions (e.g. Soergel, 1940; Garutt, 1964; Vereshchagin and Baryshnikov, 1982; Guthrie, 1990a and references therein). For the Palaearctic branch of Mammoth Faunas two species, both named by Blumenbach (1799, p. 697), became eponymous – *Mammuthus primigenius*, the woolly mammoth, and *Coelodonta antiquitatis*, the woolly rhinoceros. After Pei (1957) initially used the expression “*primigenius–antiquitatis* fauna” for Asian cold adapted mammal assemblages of Late Pleistocene age, Chow et al. (1959) introduced the name “*Mammuthus–Coelodonta* fauna”. The closely similar term *Mammuthus–Coelodonta* Faunal Complex, designating transregional expanded, cold-adapted large mammal assemblages of the Eurasian Pleistocene with similar or identical faunistic structures, was proposed by R.-D. Kahlke (1994).

Based on the model of the Eurasian Mammoth Steppe and its end-Pleistocene breakup (Guthrie, 1990b), preliminary ideas on the origin of the *Mammuthus–Coelodonta* Faunal Complex have been sketched by R.-D. Kahlke (1994, 1999). Since then, knowledge of Quaternary climate and faunal history has increased tremendously. Both the evolution and dispersal of *Mammuthus* and *Coelodonta* have been subjects of recent research (Lister et al., 2005; Kahlke and Lacombat, 2008; Álvarez-Lao et al., 2009; Deng et al., 2011), as have been other species involved in Palaearctic Mammoth Faunas. However, an up-to-date synopsis on the origin of the Eurasian *Mammuthus–Coelodonta* Faunal Complex as a whole is still missing. Such a synopsis requires the determination of the variety of transregional processes that caused the principal palaeoenvironmental preconditions of the formation of Eurasia's Mammoth Faunas. A closer look at the palaeoecological circumstances of the origins of its key species reveals principal prerequisites needed to qualify mammals as potential candidates to join the future *Mammuthus–Coelodonta* Faunal Complex. In order to clarify its main faunistic sources, the contexts from where its most significant members derived must be elucidated. Tracing back through their evolution and distribution makes it possible to draw a general picture of the significance of pan-Eurasian Mammoth Faunas.

2. Preconditions of the origin of Eurasian Mammoth Faunas

2.1. Aridification

After the African and Indian tectonic plates had broken away from Gondwana – the southern of the two precursor continents that split off the huge Pangaea supercontinent during the Mesozoic – they moved into the Northern Hemisphere. The resulting collision with Eurasia started during the Eocene at c. 53–49 Ma. This collision gave rise to an orogenic belt that extends from the Atlantic to the Pacific Ocean. In Central Asia the Tibetan plateau and the Himalaya mountains were raised up, increasingly preventing the influx of moisture from the Indian and western Pacific Oceans into Asia's interior (Ruddiman and Kutzbach, 1989; Guthrie, 1990b, 2001; Ramstein et al., 1997; Burbank et al., 2003, Fig. 2; Molnar, 2005; Wang et al., 2006 etc.). The onset of the Indian and East Asian monsoons is dated at around 9–8 Ma (An et al., 2001). Regions north of the Himalayan–Tibetan uplift, located in the monsoonal shadow, gradually suffered aridification. The Central Asian core steppe formed and was controlled by an enormous, stable high-pressure system (Guthrie, 2001). Successive expansions of steppe landscapes in Asia and, moreover, in Eurasia as a whole, are clearly reflected in the Neogene mammal record (Fortelius et al., 2006; Zhang, 2006).

Progressive aeolian deposition north of the Himalaya, documented by increasing dust accumulation rates within loess and red-earth sequences (Guo et al., 2002, 2004), establish that rising aridity occurred from the onset of the Pleistocene at 2.6 Ma

onwards. During Pleistocene cold periods the aridification of the Palaearctic was supported by advances of the Scandinavian ice shield and ice coverage of the North Atlantic, both of which reduced the inflow of moisture to the continent (Guthrie, 2001).

2.2. Cooling and continentality

The Cenozoic is characterised by a trend of decreasing global temperatures that started after the Paleocene–Eocene Thermal Maximum around 56–55 Ma. Following the Mid-Miocene Climatic Optimum, a warm interlude from 17 to 15 Ma, global cooling intensified to culminate during the glacial periods of the Pleistocene (Zachos et al., 2001). Progressive increases of ice-rafted debris occurred in the North Atlantic from 3.0 Ma onwards, with a synchronous ice sheet development in Greenland, Scandinavia and North America around 2.7 Ma (Flesche Kleiven et al., 2002). Thierens et al. (2011) have established the occurrence of contemporaneous expansion of both high- and mid-latitudinal ice sheets in the North Atlantic region from 2.6 Ma onwards. Similar records of ice rafting provide evidence of a more or less synchronous increase of glaciation in the North Pacific area (Krissek, 1995). During the 2.8–2.7 Ma interval, sea surface winter temperatures of the Subarctic Pacific Ocean dropped significantly and winter floating ice became more abundant (Haug et al., 2005). In adjacent areas of north-east Siberia and north-west North America (Western and Eastern Beringia at that time) permafrost was formed for the first time, as has been confirmed by ice wedge pseudomorphoses, e.g. from 2.9 to 2.7 Ma old sediments of Quartz Creek near Dawson City (Yukon Territory, Canada; Westgate and Froese, 2003), and from those of the Kutuyakh Beds at the Krestovka River (Yana-Kolyma lowland, Yakutia, Russian Federation) dated at around 2.5 Ma (Sher et al., 1979; Sher, 1987 and pers. comm. to the author 2003; Fig. 1).

In addition to the successive aridification of major parts of Eurasia paralleled by global cooling, the Paratethys shrinkage had a drastic consequence for climate change, driving the Neogene/Quaternary environmental conditions across Asia and Eastern Europe to increasing continentality (Ramstein et al., 1997). During glacial periods, lowered sea levels exposed a large continental shelf along Eurasia's northern and north-eastern edges that led to increased continentality at higher latitudes. Moreover, during periods of advancing glaciations, the periodical deflection of larger portions of the Gulf Stream southward up to the African coast reduced the temperatures and moisture that the Atlantic current brought into Europe (Guthrie, 2001).

3. Faunal resources of Eurasian Mammoth Faunas

3.1. The general view

In order to clarify the main faunistic sources of Eurasia's Mammoth Faunas, a review of the regions where its most significant members originated from is helpful. Based on the earliest fossil records, it becomes evident that the majority of genera that produced significant elements of cold adapted Mammoth Faunas, such as *Saiga*, *Bison*, *Alces*, *Megaloceros* and *Coelodonta*, originated during the Plio- to early Middle Pleistocene periods in the Palaearctic, particularly in Asia (R.-D. Kahlke, 1999, pp. 67ff., Table 3; Lister, 2004, p. 223; see also Section 3.2.). Occasionally, as in the case of *Ovibos*, *Rangifer* and *Alopex*, a clear establishment of Palaearctic or Beringian origins seems impossible – a problem which might be a purely academic one.

A number of genera with Ethiopian roots, such as *Mammuthus*, *Crocota* and *Panthera*, in addition to different groups of horses (*Equus*) which undoubtedly originated in the Nearctic, also

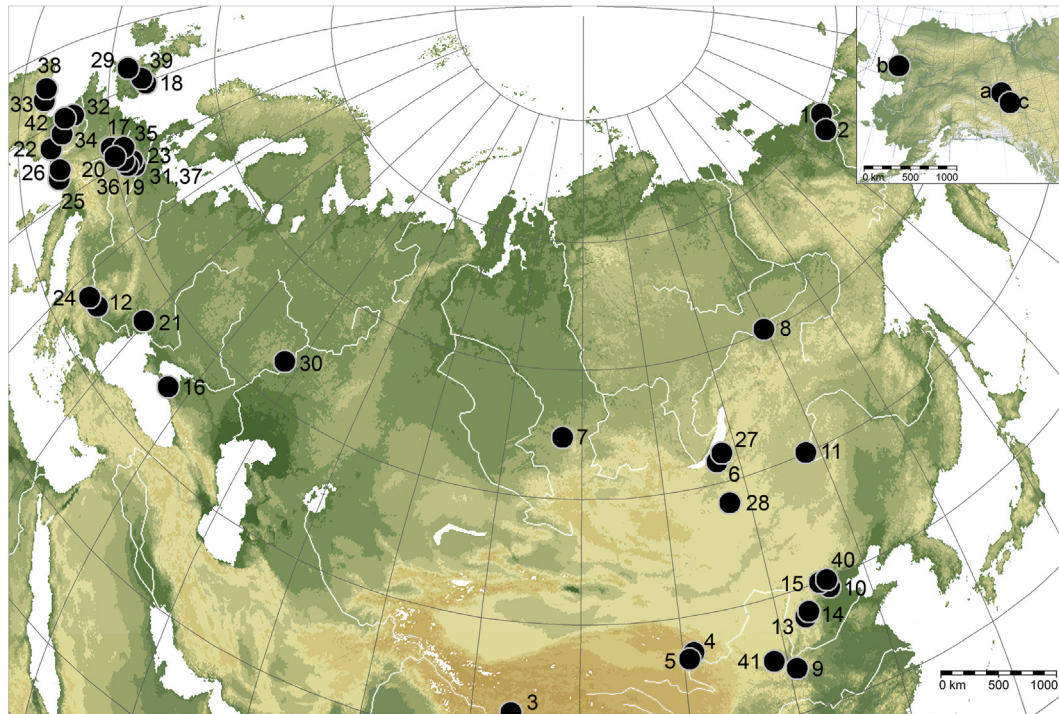


Fig. 1. Plio-/Pleistocene key sites in the order of appearance in the text. Palaeartic: 1 – Krestovka River; 2 – Kolyma (Olyorian complex); 3 – Zanda Basin; 4 – Longdan; 5 – Shitougu; 6 – Tologoj 2.5; 7 – Kuznetsk Basin; 8 – Olekminsk; 9 – Hsihoutu (=Xihoudu); 10 – Zhoukoudian, Loc. 1, 9 and 12; 11 – Zhailainoer; 12 – Cernastesti; 13 – Ch'in Hsien (Qinxian); 14 – Liyucun; 15 – Majuangou; 16 – Sinaya Balka; 17 – Dorn–Dürkheim 3; 18 – West Runton; 19 – Süßenborn; 20 – Mosbach 2; 21 – Kolkotova Balka; 22 – Arago cave; 23 – Bad Frankenhausen; 24 – Kozarnika; 25 – Le Vallonnet; 26 – l'Escale; 27 – Zazukhino 2 and 3; 28 – Nalaikha; 29 – Westbury-sub-Mendip; 30 – Ulushka; 31 – Freyburg/Unstrut; 32 – Grotte de la Chaise, Abri Suard; 33 – Abauntz cave; 34 – La Fage; 35 – Ariendorf 1; 36 – Weimar-Ehringsdorf; 37 – Markkleeberg; 38 – La Parte; 39 – Crayford; 40 – Yuxian; 41 – Gaoling; 42 – Fontéchevade. Nearctic: a – Quartz Creek; b – Cape Deceit; c – Fort Selkirk.

contributed to Eurasia's Mammoth Faunas. However, species of these groups were indigenous elements of Palaeartic faunas long before cold adapted Mammoth Faunas evolved. For example, *Mammuthus* is known from Old World sites going back to the Late Pliocene (see Section 3.2.). Eurasia's first pantherine cats, the Eurasian jaguars (*Panthera onca* ssp.) appeared during the Early Pleistocene Olduvai polarity subchone, i.e. between 1.95 and 1.77 Ma (Hemmer et al., 2010). Large lions (*Panthera fossilis*), descendants of African ancestors, have been documented in western Palaeartic interglacials from 680 to 600 ka BP onwards (García García, 2003; Hemmer, 2011). *Equus* immigrated via Beringia at around roughly 1.5 Ma, and the first caballine horses are stated to have been in Asia by, at least, around 700 ka (Eisenmann, 2006). Spotted hyenas arrived from Africa shortly prior to the onset of the Middle Pleistocene at 800 ka (R.-D. Kahlke et al., 2011). All of these early immigrants gave rise to native Palaeartic descendants which developed special adaptations and matured into the elements of Mammoth Fauna assemblages.

The autochthonous character of Old World Mammoth Faunas becomes even more evident when considering the species/sub-species level of the taxa involved. According to the stratigraphically earliest records, nearly all of the larger mammal species that were distributed in transregional belts within the range of Eurasian Mammoth Faunas were of Palaeartic origin, in some cases inclusive of the Beringian landmass as a whole. This applies in particular to *Saiga* and *Ovibos* (see Sections 3.2. and 3.3.), a wide variety of *Bison priscus* subspecies, *Alces alces*, megacerine deer species of the subgenera *Megaloceros* and *Sinomegaceros*, woolly rhinoceroses (*Coelodonta*; see Section 3.2.), numerous forms of caballine equids, Old World steppe and woolly mammoths (*Mammuthus*; see Section 4.2.), pantherine cat species of the cave lion group (*P. fossilis*, *P. spelaea*), northern forms of spotted hyenas and evolved cave hyenas

(*Crocota crocuta* ssp., *C. crocuta spelaea*), as well as polar fox (*Alopex lagopus*, see Section 3.3.) (R.-D. Kahlke, 1999, pp. 68ff.).

3.2. Faunal elements of inner continental origin

Phylogenetic ancestors of a significant number of trace species of Eurasian Mammoth Faunas, such as saiga (*Saiga borealis*), woolly rhinoceroses (*Coelodonta tologoiensis*, *C. antiquitatis*) and steppe mammoth (*Mammuthus trogontherii*) descended from species of Central Asian origin.

Whereas an immediate phylogenetic ancestor of *Saiga* has not yet been discovered, the genus most probably originated in Central Asia, as is indicated by the closely related extant chiru, also called orongo or Tibetan antelope (*Pantholops hodgsonii*), living in the steppe of the Tibetan high plateau. In respect to the saigas' specialised anatomy, with extremely reduced nasal alae, it appears that the genus had already been undergoing autonomous evolution since the Miocene, a view that was first held by Bannikov (1963). Nevertheless, the earliest evidence of saiga (*Saiga* sp.) in the fossil record known to date is reported from the late Early to early Middle Pleistocene of the Olyorian complex (1.2–0.6 Ma BP) at the lower reaches of the Kolyma River (Yakutia, Russian Federation; Sher, 1987). During the late Middle and Late Pleistocene cold periods *Saiga* spread far into the western Palaeartic (see Section 4.4.).

Based on the skull morphology, different chronological and/or geographic types of *Saiga* are distinguishable. The separation of a slightly larger, northern and western distributed group of *S. borealis* (with subspecies), inhabiting mammoth steppe biomes (see Section 5.2.), from a smaller and lighter built group of *Saiga tatarica* (with subspecies) from Central Asian steppe to semidesert habitats was substantiated by Baryshnikov and Tikhonov (1994). Recent analyses

of ancient DNA sequences (Campos et al., 2010b) do not contradict such a model.

A significant mammalian genus with which to trace back the evolutionary history of the Eurasian Mammoth Fauna is *Coelodonta*. Its earliest representative, *Coelodonta thibetana*, recently dated at c. 3.7 Ma, is represented by a complete skull and skeletal elements from the Zanda Basin in the foothills of the Himalayas in SW Tibet (Deng et al., 2011). Its morphology shows the principal traits of *Coelodonta*, such as dolichocephalic skull proportions, a strong nasal horn boss in addition to a smaller one for the frontal horn, and an occiput indicating a habitual low-slung head position for feeding at ground level. Remains of a stratigraphically younger species, *Coelodonta nihowanensis*, dated at 2.55–2.16 Ma, were discovered in loess deposits at Longdan and Shitougou (Gansu, China; Deng, 2002; Qiu et al., 2004). These cursorial rhinos were still smaller in size than early Middle to Late Pleistocene *Coelodonta* and possessed extremely slender limbs (Deng, 2006). Further discoveries of *C. nihowanensis* have been reported from several Chinese localities in the provinces of Hebei, Shanxi and Qinghai, 2.4–1.0 Ma in age (compilation in Kahlke and Lacombe, 2008). All of these records indicate a phylogeographic origin of *Coelodonta* in continental regions of Central Asia.

A more evolved form, *C. tologojensis*, is described from Tologoj 2.5 in western Transbaikalia (Buryatia, Russian Federation; Belyaeva in Vangengejm et al., 1966) immediately above the Early-/Middle Pleistocene (Matuyama/Brunhes) boundary (Alexeeva et al., 2001) and from additional sites in Transbaikalia and Mongolia (compilation in Kahlke and Lacombe, 2008). An isolated find from the Kuznetsk Basin (Foronova, 1999) indicates the initial westward expansion of this group of rhinoceroses into south-west Siberia around the onset of the Middle Pleistocene. *Coelodonta* probably did not spread into northern Asia before 600 ka, as rhinoceros remains are completely lacking in the extended fossil record of the Olyorian fauna (1.2–0.6 Ma; Sher, 1986, 1987; Lister and Sher, 2001). One single find, from the vicinity of the town of Olekminsk on the Lena River (southern Yakutia, Russian Federation), may indicate *Coelodonta*'s first advance to the north during the early Middle Pleistocene (Boeskorov, 2001). Following the restriction of the range of the genus to continental Asia for more than three million years, at around 460 ka during MIS 12, an extended phase of low temperature and aridity prevailed in western Eurasia, providing, for the first time, an opportunity for a far westward directed spread of woolly rhinoceroses of *C. tologojensis* evolutionary level (see Section 4.3.).

A separate group of little-studied large and slender *Coelodonta* survived in more temperate habitats south of areas occupied by *C. tologojensis*/*C. antiquitatis*, and probably never spread out of this area. The skull from Hsihoutu (= Xihoudou, Shanxi; Chia and Wang, 1978, pp. 28ff.), of uncertain Early Pleistocene age (1.27 Ma after Zhu et al., 2003), might belong to this group of lightly built *Coelodonta*, along with finds described as *C. antiquitatis yenshanensis* from Zhoukoudian, Loc. 1 (Sinanthropus Site), 9 and 12 (Hebei; Chow, 1978, 1979) and two skeletons from Zhalaioer in northern Inner Mongolia (R.-D. Kahlke, 2006, Fig. 2).

Members of the genus *Mammuthus* (*M. trogontherii*, *M. primigenius*) were key elements of the Middle and Late Pleistocene *Mammuthus*–*Coelodonta* Faunal Complex. Mammoth evolution began in the African Pliocene some 4.0 Ma BP with *Mammuthus subplanifrons*, an initial form with 7–9 plates in its M3 (Maglio, 1973; Kalb and Mebrate, 1993; Markov, 2010 and references therein). During the 3.5–2.5 Ma (Late Pliocene to earliest Pleistocene) interval, the first mammoths migrated from Africa via the Levantine corridor into the western Palaeartic. These finds are commonly merged as *Mammuthus rumanus*, with 8–10 plates in their M3 (Lister and van Essen, 2003; Lister et al., 2005; Van Essen,

2011). Material from Cernătești (= Dealul Calului, Dolj, Romania) of 3.2–3.0 Ma, recently described under the name *Archidiskodon stefanescui* by Obada (2010; no complete M3 available so far), might represent the earliest (i.e. Early Villafranchian) evolutionary stage of mammoths in Europe. There is also evidence for the early spread of mammoths of the *rumanus*-group to the east, as far as northern China (Wei et al., 2006). An upper M3 from Ch'in Hsien (Qinxian, Shanxi, China) contains 9 plates. Moreover, one of Asia's earliest mammoth records, the find from Liyucun (Yushe Basin, Shanxi), is roughly dated to between 3.4 and 2.8 Ma.

Between 2.6 and 0.7 Ma, *Mammuthus meridionalis* [sensu Lister et al., 2005, i.e. inclusive of fossils formerly separated as *Mammuthus gromovi* with 11(upper)/12(lower)–15 plates in the M3; see Garutt and Bajguševa, 1981, Table 2] dispersed over most of Eurasia's moderate latitudes. During this span of time molar hypsodonty and lamellar frequency increased, paralleled by a corresponding decrease of enamel thickness and a change of cranial proportions towards higher peaked skulls (for data see Lister and Sher, 2001; Lister et al., 2005 and references therein). During the Olduvai polarity subchron, around 1.7 Ma, *M. meridionalis* entered the New World via Beringia (Agenbroad, 1985; Morgan et al., 1998; Van Essen, 2011), thus forming the ancestry of an independent American branch of mammoth evolution. Advanced forms of Eurasian *M. meridionalis*, described under various (local) subspecific names (evaluation in Van Essen, 2011, pp. 132ff.), appeared until 700 ka. *M. meridionalis tamanensis* of Eastern Europe had 13–18 plates in the M3 (Garutt, 1986).

Whereas late forms of *M. meridionalis* survived in zones of more or less moderate climatic conditions well into the early Middle Pleistocene, as early as 1.8–1.7 Ma, Central Asia's continental environment caused an evolutionary thrust towards more advanced forms of mammoth. The earliest record of *M. trogontherii*, with 17 plates in its M3, was recovered from sediments of the 1.36–1.66 Ma interval at Majuangou (Nihewan Basin, Hebei, China; Wei et al., 2003, 2006). Following Cai et al. (2008, p. 141), the Majuangou fossils might even predate 1.8 Ma, but such a date has been questioned (Deng et al., 2009, p. 22). However, *trogontherii* mammoths obviously originated during the Early Pleistocene, between the Olduvai and the Jaramillo subchrons, in continental steppe regions north of the Himalayan–Tibetan uplift, to become candidates of the later *Mammuthus*–*Coelodonta* Faunal Complex. A major spread of *M. trogontherii* into Asia's North is to be assumed around 1.2 Ma, recorded by finds with 19–22 M3 plates from the north-east Siberian Early Olyorian (1.2–0.8 Ma; Sher, 1987, named *Arctelephas* sp. at that time; Lister and Sher, 2001).

More or less synchronously, at the onset of the Epivillafranchian, *M. trogontherii* also occurred in the western Palaeartic. The mammoth molars from the site of Sinaya Balka (southern Russia), dated to c. 1.2 Ma (Shchelinsky et al., 2010), range in their mean measurements, intermediating between typical *M. meridionalis* and *M. trogontherii* (Lister, 1996). However, Lister et al. (2005) point to the bimodal variety in the M3 plate number (14–19) and hypsodonty index. Something similar was found in the mammoth molar series of Dorn-Dürkheim 3 (Rheinland-Pfalz, Germany), dated to immediately before the onset of the Brunhes chron, at around 800 ka (Franzen et al., 2000). By excluding taphonomic processes as an explanation for the repeated occurrence of bimodal morphology in mammoth molars at various western Palaeartic sites of late Early Pleistocene age, populations of both *M. meridionalis* and *M. trogontherii* may have synchronously occupied different areas of the region during the 1.2–0.8 interval. Most probably, the fossil record reflects populations of different evolutionary level, shifting their distribution seasonally or with short-term climatic circles to either replace each other in corresponding areas, or even interbreed occasionally in hybrid zones, as

might be indicated by individuals with obvious mosaic morphology (Lister, 1996; Van Essen, 2003; Lister et al., 2005).

Mammoths of typical *M. trogontherii* morphology regularly occurred in western Palaearctic regions during the 800 to 400 ka interval. Prominent finds are the skeleton from Kostolac (Serbia), between 1.0 Ma and 400 ka in age, and that from West Runton (Norfolk, UK) of c. 700 ka (Lister and Stuart, 2010; Lister et al., 2012). Also remarkable are extended dental series from Süßenborn (Thüringen, Germany) of probably MIS 16 age (c. 640–620 ka; absolute data of isotope stages rounded after Bassinot et al., 1994), from Mosbach 2 (Hessen, Germany) of MIS 15 or 13 (c. 620–480 ka) and those from Kolkotova Balka (Tiraspol, Transnistria) of similar chronostratigraphic position (compilation in R.-D. Kahlke et al., 2011). The morphometric analyses of early Middle Pleistocene trogontheroid mammoths, which are especially well studied in Europe, do not support the idea of gradualistic mammoth evolution in the western Palaearctic. Rather, they suggest a model of a complex pattern of change and replacement of populations with repeated immigrations of advanced forms from Asia (Lister and Stuart, 2010). Whereas the hypsodonty index and plate count in western Palaearctic late Middle Pleistocene (c. 450–200 ka) mammoths resemble typical *M. trogontherii*, their body size was smaller, thus producing a lamellar frequency similar to that of later *M. primigenius*. Accordingly, it seems to be reasonable to assign late Middle Pleistocene mammoths of the western Palaearctic until c. 200 ka to late forms of *M. trogontherii* (Lister et al., 2005). Such a view is supported by a restudy of late Middle to Late Pleistocene material of north-eastern Chinese ‘*Mammuthus sungari*’, a species accepted by most Chinese authors (e.g. Liu and Li, 1989) as a local mammoth form. We et al. (2010) have now assigned less advanced *sungari*-representatives to *M. trogontherii*. Whereas *M. trogontherii* most probably originated in northern China, persisting there for more than one million years, the well studied region of the Nihewan Basin was never occupied by *M. primigenius* (Tong, 2010a).

3.3. Faunal elements of Arctic origin

Synchronously with a marked drop of global temperatures from about 2.7 Ma onwards, and with the progressing development of glacial phenomena in high latitudes, permafrost formed in northernmost Asia and northern North America (see Section 2.2.). For the first time a circumpolar tundra belt evolved. This new type of landscape opened up ecological niches into which new groups of plants and animals were able to spread. As a result, a number of specialised mammal species originated which were adapted to the new tundra biocoenoses. Key species of the later Eurasian Mammoth Faunas with Far Northern faunal roots were musk ox (*Ovibos moschatus*), reindeer (*Rangifer tarandus*), woolly mammoth (*M. primigenius*) and polar fox (*Alopex lagopus*).

There is little clarity concerning the origin of the musk oxen. Several forms of *Ovibovini* are known from the Neogene (compilation in R.-D. Kahlke, 1999, p. 65), although their skull morphology does not render it very likely that any of them can be considered as the immediate stem form of Pleistocene musk oxen. Whereas even the phylogenetic relationship between the well recorded genera *Praeovibos* and *Ovibos* is not yet clarified, the former is documented by stratigraphically older finds. *Praeovibos mediterraneus* appeared during the Early Pleistocene, approximately between 1.8 and 1.0 Ma, especially in Mediterranean influenced regions (compilation in Crégut-Bonnoure, 2007, p. 82). A younger form, *Praeovibos priscus*, was distributed over most of the Palaearctic and beyond into Eastern Beringia during the 900–400 ka interval (compilations in Crégut-Bonnoure, 1984, 2007, p. 84; McDonald et al., 1991). This species has been recorded mainly in open landscapes with cool and/or continental influenced climatic conditions. Outstanding

material was found in the Arago cave (Pyrénées-Orientales, France; Crégut and Guérin, 1979) and near Bad Frankenhausen (Thüringen, Germany; Staudinger, 1908). A third species, *P. beringiensis*, obviously adapted to open landscapes in higher latitudes, is recorded from Beringia some time between 1.2 and 0.8 Ma (Sher, 1971, 1987; McDonald et al., 1991). DNA and protein analyses by Campos et al. (2010a) support a close phylogenetic relationship between *Praeovibos* and *Ovibos*.

The origin of evolved musk ox (*Ovibos moschatus* ssp.) most probably paralleled the genesis of the first Holarctic tundra belt from c. 2.7 Ma onwards. Accordingly, the hypothetical centre of musk ox origin is presumed to lie in the circumpolar tundra zone. Nevertheless, the earliest evidence of fossil *Ovibos* known to date is recorded from riverine gravels at the site of Süßenborn (Thüringen, Germany; H.-D. Kahlke, 1963a), probably of MIS 16 age (c. 640–620 ka). The sporadic occurrence of musk oxen remains within the rich fossil vertebrate assemblage of this Central European site seem to reflect the occasional appearance of seasonal (winter) immigrants from Arctic regions (Soergel, 1939; R.-D. Kahlke, 1999).

Another animal of Arctic origin that joined with the Palaearctic Mammoth Fauna was the reindeer, *Rangifer tarandus*. This species is a highly specialised telemetacarpal deer of the subfamily Odocoileinae. Based on mitochondrial cytochrome b genetic analysis, Randi et al. (1998) have proposed that a split of Odocoileini and Rangiferini tribes had already occurred during the Middle Miocene. The earliest fossils of caribou, described as *Rangifer* sp., are recorded from Eastern Beringia, namely from the Early Pleistocene of Cape Deceit (Seward Peninsula, Alaska) of perhaps 1.8 Ma (Guthrie and Matthews, 1971, p. 496; Storer, 2002, 2003) and from the slightly younger site of Fort Selkirk (Yukon, Canada), dated at around 1.7–1.5 Ma BP (Storer, 2003, 2004; Harington, 2011). Late Early to early Middle Pleistocene finds of *Rangifer* ex gr. *tarandus* have also been identified in Western Beringia, in the 1.2–0.6 Ma dated Olyorian sequence of north-east Siberia (Sher, 1987). As assumed for the musk ox, *Rangifer* is also believed to have originated in the northern tundra belt. However, because of the general scarcity of larger mammal remains of Plio-/Early Pleistocene age in boreal and Arctic regions, the origin of reindeer/caribou can not be yet dated with any certainty. Nevertheless, its parallel evolution with the developing tundra from c. 2.7 Ma onwards appears the most reasonable scenario.

Over a long span of time, from the Early Pleistocene to the late Middle Pleistocene, *M. trogontherii* found suitable enough environmental conditions in order to persist in the majority of the western and central parts of the Palaearctic (see Sections 3.2. and 4.4.). Synchronously, between 800 and 600 ka BP (Late Olyorian), in north-eastern Eurasia indigenous *M. trogontherii* started to transform into more evolved forms of mammoth, as is expressed by an increase of M3 plate numbers to 22–24 (Lister et al., 2005). Continuous cold conditions, which probably fluctuated less on an annual and interannual basis than in inner continental regions of Eurasia, in combination with Far Northern vegetation phaeology, caused the speciation of *M. primigenius*. The *primigenius* stage was present in NE Asia from 400 ka onwards, i.e. at least 200 ka earlier than in the western Palaearctic (Lister and Sher, 2001).

Having been a regular element of the *Mammuthus*–*Coelodonta* Faunal Complex, the polar fox *Alopex lagopus* is clearly a carnivore of northern origin. Nevertheless, earliest Palaearctic fox remains of the genus *Vulpes* are reported from the Ruscinian/Villafranchian transition (c. 3.4 Ma) and the onset of the Villafranchian (Spassov, 2000 and references therein). Recorded from Middle to Late Villafranchian (2.6–1.2 Ma) western Palaearctic faunal assemblages (compilation in Koufos, 1993; Garrido, 2008), *Vulpes alopecoides* is commonly held to be the stem species of the evolutionary line towards cold adapted (“polar”) foxes. *V. alopecoides* was an animal

of a size similar to that of the extant polar fox and with a certain preference of open steppe-like habitats (R.-D. Kahlke, 1999, pp. 96f.). From the beginning of the Pleistocene onwards it developed and expanded parallel to the spread of open landscapes (R.-D. Kahlke et al., 2011). A form of probably analogous evolutionary level was described under the name *Vulpes chikushanensis* from contemporaneous sites in China (discussion in Qiu et al., 2004, pp. 171f.).

The scarcity of fossil fox remains of late Early to Middle Pleistocene ages causes uncertainties in our knowledge about the origin and early evolution of the polar fox. Whereas Bonifay (1971, p. 143) regards *Vulpes praeglacialis* as a synonym of *V. alopecoides*, other students separate the former as a more evolved species from the latter (e.g. Spassov, 1999). *V. praeglacialis* is recorded from various European sites of the 1.2–0.4 Ma interval, such as the lower levels of Kozarnika (north-western Bulgaria), Le Vallonnet (Alpes-Maritimes, France) and l'Escale (Bouches-du-Rhône, France) (compilation in R.-D. Kahlke et al., 2011). Whereas this species obviously survived the MIS 12 (Elsterian) cold stage, it is unlikely that its latest representatives gave rise to the origin of *Alopex*. However, the remains of a fox from the Olyorian (1.2–0.6 Ma) fauna of north-east Siberia, published as *Alopex* sp. (Sher, 1987, p. 100), imply that the centre of origin of polar foxes is to be found within the late Early to early Middle Pleistocene Arctic tundra belt.

4. Precursors and stages of Eurasian Mammoth Faunas

4.1. Early Asian steppe faunas

The Early Pleistocene global temperature fluctuations that followed a 41 ka periodicity (Lisiecki and Raymo, 2005) did not obviously affect the principal tendency of aridification of Central Asia. A series of Early to earliest Middle Pleistocene (c. 2.6–0.7 Ma) fossil vertebrate sites illustrate the faunal character of the inner Asian steppe before the formation of pan-Eurasian Mammoth Faunas. Of particular interest are the Middle Villafranchian finds from Longdan (Gansu, China; Deng, 2002; Qiu et al., 2004), the Late Villafranchian assemblages of the Nihewan Basin (Hebei, China; compilations in Qiu, 2000; Wei, 2009), the Late to Epivillafranchian faunas of Zazukhino 2 and 3 in western Transbaikalia (Buryatia, Russian Federation; Vangengejm et al., 1990), those from the late Early Pleistocene (>900 ka) deposits of Nalaikha near Ulaan Baatar (Mongolia; Zhegallo et al., 1982; Sotnikova, 1988; Eisenmann and Kuznetsova, 2004), and finds from the earliest Middle Pleistocene fossil layer of Tologoj 2.5 at the Selenga river (Buryatia; Vangengejm et al., 1966; Alexeeva et al., 2001; Alexeeva and Erbajeva, 2006).

The bovids of these sites are predominantly represented by forms increasingly adapted to continental steppe or semi-arid environments, such as the multiform genus *Gazella* (Longdan, Nihewan, Nalaikha, Tologoj 2.5) and the group of spiral-horned antelopes, from *Spirocerus wongi* to *S. kiakhtensis* (Nihewan, Zazukhino 2 and 3, Nalaikha, Tologoj 2.5). Moreover, *Leptobos* was successively replaced during the Middle and Late Villafranchian by early members the genus *Bison*, a process which has also been observed in western Palaearctic regions (R.-D. Kahlke, 2007a). This substitution probably reflects a transcontinental expansion of steppe-like environments.

Some ecological differences between the Chinese large mammal associations and the Transbaikalian and Mongolian ones, probably caused by chronological as well as palaeogeographical reasons, are apparent. Thus the faunas from Longdan and Nihewan include several cervid genera, such as *Eucladoceros*, *Rusa* and *Elaphurus*, with at least partial forest adaptation, which do not occur in more northerly sites of Central Asia. Accordingly, the areas covered by the Chinese sites may have been characterized at certain times by, at

least, some woodland. However, from the Transbaikalian Zazukhino 3 site the remains of *Capreolus* cf. *suessenbornensis*, *Alces* cf. *latifrons* and those of an indeterminable megacerine have been recovered. All of these species are attributable to a more or less open landscape.

Early forms of *Coelodonta* were the dominating rhinoceroses in all of the key site faunas (see Section 3.2.). However, they did not spread out of Central Asia until 600 ka. The life style of Early Pleistocene *C. nihewanensis* was that of a cursorial mixed feeder with a certain preference for grazing behaviour. Early Middle Pleistocene *C. tologojensis* continued to develop the feeding strategy of a grazer in meadow to forest steppes (Kahlke and Lacombat, 2008). Other species indicating open environments are the equids, represented in most cases by the morphologically variable *Equus sanmeniensis* group (Nihewan, Zazukhino 3, Tologoj 2.5). The large horse from Longdan, *Equus eisenmanni*, has been identified as a hard grass feeder (Qiu et al., 2004). *E. nalaikhaensis* from Mongolia shows some hemione-like features (Eisenmann and Kuznetsova, 2004) which also may suggest a grazing life style.

Most of the mentioned Central Asian key sites produced some remains of *Mammuthus*, although dental remains suitable for detailed investigations are usually lacking. In any case, the earliest record of steppe mammoth *M. trogontherii* originates from the Nihewan basin (see Section 3.2.).

The range of genera from the above localities includes a variable multiplicity of carnivores. Characteristic felids are early pantherine cats (*Panthera* ex gr. *palaeosinensis*), early cheetahs (*Acinonyx pardensis* s. l.; Hemmer et al., 2011) and dirk toothed cats (*Megantereon*). A variety of small canids seem to have been the result of prevailing open landscapes (Longdan, Nihewan). Other species, such as *Pachycrocuta* ex gr. *brevirostris/sinensis* (Longdan, Nihewan, Zazukhino 3, Nalaikha), *Canis* (*Xenocyon*) ex gr. *lycaonoides* (Zazukhino 3, Nalaikha) and *Canis variabilis* (Zazukhino 3, Nalaikha), were not restricted to the Central Asian steppe zone but had a wider range of habitat preferences (R.-D. Kahlke et al., 2011; see Section 4.2.).

For Early Pleistocene to earliest Middle Pleistocene periods the picture which emerges is one of a relatively independent evolution of continental Asian steppe faunas, which ranged from the foothills of the Himalaya up to Mongolia and Transbaikalia. Only a few species have also been recorded from the contemporaneous faunas of the Arctic tundra (see Section 4.2.). Over long spans of time both faunal complexes were substantially separated from each other by taiga-like forest belts (Arkhipov et al., 2005; Fradkina et al., 2005; Nikitin, 2006).

4.2. Early Beringian tundra faunas

Mammal fossils of Early Pleistocene age are rare in the Far North. Therefore the influence of global climate variability, inclusive of the recently recorded Arctic “super interglacials” (Melles et al., 2012), on the evolution and spatial distribution of early tundra faunas is relatively unknown. Palaearctic vertebrate records have mainly been obtained from sections in the north-east Siberian Yana-Kolyma lowland (Sher, 1986, 1987, 1992). Quite diverse material was collected from sites of the Epivillafranchian to early Middle Pleistocene Olyorian complex (1.2–0.6 Ma BP; Sher, 1986, 1987). The Early Olyorian (= Chukochyan), covering the 1.2–0.8 Ma span, is separated from the Late Olyorian (= Akanian) of 800–600 ka.

During the Early Olyorian the abundant group of musk oxen comprised different forms of *Praeovibos* (*P. beringiensis*, *P. cf. priscus*, *P. sp.*; Sher, 1987), which had probably developed different affinities to open landscapes. Compared to *Ovibos*, members of *Praeovibos* apparently possessed a greater ecological variability, so that the latter genus was widely dispersed from south-west Europe to north-east Siberia during the Early Pleistocene. Remains of

sympatric *Ovibos* with strict adaptation to tundra landscapes have not yet been recorded at high altitudes, but are assumed to be there (see Section 3.3.). Another typical Beringian bovid, *Soergelia* sp., an animal the size of the western Palaearctic *Soergelia elisabethae* but with a slightly different morphology of its horn cores (H.-D. Kahlke, 1969a; Sher, 1987; R.-D. Kahlke, 2007b), was not adapted to extreme cold and/or corresponding aridity. Like *Praeovibos*, it did not survive the Middle Pleistocene.

During the whole span of the Olyorian, the early reindeer *Rangifer* ex gr. *tarandus* with its clear tundra adaptation was abundant, in some cases accompanied by elks of the *Alces latifrons* group (Sher, 1986, 1987), which are also indicators of open environments. As a rare faunal element of at least the Akanian period, an early form of elaphine deer (*Cervus* ex gr. *acoronatus*) appeared more or less synchronously with its correspondingly earliest records in the western Palaearctic (R.-D. Kahlke et al., 2011). However, its ecological niche is still little-known.

Whereas rhinoceroses were completely lacking in Olyorian assemblages (see Section 3.2.), the fossil record illustrates the abundance of different species of horses. Particularly prevalent was *Equus verae* and its related forms, in addition to more advanced caballines close to *E. mosbachensis* (Sher, 1971, 1987), a group which predominantly dispersed under cool to cold environmental conditions in grasslands. *Mammuthus trogontherii* first appeared in Beringia around 1.2 Ma BP (Lister and Sher, 2001) to transform during the Middle Pleistocene into *M. primigenius* (Lister et al., 2005) (see Section 3.3.).

The guild of Olyorian carnivores, as far as is known, appears to be less indicative of the tundra environment. It comprises a number of ubiquitous forms, such as *Homotherium* sp., *Gulo* cf. *schlosseri*, *Ursus* sp. (“spelaeoid”, *U. savini nordostensis*), *Canis mosbachensis* and *Canis (Xenocyon) lycaonoides* (Sotnikova, 1978, 1982, 1988; Sher et al., 2011). Nevertheless, the Olyorian record of *Alopex* sp. provides evidence for the Beringian origin of polar foxes (see Section 3.3.).

4.3. Steppe/tundra faunal exchange and first pan-Eurasian Mammoth Fauna

The interval of globally unstable climatic conditions between 1.2 and 0.9 Ma BP (Lisiecki and Raymo, 2005) seems to be the result of a transition linking the 41 ka with the following 100 ka periodicity. In wide regions of the Palaearctic it created an increasing diversity of habitats and a distinctive character of resulting (Epivillafranchian) faunas (R.-D. Kahlke, 2007a). From 900 ka onwards the climatic cycling finally switched to a 100 ka periodicity. Correspondingly, prolonged climatic cycles, which appeared as extended phases of climatic stability, caused drastic changes in the structure of mammal faunas (R.-D. Kahlke et al., 2011).

A major spread of steppe mammoth, *M. trogontherii*, into the Asian Arctic took place at around 1.2 Ma B.P. (see Section 3.2.). During that time, i.e. around the onset of the Epivillafranchian at the latest, this species also occurred in the western Palaearctic. The conceptual model of repeated, climate-controlled mutual replacement of *M. meridionalis* and *M. trogontherii* populations in most of Europe (see Section 3.2.) seems reasonable. From 800 ka onwards *M. trogontherii* became the dominating mammoth species across the entire Palaearctic. Roughly around that time *Saiga* also appeared in high latitudes (see Section 3.2.).

In return, occasional appearances of immigrants from the Arctic regions in Europe’s mid-latitudes (Germany, British Islands, France) during the 640–480 ka span (MIS 16–13) indicate a temporal opening of migration routes for cold adapted species into temperate regions. Scarce early Middle Pleistocene musk ox material of probably MIS 16 (c. 640–620 ka) age has been recorded from the site of Süßenborn (Thüringen, Germany) (see Section 3.3.), which

shows a far-reaching morphological proximity to Late Pleistocene and extant forms. The more slender metapodials of the Süßenborn animals provide the main argument for a subspecific separation as *Ovibos moschatus suessenbornensis* (H.-D. Kahlke, 1963a).

In addition, earliest western Palaearctic reindeer finds were also recovered from the Süßenborn gravels. Based on antler morphology these remains were attributed to early representatives of tundra reindeer (H.-D. Kahlke, 1969b). A skull with attached antlers from the Mosbach 2 fauna (Hessen, Germany) of MIS 15 or 13 age (c. 620–480 ka) belongs to the same morpho-group. Based on the latter find, the early Middle Pleistocene subspecies *R. tarandus stadelmanni* was established (H.-D. Kahlke, 1963b; R.-D. Kahlke, 1999, pp. 53f.). Furthermore, a single antler-base of reindeer was reported from the top of the Westbury-sub-Mendip sequence (Somerset, UK; Gentry, 1999). The low quantities of *Rangifer* finds within the extended fossil assemblages, particularly at the sites of Süßenborn and Mosbach, led to the interpretation of the recorded individuals as occasional winter visitors from Subarctic or Arctic regions, as was similarly assumed for contemporaneous musk oxen (see Section 3.3.).

Moigne et al. (2006) discussed the first reindeer spread as far as Western Europe during MIS 14 (Arago cave, Complex moyen, ensemble I). During the cold period of MIS 12, around 460 ka, *Rangifer* became, for the first time, a regular faunal element of the Palaearctic Mammoth Fauna, as recorded from the fossil assemblage of Bad Frankenhausen (Thüringen, Germany; Kahlke and Lacombat, 2008, p. 1953: *R. tarandus* ssp.). Roughly synchronous finds of reindeer remains are known from several Western and North Western European sites (compilation in R.-D. Kahlke, 1999, p. 54; Moigne et al., 2006, Arago cave, Complex moyen, ensemble III).

The long-lasting cold and continental climatic conditions of MIS 12 between 480 and 400 ka (Elsterian, Anglian, Okian) changed the Palaearctic faunal pattern drastically. Species of Central Asian steppe origin spread into northern and western Palaearctic regions, among them members of the *Coelodonta* group (see Section 3.2.). Single records of their first “far western” expansion are documented from at least seven western Palaearctic sites in the Romanian Brasov depression and in Central Germany (Rădulescu and Samson, 1985; Kahlke and Lacombat, 2008). In addition to *C. tolgajensis*, the faunal record of meltwater gravels deposited around 460 ka BP (isotopic events 12.4–12.3 sensu Bassinot et al., 1994) in the vicinity of the advancing Elsterian ice sheet near Bad Frankenhausen (Thüringen, Germany) comprise more species adapted to cold and continental environments, such as *Bison* sp., *Soergelia elisabethae*, *Praeovibos priscus*, *Rangifer tarandus* ssp., *Equus* sp. and *Mammuthus trogontherii* (Kahlke and Lacombat, 2008 and references therein). Elements of steppe as well as of tundra origin co-occurred, and for the first time the structure of a Mammoth Fauna appeared. This allows the conclusion to be drawn that similar assemblages existed concurrently, ranging from Central Europe (at least 11°E) in the west, up to Central and northern Asia in the east, thus forming the first pan-Eurasian Mammoth Fauna. The merger of essential parts of faunas, hitherto limited to Arctic and continental Asian regions respectively during MIS 12, probably took place slightly earlier in the eastern Palaearctic than in Europe.

4.4. Late Middle and Late Pleistocene Eurasian Mammoth Faunas

From 400 ka BP onwards, the faunal evolution was controlled by the continuing 100 ka climatic cyclicity. Long and usually relatively stable cold and warm climatic intervals, modulated by a general trend of global cooling (see Raymo and Nisancioglu, 2003, Fig. 1; Lisiecki and Raymo, 2005, Fig. 4), led to the origin and expansion of ecologically specialized mammal species. Western and easternmost regions of the Palaearctic in particular were characterized by

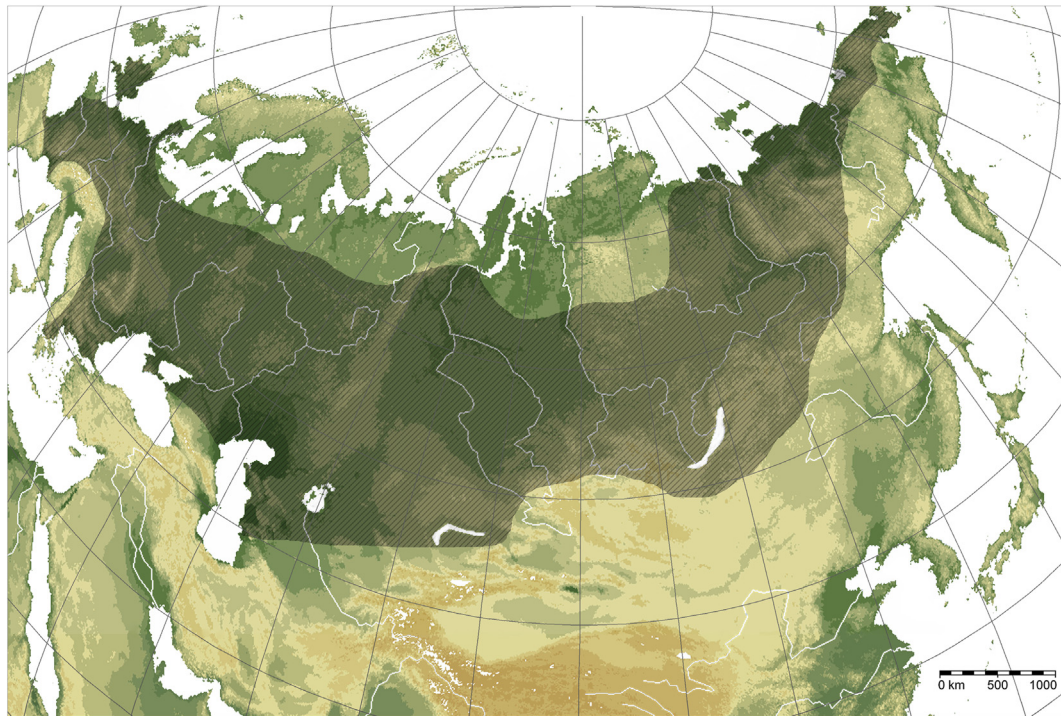


Fig. 2. Last Glacial (MIS 5d–MIS 2, Weichselian, Devensian, Valdaian) maximum distribution of *Saiga borealis*/*Saiga tatarica* in the Palearctic (after R.-D. Kahlke, 1999; additions after Álvarez-Lao and García, 2011a).

dramatic alterations between cold and warm adapted faunal assemblages (Xue, 1991; R.-D. Kahlke, 1999, pp. 117f.; R.-D. Kahlke et al., 2011). During cool to cold climatic periods, all groups of animals considered in this study expanded their habitats significantly, thus becoming faunal elements of corresponding Mammoth Faunas.

After the first appearance of *Saiga* in north-east Siberia during the late Early to early Middle Pleistocene (see Section 3.2.), a long gap in the information on the distribution of this species follows. It is only from the late Middle Pleistocene onwards, during colder climatic periods with pronounced continental conditions, that saigas are known to have repeatedly expanded from their, probable, Central Asian refugia northwards into Subarctic and Arctic latitudes, as well as westward into Europe. Corresponding remains are recorded from East, Central and Western European sites, such as Ulushka (Volgograd, Russia), Freyburg/Unstrut (Sachsen-Anhalt, Germany), and the Grotte de la Chaise, Abri Suard (Charente, France) (R.-D. Kahlke, 1990, 1992). During the Last Glacial (MIS 5d–MIS 2) *Saiga* experienced its maximum geographical distribution (Fig. 2). In Europe the Alps and Pyrenees constituted barriers to migration and the Apennine and the Iberian Peninsula were not occupied. Single saiga finds from a Magdalenian context of the Abantz cave (Navarra, Spain) are interpreted as having been brought by human hunters from elsewhere (Álvarez-Lao and García, 2011a). The Ural Mountains were colonized as far as 62° N (Kuzmina, 1971, pp. 101, 109), and in north-east Siberia *Saiga* expanded up to Yakutia (Lazarev, 2008, Fig. 46). From at least 39 ka BP onwards saiga entered Eastern Beringia (Harington, 1998, 2011). The principal limiting factors to its expansion included high reliefs, forested habitats, regions of deep or crusted snow covers and deserts.

After *Coelodonta tologojensis* was involved in the formation of the initial pan-Eurasian Mammoth Fauna, which expanded during MIS 12 to Central Europe (see Section 4.3.), it retreated from western Palearctic areas during most of the subsequent warm-

humid periods, to re-occupy huge territories of Eurasia in successively evolving stages during all of the following cold and continental influenced periods. During MIS 10 and 8 *Coelodonta* advanced into the steppe-like environments of Central and even, temporarily, Western Europe, as demonstrated by finds from e.g. La Fage (Corrèze, France; Guérin, 1973), Ariendorf 1 (Rheinland-Pfalz, Germany; Turner et al., 1997, pp. 69ff.), Weimar-Ehringsdorf (basal gravels below the travertine sequence with mammal fauna 1; Thüringen, Germany; R.-D. Kahlke et al., 2002, p. 163) and Markkleeberg (Sachsen, Germany; Eissmann, 2002, p. 1307). During MIS 6, *C. antiquitatis* entered the Iberian Peninsula for the first time, as recorded from the site of La Parte (Asturias, Spain; Álvarez-Lao and García-García, 2006). The range of *Coelodonta*'s ecological tolerance meant that woolly rhinoceroses were also present in Central and North Western Europe during the dryer and cooler periods of MIS 7 and 5, e.g. at Crayford (Kent, UK; Schreve, 2001, p. 1702) and Weimar-Ehringsdorf (Upper Travertines I and II with mammal faunas 7 and 8; Thüringen, Germany; R.-D. Kahlke et al., 2002, p. 172), as long as the available habitats comprised sufficient amounts of open grassland. During the later Middle Pleistocene *C. antiquitatis* expanded into the eastern Palearctic as far north as Yakutia and Chukotka (Russian Federation; Boeskorov, 2001).

During the Last Glacial (MIS 5d–MIS 2), *C. antiquitatis* ranged through most of northern and middle Eurasia from the Iberian Peninsula, France and England in the west, via Denmark, Central Europe, Italy, the Balkans, most of Eastern Europe up to the Caucasus and the Urals, northern and north-eastern Kazakhstan as far as Kyrgyzstan, Western Siberia, through the Baikal region and northern Outer Mongolia to the far-eastern Primorski Krai of the Russian Federation, southern Korea and northern and north-eastern provinces of China. The northward expansion once more reached Yakutia, the New Siberian Islands, Chukotka and Kamchatka (R.-D. Kahlke, 1999; Kahlke and Lacomat, 2008; additions after Pereladov and Shpanskiy, 1997; Savinevskiy and Ptashinskiy, 1999; Álvarez-Lao and García, 2011a,b) (Fig. 3). Principal limiting

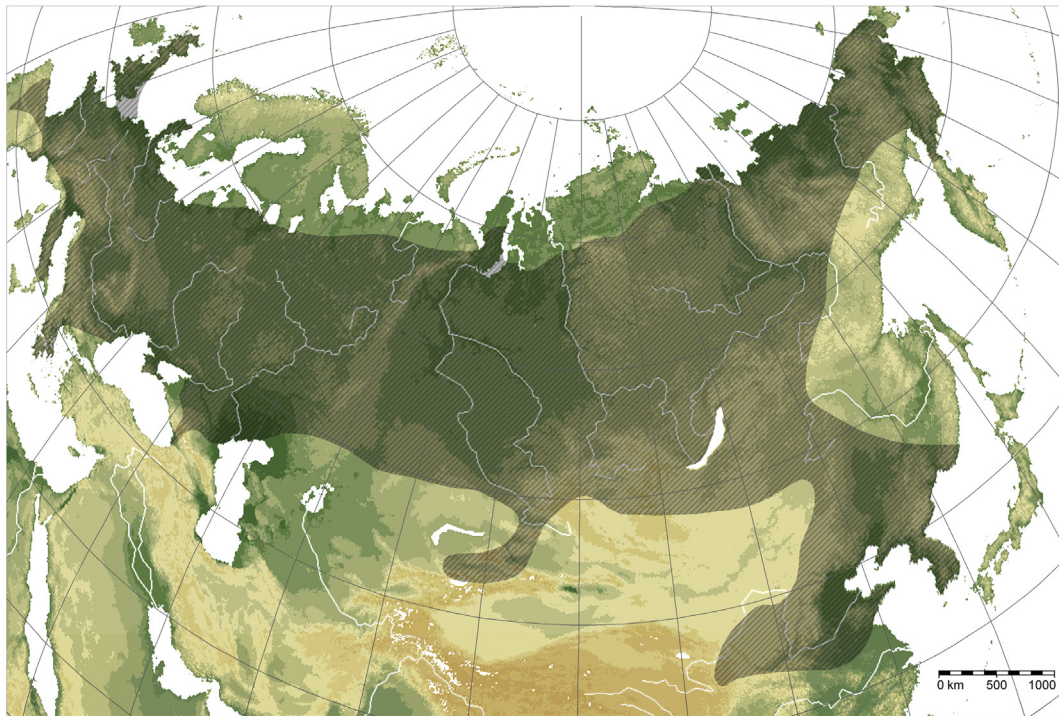


Fig. 3. Last Glacial (MIS 5d–MIS 2, Weichselian, Devensian, Valdaian, Dalian) maximum distribution of *Coelodonta antiquitatis* in the Palearctic (after Kahlke and Lacombe, 2008; additions after Pereladov and Shpanskiy, 1997; Savinevskiy and Ptashinskiy, 1999; Álvarez-Lao and García, 2011a).

factors to the woolly rhinos' expansions were dense forests, swampy areas and open water bodies on the one hand, and semi-deserts and deserts on the other. A moisture barrier, particularly the seasonal formation of stagnant waters on top of permafrost soils towards Eastern Beringia, may have prevented *Coelodonta*'s immigration to the Nearctic (R.-D. Kahlke, 1999, p. 46; Mol et al., 2006; see Section 5.2.).

Steppe mammoths (*M. trogontherii*) were abundant faunal elements of late Middle Pleistocene Mammoth Faunas until 200 ka (see Section 3.2.), expanding and contracting their habitats parallel to alternating colder/drier and warmer/wetter environmental conditions. In eastern Palearctic refugia, *M. trogontherii* probably survived much longer than in the west, as is indicated by recent finds of Late Pleistocene age from Yuxian (Hebei; Tong, 2010b) and from Gaoling County (Shanxi; We et al., 2010; see Section 5.2.). In Europe, developed *M. primigenius* appeared during late MIS 7 or early MIS 6, between 200 and 160 ka. The fossil record indicates an oscillating movement of synchronous western Palearctic *M. trogontherii* and *M. primigenius* populations (Lister et al., 2005), similar to that of Early Pleistocene shifting of *M. meridionalis* and *M. trogontherii* between 1.8 and 1.2 Ma BP (see Section 3.2.), except for a shorter interval. However, an unambiguous assignment of isolated finds to one of the aforementioned species is possible, though not in every case.

M. primigenius became a trace species for the latest Middle to Late Pleistocene Palearctic Mammoth Faunas. It reached its maximum distribution during the Late Pleistocene cold period (MIS 5d–MIS 2), developing a Holarctic belt of woolly mammoth distribution. Its habitats stretched from the Iberian Peninsula, North Western Europe, the southern bight of the North Sea and Scandinavia via Central, Southern and South Eastern Europe, the Russian Plain, the Ukraine as far as the Black Sea, Transcaucasia, the Urals and Bashkiria to south-eastern Kazakhstan, Xinjiang in westernmost China, northern Outer Mongolia, Eastern Siberia, north-eastern China, the northernmost part of South Korea, Sakhalin and

Hokkaido and to Yakutia and Kamchatka, as well as into northern North America and the Northern Plains of the United States (compilation and references in R.-D. Kahlke, 1999, 36f.; Álvarez-Lao et al., 2009, pp. 65ff.). The southern expansion of *M. primigenius* during the Late Pleistocene extended to similar latitudes of c. 37°N in Europe and Asia (Álvarez-Lao et al., 2009). Its southernmost spreads were limited by unsuitable vegetational conditions and the configuration of high mountain chains, arid zones and marine shorelines (Fig. 4).

A first continuous occupation of wide, non-Arctic territories by musk oxen is recorded for the late Middle Pleistocene cold stages (MIS 8, 6), when *Ovibos moschatus* temporarily ranged from Siberia up to North Western Europe (compilation in Sher, 1971, pp. 251f.; Raufuss and von Koenigswald, 1999). It had replaced *Praeovibos*, the dominant ovibovine of early Middle Pleistocene faunas, to become a regular element of the *Mammuthus*–*Coelodonta* Faunal Complex. Whereas *Ovibos moschatus* survived late Middle to Late Pleistocene temperate and more humid periods in Arctic to subarctic refugia – which in fact are the habitats of its origin – the species re-advanced into middle latitudes of Eurasia during each significant climate cooling span. During the coldest periods of the Last Glacial (MIS 5d–MIS 2) musk oxen reached their largest ever range of distribution. The species is recorded from the Iberian Peninsula in the west (Álvarez-Lao and García, 2011a) and France, England, the southern bight of the North Sea, the entire Central European area, southern Scandinavia, Moldova, the Russian Plain to the Urals and West and north-east Siberia to the Liakhov and the New Siberian Islands into the New World (R.-D. Kahlke, 1999, p. 66). Principal limiting factors of its spatial expansion were the configurations of the ice advances from the north, arid areas in Central Eurasia and probably relatively high amounts of annual precipitation in Southwestern Europe (Fig. 5).

During colder and dryer periods, especially of MIS 10, 8 and 6, *Rangifer* also expanded from its original Arctic or boreal habitats deep into Eurasia. Scattered finds from Siberia, especially from the Kuznetsk Basin up into the Volga region in European Russia, in

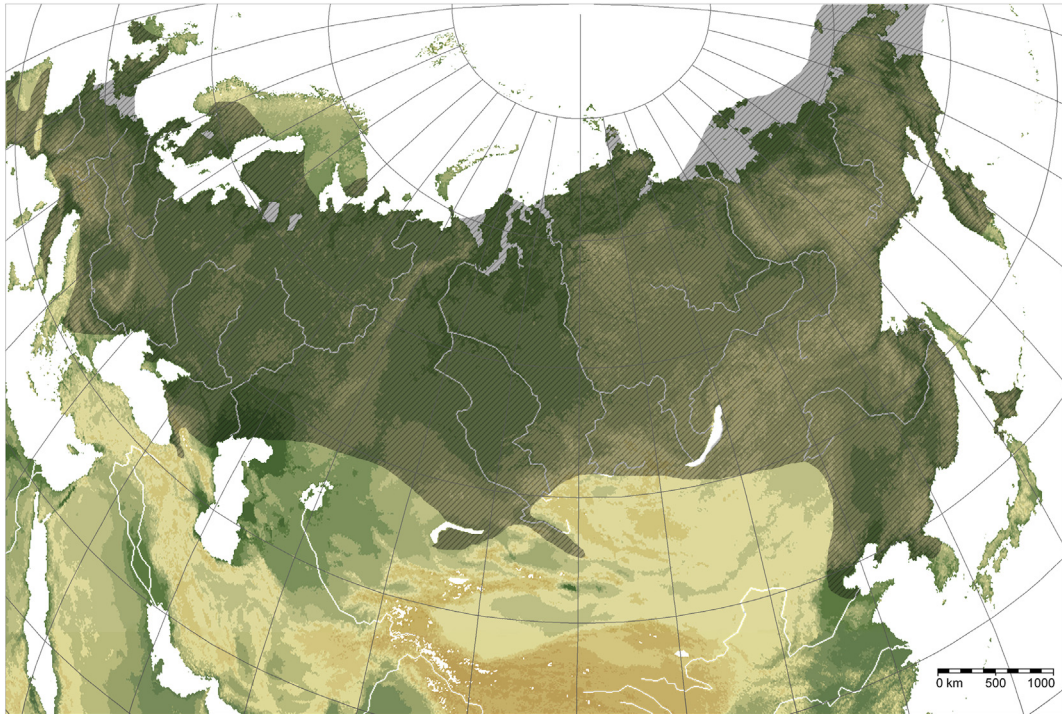


Fig. 4. Last Glacial (MIS 5d–MIS 2, Weichselian, Devensian, Valdaian, Dalian) maximum distribution of *Mammuthus primigenius* (adapted after R.-D. Kahlke in Álvarez-Lao et al., 2009, Fig. 8).

combination with records from Western and North Western Europe (compilation in R.-D. Kahlke, 1999, p. 54), suggest extended distribution ranges of reindeer comparable to those of the Late Pleistocene. A number of finds from Eastern Beringia establish late Middle Pleistocene caribou occurrence in the Nearctic (Péwé and Hopkins, 1967). Palaeartic fossil *R. tarandus* finds of Late

Pleistocene (MIS 5d–MIS 2) ages are known in extremely large numbers, especially towards the end of this period. Fossil localities have redrawn huge belts of reindeer occurrences from the Iberian Peninsula and the British Isles in the west, the southern bight of the North Sea, almost the entire territory of France and Central Europe, southern Scandinavia, the north of

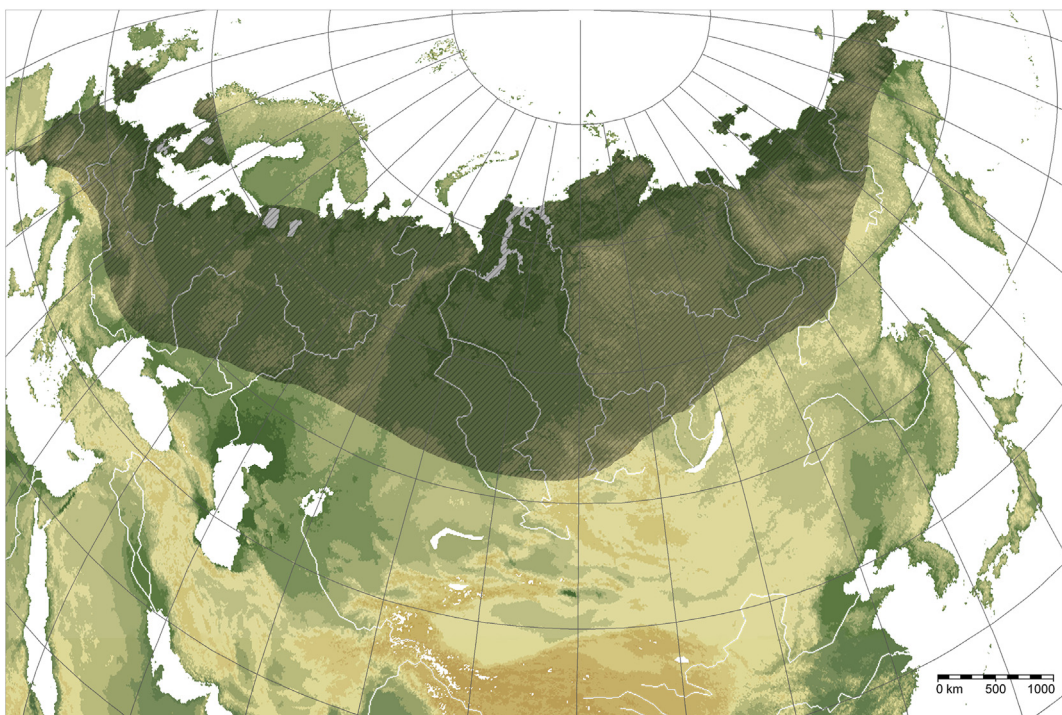


Fig. 5. Last Glacial (MIS 5d–MIS 2, Weichselian, Devensian, Valdaian) maximum distribution of *Ovibos moschatus* (after R.-D. Kahlke, 1999, additions after Álvarez-Lao and García, 2011a).

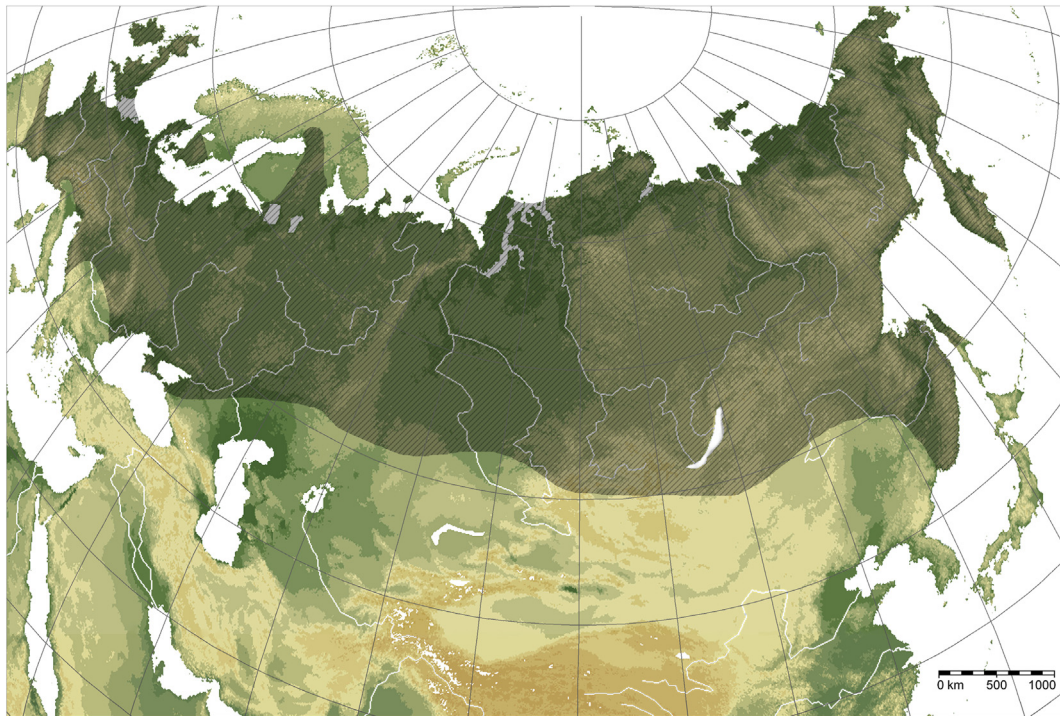


Fig. 6. Last Glacial (MIS 5d–MIS 2, Weichselian, Devensian, Valdaian) maximum distribution of *Rangifer tarandus* (after R.-D. Kahlke, 1999; modifications after Sala, 1983; Álvarez-Lao and García, 2011a).

South Eastern Europe, the Russian Plain as far as the Crimea, the Urals and its foreland, northern Kazakhstan, Western and Eastern Siberia, the Far East of the Russian Federation, Yakutia, the New Siberian Islands, and beyond into Eastern Beringia (R.-D. Kahlke, 1999, p. 54f.). The principal limiting factors to its expansion appear to be similar to that of the musk oxen: the shape of northern

ice advances, the aridity in central Eurasia and probably a high amount of annual precipitation combined with corresponding vegetation in regions of marine climatic influence (Fig. 6).

Following the recorded incidence of an early representative of polar foxes (*Alopex* sp.) in the north-east Siberian Olyorian along with some late Early to early Middle Pleistocene fox remains of

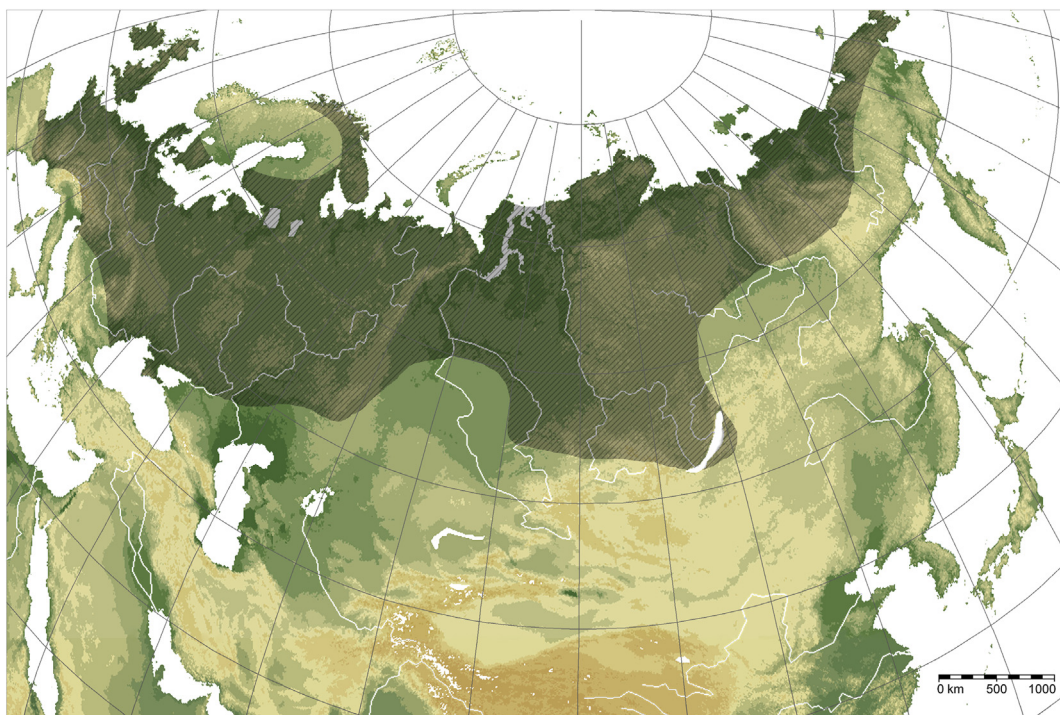


Fig. 7. Last Glacial (MIS 5d–MIS 2, Weichselian, Devensian, Valdaian) maximum distribution of *Alopex lagopus* (after R.-D. Kahlke, 1999; additions after Álvarez-Lao and García, 2011a).

uncertain phylogenetic position from Europe (see Section 3.3.), there is a long gap in the fossil evidence. Arambourg (1958, pp. 209ff., tab. XIV, 4) referred a number of mandibular fragments from Fontéchevade (Charente, France) to *A. cf. lagopus*. Following Bonifay's (1983, p. 113) dating of the fossils to late Middle Pleistocene age, for a long time these finds were considered to represent the oldest records of evolved polar fox (R.-D. Kahlke, 1999, p. 20). More recent data, however, have almost certainly assigned the site to MIS 3 (Chase et al., 2007), which would not support a first immigration of *A. lagopus* into the western Palaearctic before the Late Pleistocene. However, given the wide spread of *Ovibos* and *Rangifer* during appropriate late Middle Pleistocene spans of time, a parallel expansion of polar foxes into the Mammoth Fauna can not be generally excluded. As a regular member of the Late Pleistocene (MIS 5d–MIS 2) *Mammuthus*–*Coelodonta* Faunal Complex, evolved *A. lagopus* occupied large areas of Eurasia. It is recorded in the Pyrenees, France and the British Isles in the west, across Central and Eastern Europe, ice free parts of Scandinavia as far as the Altai, the Baikal region, north-east Siberia, the Liakhov Islands and beyond into the New World (R.-D. Kahlke, 1999, p. 20; Fig. 7). Because the polar fox is capable of traversing long distances over frozen water, future finds from a larger number of islands within the northern polar circle are to be expected. Towards the south, in moderate regions, Late Pleistocene polar fox was replaced by *Vulpes vulpes* and in dryer steppe habitats of Central to East Asia by *V. corsac*.

5. Discussion

5.1. Preconditions and precursors

The origin and evolution of Eurasian Mammoth Faunas and their precursors are the result of geological and climatic processes of global dimension that started well before the onset of the Quaternary. The collision of the African and Indian tectonic plates with Eurasia began as early as during the early Cenozoic. It resulted in the rise of a massive, continent-spanning orogen, which prevented the influx of moist air from the Indian and western Pacific Oceans into Asia's interior. At least since the late Miocene, the aridification of Central Asia, north of the Himalayan–Tibetan uplift, had a fundamental impact on the evolution of corresponding mammalian faunas. Moreover, from c. 15 Ma onwards, a trend of global cooling also strongly affected Eurasia's faunal evolution. Roughly between 2.9 and 2.6 Ma, a circumpolar extended tundra belt was formed, opening ecological niches for mammals that could increasingly endure high Arctic climate and vegetation conditions. The configuration of the Eurasian landmass as a whole, with its wide east–west-extension in mid- and high latitudes of the Northern Hemisphere, formed the basis for the development of pronounced continentality in regions of greater distances to the oceans and with stable atmospheric high-pressure conditions. A number of geographic factors, such as temporal ice advances, sea level lowering with resulting shelf exposure, and changes in the ocean current system supported the increase of continentality (see Sections 2.1. and 2.2.).

Species with progressing adaptation to pronounced aridity, decreasing temperatures and rapid temperature fluctuations inclusive of intervals of extreme cold, met the principal requirements to evolve into elements of Mammoth Faunas. This is the case for a number of herbivores which originated in the continental, open landscape of Central Asia, such as *Saiga* and *Mammuthus trogontherii* (see Section 3.2.). Most of these species did not primarily originate in high-altitude regions. The majority of larger mammals of Tibetan/Himalayan origin, such as argali (*Ovis ammon*), blue sheep (*Pseudois nayaur*), chiru (*Pantholops hodgsonii*), yak [*Bos (Poëphagus) mutus*], Tibetan wild ass (*Equus kiang*), and snow leopard (*Uncia uncia*) (Deng et al., 2011) have always been

restricted to the mountainous habitats of Tibet and the surrounding regions and did not disperse far into the Eurasian landmass. However, Deng et al. (2011) showed that the first member of the continental adapted rhinos, *Coelodonta thibetana*, apparently originated in the Tibetan high-plateau. So not only the dry regions north of the Himalayan–Tibetan uplift, but also the mountain region itself was part of the area of the origin of ancestors, which subsequently evolved into species of pan-Eurasian Mammoth Faunas. Another region that essentially contributed to the mammal spectrum of the Mammoth Faunas was the Far North. Species of Subarctic to Arctic origin, such as *Ovibos moschatus*, *Rangifer tarandus*, *Mammuthus primigenius* and *Alopex lagopus*, were also adapted to low temperature conditions combined with extreme seasonality inclusive of frost drought.

For a long time, faunas of both continental Asian steppe and Arctic tundra were spatially separated from each other. They shared only a few common faunal elements, such as the ubiquitous canid *Canis (Xenocyon) ex gr. lycaonoides*. Among the first large herbivorous species that occurred in both continental Eurasian steppe and in high latitude environments was *Mammuthus trogontherii*, which became the dominating Palaearctic proboscidean from the onset of the Middle Pleistocene onwards. For other large herbivores from Central Asian and Arctic faunal assemblages, which were principally adapted to open environments, a taiga-like forest belt (see Section 4.1.) acted as an effective barrier to further expansion. As a single exception among the larger mammals, early *Saiga* reached north-east Siberia via occasional migration paths, which probably opened up somewhere in the eastern Palaearctic. These early routes would have passed over patches of steppic communities that sometimes scattered into boreal habitats (Guthrie, 2001, p. 552). In return, the tundra-derived *Ovibos moschatus* and *Rangifer tarandus* appeared during the cool and relatively dry periods of the 640–480 ka span in temperate regions of Central and North Western Europe as seasonal immigrants (Soergel's "Wintergäste": Soergel, 1939, p. 834). Thus, almost like pioneers, early saiga, musk oxen and reindeer anticipated the subsequent fusion of Arctic and steppe assemblages to Eurasian Mammoth faunas.

5.2. Formation and expansion

Following a 41 ka periodicity in global temperature and climate evolution lasting millions of years, and a subsequent period of more or less irregular variations between 1.2 and 0.9 Ma BP, the Middle and Late Pleistocene was governed by a clear 100 ka periodicity (Raymo and Nisancioglu, 2003, Fig. 1; Lisiecki and Raymo, 2005, Fig. 4). The resulting prolongation of single climatic cycles extended the spans of relatively stable cold and warm conditions respectively. Such a renewed environmental framework caused drastic changes in the structure of mammal faunas and in consequence a dramatic alternation between different faunal types in wide areas of the Palaearctic (R.-D. Kahlke et al., 2011). This principal scenario was modulated by a continuing trend of global cooling.

An entirely new biogeographic situation was created by the pronounced cold period of MIS 12 (Elsterian, Anglian, Okian), between 480 and 400 ka. For the first time the forested belt separating the central Eurasian steppe from the Arctic tundra was significantly reduced or even temporarily eliminated (see Sections 4.1. and 4.2.), thus opening the way for expansions of species from both faunal assemblages. A new type of biome, the so-called tundra-steppe or mammoth steppe, evolved (Fig. 8). Although this kind of cold steppe appeared in many local variants, it has no modern large scale analogue (Guthrie, 1990b, 2001). Increased aridity, cooling and continentality allowed species of Arctic tundra origin to disperse south- and south-westwards, as species of steppe origin spread into northern and western regions of the Palaearctic. The

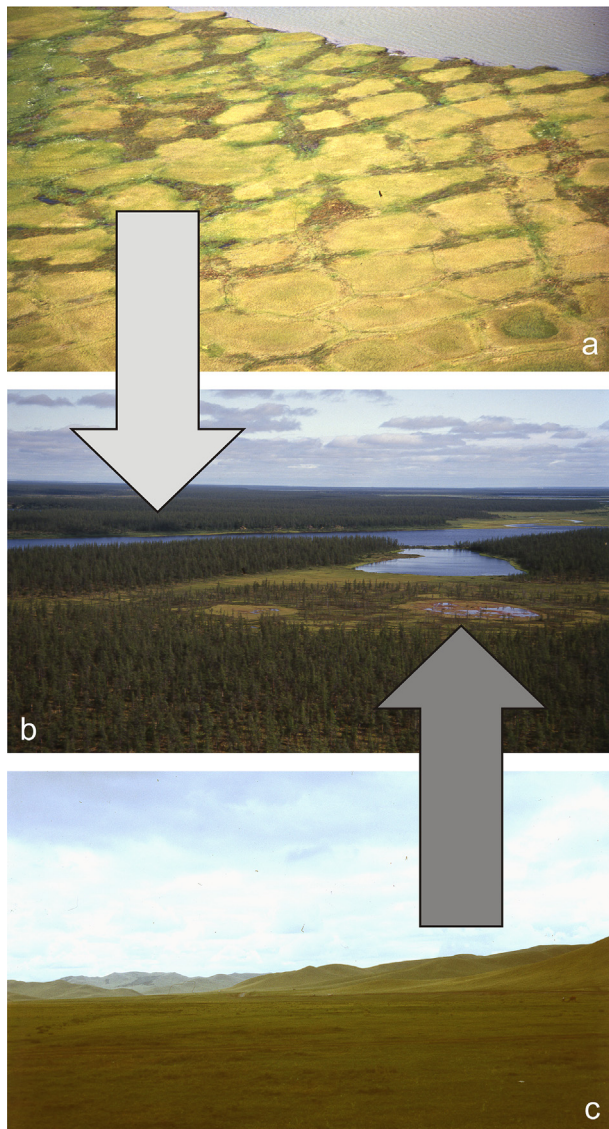


Fig. 8. Origin of a new type of biome (diagrammatic): The expansion of continental Asian steppe to the north (dark arrow) and of Arctic tundra to the south (pale arrow), both at the expense of an inserted forest belt, resulted in the formation of the Eurasian steppe-tundra. a: Arctic tundra with ice-wedge polygons (Tajmyr peninsula), b: Taiga (Yakutia), c: Central Asian steppe (Buryatia); photographs: R.-D. Kahlke.

initial formation of a pan-Eurasian *Mammuthus*–*Coelodonta* Faunal Complex is fixed by the regular sympatry of *Coelodonta tologojensis*, i.e. the first member of the woolly rhinoceros group invading the western Palaearctic, along with early *Rangifer tarandus*, in addition to the steppe mammoth *Mammuthus trogontherii*. Such a sympatry was recorded for the first time at the Bad Frankenhausen fauna in Central Europe, dated to around 460 ka BP (see Section 4.3.).

Large mammals of other origins than the two mentioned biomes benefited to a much lesser extent from the environmental changes in Eurasia's mid- and high latitudes during the Plio-/Pleistocene. Species of undoubtedly Ethiopian origin, most notably predators, arrived in the Palaearctic long before the formation of Mammoth Faunas (see Section 3.1.). After the Eurasian *Mammuthus*–*Coelodonta* Faunal Complex evolved, Africa did not contribute to its large mammal assemblages.

Although a plurality of elements of the Mammoth Fauna, such as *Ovibos*, *Saiga*, *Bison*, *Rangifer*, *Equus*, *Mammuthus* and *Alopex*, was

repeatedly distributed in continuous Holarctic belts, there are forms that permanently remained in Eurasia or North America respectively, even during most pronounced Middle- and Late Pleistocene cold periods. *Coelodonta* is believed to have never reached the New World, probably because of a moisture barrier in the Beringian region of what is now the Bering Strait (see Section 4.4.). Guthrie (2001) pointed out that the marine influence of the Bering and Chukchi seas at least partially broke the continuity of the Pleistocene mammoth steppe. As in the case of the woolly rhinoceros, the westward expansion of some Nearctic mammals, such as the musk ox *Bootherium* and the western camel *Camelops*, ended at the Bering Strait (Harington, 1997, 2002, 2003; Zazula et al., 2011).

During the warmer periods of the Middle and Late Pleistocene the mammoth steppe biome retreated from its transcontinental extension and huge areas of Palaearctic mid-latitudes were reforested (Eastern Siberia: Shichi et al., 2007; Western Siberia: Arkhipov et al., 2005; Eastern Europe: Velichko et al., 2005). Most of the elements of Eurasia's Mammoth Fauna withdrew to regions of the Asian core steppe (see Section 2.1.) or to the circumpolar tundra belt respectively. Due to scarcity, and in some cases insufficient biostratigraphic resolution of Central as well as north-east Asian Middle Pleistocene mammal sites, the scope of these interglacial refugia have not yet been redrawn in detail. With successive cooling towards the next climatic cycle there followed renewed reductions of the Eurasian taiga belt. Once more, the barriers restricting a reunion of faunal elements from the inner continental core steppe and tundra regions were torn down. A transcontinental expansion of Mammoth Faunas re-emerged, comprising almost the same spectrum of genera/species as their precursors. In most cases individual species were morphologically more evolved (R.-D. Kahlke, 1999; see Sections 3.2. and 3.3.), as has been discussed in particular for *Mammuthus primigenius* by Lister et al. (2005) and for *Coelodonta antiquitatis* by Kahlke and Lacombat (2008).

Recently, evidence has been produced of the development of some faunistic peculiarities in the Central Asian core steppe regions independent to the evolution of Eurasian Mammoth Faunas. With the realization that *Mammuthus trogontherii* survived – at least in northern China – until the Late Pleistocene (see Section 4.4.), regardless of the origin of Woolly Mammoth (*M. primigenius*) around 400 ka BP (see Section 3.3.), a new point of view on the evolutionary history of eastern Palaearctic mammoths has been opened up. *M. trogontherii*, which was adapted to continental environmental conditions, survived in Central Asian steppe regions parallel to the successively evolving *M. primigenius* in the more northern altitudes of Eurasia for more than 350 ka. A corresponding phenomenon of coexisting mammoth species, adapted to continental steppe and tundra steppe habitats respectively, is known from the New World. Here, *Mammuthus columbi* s.l. (Agenbroad, 1989), an American stage of the mammoth evolutionary line, which in many respects resembles *M. trogontherii*, occupied steppe/prairie habitats, whereas *M. primigenius* synchronously spread into the mammoth steppe. Occasionally both species were recorded to co-occur in one and the same site, as in the case of the uppermost section of a karst sinkhole filling of Hot Springs (South Dakota, USA; Agenbroad, 1994), indicating temporal replacement or short term (perhaps seasonal) sympatry of *M. columbi* by *M. primigenius* in the American Midwest around 30 ka BP.

Similar phylogeographic patterns seem to have been developed in Eurasia by saigas and the woolly rhino group. Baryshnikov and Tikhonov (1994) distinguish *Saiga borealis* as a member of Mammoth Faunas from the more gracile *S. tatarica* of inner Asian steppe assemblages (see Section 3.2.). A number of poorly known *Coelodonta* finds from northern China/Inner Mongolia indicate a branch of woolly rhinos that evolved independently from the northern

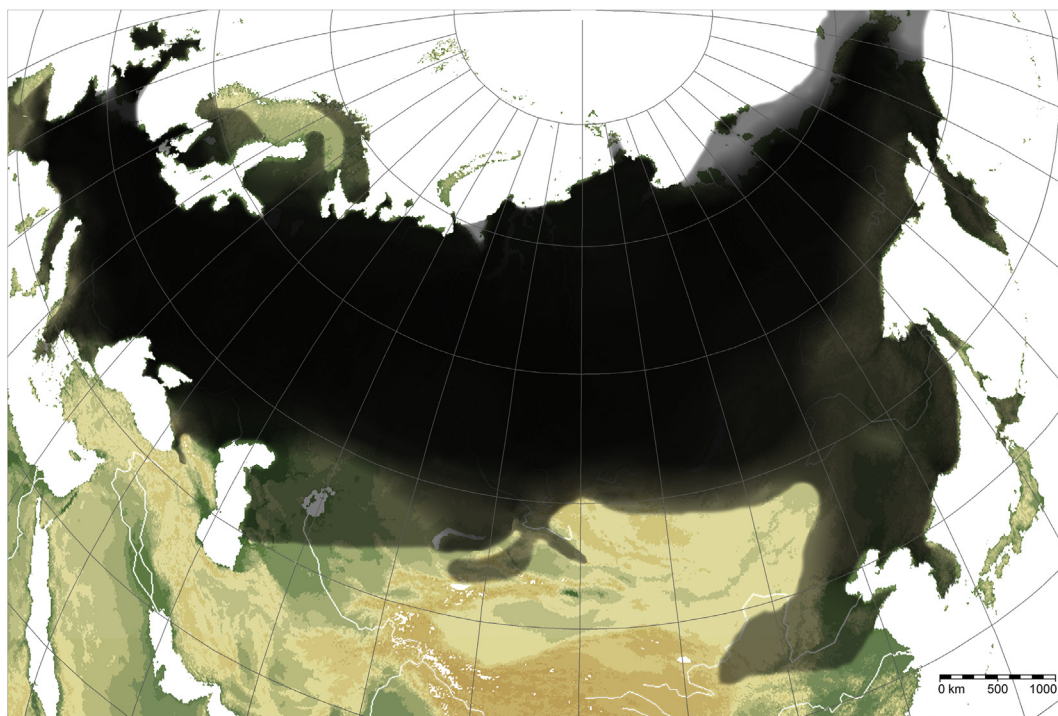


Fig. 9. Sketch of the maximum extension of the Eurasian *Mammuthus*–*Coelodonta* faunal complex during the Late Pleistocene (MIS 5d-2) according to the available fossil record of trace species (based on maps Figs. 2–7). Fading indicates reduction of amount of involved species.

C. tologijensis/antiquitatis lineage (see Section 4.2.). Detailed studies of these putative steppe forms are required to understand their phylogeny and ecology. However, it seems obvious that ecological differences between continental steppe dominated habitats and the tundra steppe caused different adaptations of sister taxa. Furthermore, it becomes clear that while Central Asia's steppe faunas essentially contributed to the mammal spectrum of the Mammoth Faunas, not all of the inner continental core steppe developed into the Middle to Late Pleistocene tundra steppe biome.

Generally speaking, the synopsis of the history of evolution and dispersal of trace mammal species proves the repeated formation and expansion of Mammoth Faunas during the late Middle and Late Pleistocene cold stages in Eurasia's mid- and high latitudes. The principally uniform species composition of the successive stages of the *Mammuthus*–*Coelodonta* Faunal Complex differs from both the Central Asian steppe and Arctic tundra assemblages, but is phylogenetically closely related to each of them. A projection of the distribution areas of essential elements of Eurasian Mammoth Faunas show its maximum extension during the Late Pleistocene, when it covered about 140 degrees of longitude and 40 degrees of latitude (Fig. 9).

6. Conclusions

The cause for the emergence of Eurasian Mammoth Faunas can not be seen to lie solely at the door of Neogene/Quaternary climate cooling. Rather, it was the result of an ensemble of tectonic, geographical, climatic, ecological and phylogenetic processes that were interacting in a unique way. Key environmental factors controlling the origin and evolution of Palaearctic cold-adapted large mammal faunas were the successive aridification of major parts of Eurasia, rhythmic global climatic cooling with prolonged and intensified cold stages, and increasing continentality.

A huge east–west expanding transcontinental orogene that rose from the Eocene onwards was the principal precondition for the

aridification of Central Asia. This mountain system, especially the prominent Himalayan–Tibetan uplift, cut off the flow of humid air from Indian and western Pacific oceans to the north. The corresponding development of Asia's core steppe turned out to be one of the most radical environmental changes in the Northern Hemisphere during the Cenozoic. A parallel tendency of global cooling resulted in synchronous ice sheet formations in different regions of the Far North from the Late Pliocene onwards. The genesis of the earliest circumpolar tundra belt, between 2.9 and 2.6 Ma, was completed by the onset of the Pleistocene. The Paratethys' shrinkage, exposure of huge areas of continental shelf, particularly in Eurasia's north and north-east due to lowered sea levels during glacial periods, in addition to the periodical deflection of larger portions of the Gulf Stream southwards, progressively affected adjacent regions by increased continentality.

Old World Mammoth Faunas were mainly composed of autochthonous Eurasian elements. The majority of involved genera, such as *Ovibos*, *Saiga*, *Bison*, *Rangifer*, *Alces*, *Megaloceros*, *Coelodonta* and *Alopex* originated in the Palaearctic inclusive of Beringia as a whole during the Plio-/Early Pleistocene. A lesser number of genera, such as *Mammuthus*, *Panthera* and *Crocota* have their phylogenetic roots in Africa or, as in the case of *Equus*, in North America. However, corresponding species were indigenous elements of Palaearctic mammal faunas well before the origin of cold adapted Mammoth Faunas. During the Early to earliest Middle Pleistocene, roughly between 2.6 Ma and 700 ka, largely independent mammal faunas were established in continental Asian steppe regions as well as in the circumpolar tundra. Both faunal complexes were adapted to open environmental conditions, but were widely separated from each other by a forested zone.

The reconstruction of the history of origins and dispersal of key species of the Middle to Late Pleistocene *Mammuthus*–*Coelodonta* Faunal Complex outlines its main faunistic resources. The principal requirements for species to evolve into members of Mammoth Faunas are progressing adaptation to aridity, decreasing

temperatures and rapid temperature fluctuations inclusive of intervals of extreme cold. A number of species, such as *Saiga tatarica* ssp., *Coelodonta tologojensis* and *Mammuthus trogontherii*, which originated in Asian steppe landscapes, fulfilled these conditions, as did others of northern origin, such as *Ovibos moschatus* ssp., *Rangifer tarandus* ssp. and *Alopex* sp. Correspondingly, Eurasian Mammoth Faunas were mainly composed of the descendants of either Central Asian steppe or Arctic tundra faunal elements. The majority of species of Central Asian origin emerged in regions north of the Himalayan–Tibetan uplift. However, a recent discovery of earliest *Coelodonta* brings the Tibetan high plateau itself into the formation region of ancestor species of future Mammoth Faunas.

During the early Middle Pleistocene 640–480 ka span, saiga, musk-ox and reindeer occasionally spread far beyond the limits of their respective traditional areas, thus anticipating the subsequent merge of steppe or tundra originated species in Eurasian Mammoth Faunas. Cooling and significant prolongation of cold climatic phases within the 100 ka temperature periodicity pattern, as well as the consequent aridification of large areas of the Eurasian landmass finally caused a regular south- and south-west directed expansion of tundra species into a newly formed type of biome, the so-called tundra-steppe or mammoth steppe. Descendants of Central Asian steppe species that could cope with the decreasing temperatures also dispersed into new habitats north and northwest of their ancestral distribution areas. As a result, faunal elements of tundra, as well as of steppe, origins co-occurred in wide areas of Eurasia. During the pronounced cold period of MIS 12, around 460 ka BP, this drastic faunal turnover led to the formation of the earliest pan-Eurasian Mammoth Fauna, which extended from eastern Asia up to Central Europe. This group shared common roots with Arctic tundra assemblages on the one hand, and with Central Asian steppe assemblages on the other.

Independent from Eurasian Mammoth Faunas, sister taxa of several involved species underwent separate evolutions in Central Asia, thus indicating ecological differences between Asian core steppe and Eurasian tundra-steppe. The phylogeny and ecology of these species is still poorly understood.

During temperate and more humid stages of the late Middle to Late Pleistocene the Palaeoarctic mammoth steppe collapsed in its transcontinental extension. Huge areas of Eurasia's mid-latitudes became reforested and the majority of Mammoth Fauna species were forced back to continental steppe or Arctic tundra refugia. With the reduction of the forested belts during the subsequent cold stages, the formation of renewed Mammoth Faunas was repeated. The temporo-spatial extension of late Middle to Late Pleistocene stages of the *Mammuthus*–*Coelodonta* Faunal Complex varied to some degree. Its maximum geographic distribution was accomplished during the Late Pleistocene (MIS 5d-2), when the Palaeoarctic Mammoth Fauna covered up to 190 degrees of longitude and 40 degrees of latitude.

Acknowledgements

The author wishes to thank the editors, H. O'Regan, S. Elton and D. Schreve, for their kind invitation to participate in this Alan Turner memorial volume. The study presented here was carried out as a part of the Senckenberg Research Institute's project group "Origin, dispersal and impoverishment of Eurasian cold adapted faunas". The paper itself is the enhanced version of a talk given during the opening session of the Vth International Conference on mammoths and their relatives, held in 2010 in Le Puy-en-Velay, France. Thanks are due to the conveners of this conference, F. Lacombe (Le Puy-en-Velay) and D. Mol (Rotterdam), who encouraged me to deal with this issue. I am grateful to F. Kienast (Weimar), I.V. Kirillova (Moscow), L. Riedel (Weimar)

and N. Spassov (Sofia) for information on different topics, G. Utschig (Weimar) for assistance with the figures and C.M. Nielsen-Marsh (Leipzig) for linguistic revision of the paper. M. Fortelius (Helsinki) and one anonymous reviewer helped to improve the paper.

References

- Agenbroad, L.D., 1985. The distribution and chronology of mammoth in the New World. *Acta Zoologica Fennica* 170, 221–224.
- Agenbroad, L.D., 1989. New World Mammoth Distribution. In: Martin, P.S., Klein, R.G. (Eds.), *Quaternary Extinctions. A Prehistoric Revolution*. The University of Arizona Press, Tucson, AZ, pp. 90–108.
- Agenbroad, L.D., 1994. Geology, Hydrology, and Excavation of the site. In: Agenbroad, L.D., Mead, J.I. (Eds.), *The Hot Springs Mammoth Site: A Decade of Field and Laboratory Research in Paleontology, Geology, and Paleoecology*. Fenske, Rapid City, SD, pp. 15–27.
- Alexeeva, N.V., Erbaeva, M.A., 2006. Tologoi Key Section: Middle Pliocene – Holocene colluvial deposits, with 13 sequential mammalian faunas (among them, the Middle Pleistocene Tologoi faunistic complex and Ivoginian fauna). In: Alexeeva, N.V., Erbaeva, M.A. (Eds.), *Stratigraphy, paleontology and paleoenvironments of Pliocene-Pleistocene of Transbaikalia and interregional correlations*, International Symposium August 28th – September 3rd 2006, Ulan Ude, Field Excursion Guidebook. INQUA Sub-commission on Asian Quaternary Stratigraphy etc., Ulan Ude, pp. 26–30.
- Alexeeva, N.V., Erbaeva, M.A., Sen, S., 2001. Geology and fauna, and preliminary correlation of sediments of the main Late Cenozoic sites of the Transbaikalia area. *Quaternary International* 80–81, 93–100.
- Álvarez-Lao, D., García-García, N., 2006. A new site from the Spanish Middle Pleistocene with cold-resistant faunal elements: La Parte (Asturias, Spain). *Quaternary International* 142–143, 107–118.
- Álvarez-Lao, D.J., García, N., 2011a. Geographical distribution of Pleistocene cold-adapted large mammal faunas in the Iberian Peninsula. *Quaternary International* 233, 159–170.
- Álvarez-Lao, D.J., García, N., 2011b. Southern dispersal and Palaeoecological implications of woolly rhinoceros (*Coelodonta antiquitatis*): review of the Iberian occurrences. *Quaternary Science Reviews* 30, 2002–2017.
- Álvarez-Lao, D.J., Kahlke, R.-D., García, N., Mol, D., 2009. The Padul mammoth finds – On the southernmost record of *Mammuthus primigenius* in Europe and its southern spread during the Late Pleistocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 278, 57–70.
- An, Z., Kutzbach, J.E., Prell, W.E., Porter, S.C., 2001. Evolution of Asian monsoons and phased uplift of the Himalaya–Tibetan plateau since Late Miocene times. *Nature* 411, 62–66.
- Arambourg, C., 1958. Les gros mammifères des couches tayaciennes. In: Vallois, H.-V., Alimen, H., Arambourg, C., Schreuder, A. La grotte de Fontécheval. Deuxième et troisième partie. *Archives de l'Institut de Paléontologie Humaine, Mémoire* 29, pp. 185–229.
- Arkipov, S.A., Volkova, V.S., Zolnikov, I.D., Zykina, V.S., Krukov, A.A., Kul'kova, L.A., 2005. West Siberia. In: Velichko, A.A., Nechaev, V.P. (Eds.), *Cenozoic Climatic and Environmental Changes in Russia*. The Geological Society of America, Special Paper 382, Boulder, Colorado, pp. 67–88.
- Bannikov, A.G., 1963. Die Saiga-Antilope (*Saiga tatarica* L.). A. Ziemsen Verlag, Wittenberg Lutherstadt.
- Baryshnikov, G., Tikhonov, A., 1994. Notes on skulls of Pleistocene saiga of Northern Eurasia. *Historical Biology* 8, 209–234.
- Bassinot, F.C., Labeyrie, L.D., Vincent, E., Quidelleur, X., Shackleton, N.J., Lancelot, Y., 1994. The astronomical theory of climate and the age of the Brunhes-Matuyama magnetic reversal. *Earth and Planetary Science Letters* 126, 91–108.
- Blumenbach, J.F., 1799. *Handbuch der Naturgeschichte*. Sechste Auflage, Dieterich, Göttingen.
- Boeskorov, G., 2001. Woolly rhino (*Coelodonta antiquitatis*) distribution in Northeast Asia. *Deinsea* 8, 15–20.
- Bonifay, M.-F., 1971. Carnivores quaternaires du Sud-Est de la France. *Mémoires du Muséum National d'Histoire Naturelle. Nouvelle Série C* 21, 43–377.
- Bonifay, M.-F., 1983. Les Canidés de Vergranne. *Annales Scientifiques de l'Université de Franche-Comté Besançon, Géologie 4 série*, 5, 111–123.
- Burbank, D.W., Blythe, A.E., Putkonen, J., Pratt-Sitaula, B., Gabet, E., Oskin, M., Barros, A., Ojha, T.P., 2003. Decoupling of erosion and precipitation in the Himalayas. *Nature* 426, 652–655.
- Cai, B.-Q., Li, Q., Zheng, S.-H., 2008. Fossil Mammals from Majuangou Section of Nihewan Basin, China and Their Age. *Acta Anthropologica Sinica* 27, 129–142 (in Chinese, with English summary).
- Campos, P.F., Sher, A., Mead, J.I., Tikhonov, A., Buckley, M., Collins, M., Willerslev, E., Gilbert, M.T.P., 2010a. Clarification of the taxonomic relationship of the extant and extinct ovibovids, *Ovibos*, *Praeovibos*, *Euceratherium* and *Bootherium*. *Quaternary Science Reviews* 29, 2123–2130.
- Campos, P.F., Kristensen, T., Orlando, L., Sher, A., Kholodova, M.V., Götherström, A., Hofreiter, M., Drucker, D.G., Kosintsev, P., Tikhonov, A., Baryshnikov, G.F., Willerslev, E., Gilbert, M.T.P., 2010b. Ancient DNA sequences point to a large loss of mitochondrial genetic diversity in the saiga antelope (*Saiga tatarica*) since the Pleistocene. *Molecular Ecology* 19, 4863–4875.

- Chase, P.G., Debénath, A., Dibble, H.L., McPherron, S.P., Schwarcz, H.P., Stafford Jr., T.W., Tournepiche, J.-F., 2007. New dates for the Fontéchevade (Charente, France) *Homo* remains. *Journal of Human Evolution* 52, 217–221.
- Chia, L.-P., Wang, C., 1978. Hsihoutu. A Culture Site of Early Pleistocene in Shansi Province. Wenwu Press, Peking (in Chinese, with English summary).
- Chow, B., 1978. The Distribution of the Woolly Rhinoceros and Woolly Mammoth. *Vertebrata Palasiatica* 16, 47–59 (in Chinese, with English summary).
- Chow, B., 1979. The Fossil Rhinocerotides of Locality 1, Choukoutien. *Vertebrata Palasiatica* 17, 256–258 (in Chinese, with English summary).
- Chow, M., Chang, Y.P., Hu, C.K., Liu, H.I., Hsu, Y.H., Chou, P.H., Lee, Y.C., Hsien, H.H., 1959. Pleistocene mammalian fossils from the northeastern provinces. Institute of Vertebrate Paleontology, Academia Sinica, Beijing (in Chinese, with English summary).
- Crégut-Bonnoure, E., 1984. The Pleistocene Ovipovinae of Western Europe: Temporal-spatial Expansion and Paleoecological Implications. In: *Biological Papers of the University of Alaska, Special Reports* 4, pp. 136–144.
- Crégut-Bonnoure, E., 2007. Apport des Caprinae et Antilopinae (Mammalia, Bovidae) à la biostratigraphie du Pliocène terminal et du Pléistocène d'Europe. *Quaternaire* 18, 73–97.
- Crégut, E., Guérin, C., 1979. Première découverte en Europe sud-occidentale de *Praeovibos priscus* (Mammalia, Artiodactyla, Ovipovinae) dans le gisement pléistocène moyen anté-rissien de la Caune de l'Arago (Tautavel, Pyrénées-Orientales, France). *Geobios* 12, 459–465.
- Deng, C., Wei, Q., Mei, H., 2009. Excursion North Line to Nihewan. In: *International Symposium on Paleoanthropology in Commemoration of the 80th Anniversary of the Discovery of the First Skull of Peking Man and the First Asian Conference on Quaternary Research*. Beijing, pp. 3–27.
- Deng, T., 2002. The earliest known woolly [sic] rhino discovered in the Linxia basin, Gansu Province, China. *Geological Bulletin of China* 21, 604–608 (in Chinese, with English summary).
- Deng, T., 2006. Neogene Rhinoceroses of the Linxia Basin (Gansu, China). In: Kahlke, R.-D., Maul, L.C., Mazza, P.P.A. (Eds.), *Late Neogene and Quaternary biodiversity and evolution: Regional developments and interregional correlations*, Volume I. Courier Forschungsinstitut Senckenberg 256, pp. 43–56.
- Deng, T., Wang, X., Fortelius, M., Li, Q., Wang, Y., Tseng, Z.J., Takeuchi, G.T., Saylor, J.E., Sällä, L.K., Xie, G., 2011. Out of Tibet: Pliocene Woolly Rhino Suggests High-Plateau Origin of Ice Age Megaherbivores. *Science* 333, 1285–1288.
- Eisenmann, V., 2006. Pliocene and Pleistocene Equids: palaeontology versus molecular biology. In: Kahlke, R.-D., Maul, L.C., Mazza, P.P.A. (Eds.), *Late Neogene and Quaternary biodiversity and evolution: Regional developments and interregional correlations*, Volume I. Courier Forschungsinstitut Senckenberg 256, pp. 71–89.
- Eisenmann, V., Kuznetsova, T., 2004. Early Pleistocene equids (Mammalia, Perissodactyla) of Nalaikha, Mongolia, and the emergence of modern *Equus* Linnaeus, 1758. *Geodiversitas* 26, 535–561.
- Eissmann, L., 2002. Quaternary geology of eastern Germany (Saxony, Saxon-Anhalt, South Brandenburg, Thuringia), type area of the Elsterian and Saalian Stages in Europe. *Quaternary Science Reviews* 21, 1275–1346.
- Flesche Kleiven, H., Jansen, E., Fronval, T., Smith, T.M., 2002. Intensification of Northern Hemisphere glaciations in the circum Atlantic region (3.5–2.4 Ma) – ice-rafted detritus evidence. *Palaeogeography, Palaeoclimatology, Palaeoecology* 184, 213–223.
- Foronova, I.V., 1999. Quaternary mammals and stratigraphy of the Kuznetsk Basin (South-western Siberia). *Anthropozoikum* 23, 71–97.
- Fortelius, M., Eronen, J.T., Liu, L., Pushkina, D., Tesakov, A., Vislobokova, I.A., Zhang, Z., 2006. Late Miocene and Pliocene large land mammals and climatic changes in Eurasia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238, 219–227.
- Frédérina, A.F., Alekseev, M.N., Andreev, A.A., Klimanov, V.A., 2005. East Siberia (Based on data obtained mainly in central Yakutia). In: Velichko, A.A., Nechaev, V.P. (Eds.), *Cenozoic Climatic and Environmental Changes in Russia*. The Geological Society of America, Special Paper 382, Boulder, Colorado, pp. 89–103.
- Franzen, J.L., Gliozzi, E., Jellinek, T., Scholger, R., Weidenfeller, M., 2000. Die spät-altpleistozäne Fossilagerstätte Dorn-Dürkheim 3 und ihre Bedeutung für die Rekonstruktion der Entwicklung des rheinischen Flußsystems. *Senckenbergiana lethaea* 80, 305–353.
- García García, N., 2003. Osos y otros carnívoros de la Sierra de Atapuerca. Fundación Oso de Asturias, Oviedo.
- Garrido, G., 2008. The fossil record of *Vulpes alopecoides* (Forsyth-Major, 1877), *Canis etruscus* Forsyth-Major, 1877 and *Canis cf. falconeri* Forsyth-Major, 1877 (Canidae, Carnivora, Mammalia) at the Fonelas P-1 site (Guadix Basin, Granada). In: Arribas, A. (Ed.), *Vertebrados del Plioceno superior terminal en el suroeste de Europa: Fonelas P-1 y el Proyecto Fonelas*. Instituto Geológico y Minero de España, Madrid, pp. 159–186.
- Garutt, W.E., 1964. Das Mammut. A. Ziemsen Verlag, Wittenberg Lutherstadt.
- Garutt, V.E., 1986. Proiskhozhdenie slonov Elephantidae i puti ikh filogenii. *Trudy Zoologicheskogo Instituta AN SSSR* 149, 15–32 (in Russian).
- Garutt, V.E., Bajguseva, V.S., 1981. *Archidiskodon gromovi* Garutt et Alexeeva – der älteste Elefant der Mammutlinie in Eurasien. *Quartärpaläontologie* 4, 19–25.
- Gentry, A.W., 1999. Fossil Ruminants (Mammalia, Artiodactyla) from Westbury Cave. In: Andrews, P., Cook, J., Currant, A., Stringer, C. (Eds.), *The Natural History Museum excavations 1976–1984*. Western Academic & Specialist Press Ltd., Bristol, pp. 139–174.
- Guérin, C., 1973. Les trois espèces de rhinocéros (Mammalia, Perissodactyla) du gisement pléistocène moyen des Abîmes de La Fage (Corrèze). *Nouvelles Archives du Muséum d'Histoire naturelle de Lyon* 11, 55–84. pl. 5–17.
- Guo, Z., Peng, S., Hao, Q., Biscaye, P.E., An, Z., Liu, T., 2004. Late Miocene–Pliocene development of Asian aridification as recorded in the Red-Earth Formation in northern China. *Global and Planetary Change* 41, 135–145.
- Guo, Z.T., Ruddiman, W.F., Hao, Q.Z., Wu, H.B., Qiao, Y.S., Zhu, R.X., Peng, S.Z., Wei, J.J., Yuan, B.Y., Liu, T.S., 2002. Onset of Asian desertification by 22 Myr ago inferred from loess deposits in China. *Nature* 416, 159–163.
- Guthrie, R.D., 1990a. Frozen Fauna of the Mammoth Steppe. The Story of Blue Babe. The University of Chicago Press, Chicago, London.
- Guthrie, R.D., 1990b. Late Pleistocene faunal revolution – a new perspective on the extinction debate. In: Agenbroad, L.D., Mead, J.L., Nelson, L.W. (Eds.), *Mega fauna & Man. Discovery of America's Heartland*. Scientific Papers, 1. The Mammoth Site of Hot Springs, South Dakota, pp. 42–53.
- Guthrie, R.D., 2001. Origin and causes of the mammoth steppe: a story of cloud cover, woolly mammal tooth pits, buckles, and inside-out Beringia. *Quaternary Science Reviews* 20, 549–574.
- Guthrie, R.D., Matthews Jr., J.V., 1971. The Cape Deceit Fauna – Early Pleistocene Mammalian Assemblage from the Alaskan Arctic. *Quaternary Research* 1, 474–510.
- Harington, C.R., 1997. Ice Age Yukon and Alaskan Camels. *Beringian Research Notes* 10, 1–4.
- Harington, C.R., 1998. North American Saiga. *Beringian Research Notes* 11, 1–4.
- Harington, C.R., 2002. Helmeted Muskox. *Beringian Research Notes* 13, 1–4.
- Harington, C.R. (Ed.), 2003. *Annotated Bibliography of Quaternary Vertebrates of Northern North America – with Radiocarbon Dates*. Toronto University Press, Toronto, Buffalo, London.
- Harington, C.R., 2011. Pleistocene vertebrates of the Yukon Territory. *Quaternary Science Reviews* 30, 2341–2354.
- Haug, G.H., Ganopolski, A., Sigman, D.M., Rosell-Mele, A., Swann, G.E.A., Tiedemann, R., Jaccard, S.L., Bollmann, J., Maslin, M.A., Leng, M.J., Eglinton, G., 2005. North Pacific seasonality and the glaciation of North America 2.7 million years ago. *Nature* 433, 821–825.
- Hemmer, H., 2011. The story of the cave lion – *Panthera leo spelaea* (Goldfuss, 1810) – a review. *Quaternaire, Hors-série* 4, 201–208.
- Hemmer, H., Kahlke, R.-D., Vekua, A.K., 2010. *Panthera onca georgica* ssp. nov. from the Early Pleistocene of Dmanisi (Republic of Georgia) and the phylogeography of jaguars (Mammalia, Carnivora, Felidae). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 257, 115–127.
- Hemmer, H., Kahlke, R.-D., Vekua, A.K., 2011. The cheetah *Acinonyx pardinensis* (Croizat et Jobert, 1828) s.l. at the hominin site of Dmanisi (Georgia) – A potential prime meat supplier in Early Pleistocene ecosystems. *Quaternary Science Reviews* 30, 2703–2714.
- Kahlke, H.-D., 1963a. *Ovibos* aus den Kiesen von Süßenborn. Ein Beitrag zur Systematik und Phylogenie der Ovipovini und zur Stratigraphie des Pleistozäns. *Geologie* 12, 942–972.
- Kahlke, H.-D., 1963b. *Rangifer* aus den Sanden von Mosbach. *Paläontologische Zeitschrift* 37, 277–282.
- Kahlke, H.-D., 1969a. Die *Soergelia*-Reste aus den Kiesen von Süßenborn bei Weimar. *Paläontologische Abhandlungen A, Paläozoologie* 3, 531–545. Taf. XXIII–XXVI.
- Kahlke, H.-D., 1969b. Die Cerviden-Reste aus den Kiesen von Süßenborn bei Weimar. *Paläontologische Abhandlungen A, Paläozoologie* 3, 547–610. Taf. XXVII–XXXVI.
- Kahlke, R.-D., 1990. Der Saiga-Fund von Pahren. Ein Beitrag zur Kenntnis der paläarktischen Verbreitungsgeschichte der Gattung *Saiga* Gray, 1843 unter besonderer Berücksichtigung des Gebietes der DDR. *Eiszeitalter und Gegenwart* 40, 20–37.
- Kahlke, R.-D., 1992. Repeated immigration of *Saiga* into Europe. In: Von Koenigswald, W., Werdelin, L. (Eds.), *Mammalian Migration and Dispersal Events in the European Quaternary*. Courier Forschungsinstitut Senckenberg 153, pp. 187–195.
- Kahlke, R.-D., 1994. Die Entstehungs-, Entwicklungs- und Verbreitungsgeschichte des oberpleistozänen *Mammuthus-Coelodonta*-Faunenkomplexes in Eurasien (Großsäuger). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 546, 1–164 + 23 maps.
- Kahlke, R.-D., 1999. The History of the Origin, Evolution and Dispersal of the Late Pleistocene *Mammuthus-Coelodonta* Faunal Complex in Eurasia (Large Mammals). Fenske Companies, Rapid City.
- Kahlke, R.-D., 2006. Nashörner der Kältesteppe. *Natur und Museum* 136, 245–255.
- Kahlke, R.-D., 2007a. Late Early Pleistocene European large mammals and the concept of an Epiivallanfranchian biochron. In: Kahlke, R.-D., Maul, L.C., Mazza, P.P.A. (Eds.), *Late Neogene and Quaternary biodiversity and evolution: Regional developments and interregional correlations*, Volume II. Courier Forschungsinstitut Senckenberg 259, pp. 265–278.
- Kahlke, R.-D., 2007b. *Soergelia elisabethae*. Ein eiszeitliches Faunenelement Eurasiens und Nordamerikas. *Natur und Museum* 137, 168–169.
- Kahlke, R.-D., Lacombe, F., 2008. The earliest immigration of woolly rhinoceros (*Coelodonta tologojensis*, Rhinocerotidae, Mammalia) into Europe and its adaptive evolution in Palaeoarctic cold stage mammal faunas. *Quaternary Science Reviews* 27, 1951–1961.
- Kahlke, R.-D., Maul, L.C., Meyrick, R.A., Stebich, M., Grasselt, T., 2002. The Quaternary sequence from the late Middle to Upper Pleistocene site of Weimar-Ehringsdorf. In: Meyrick, R.A., Schreve, D.C. (Eds.), *The Quaternary of Central*

- Germany (Thuringia & Surroundings). Field Guide. Quaternary Research Association, London, pp. 163–177.
- Kahlke, R.-D., García, N., Kostopoulos, D.S., Lacombat, F., Lister, A.M., Mazza, P.P.A., Spassov, N., Titov, V.V., 2011. Western Palaearctic palaeoenvironmental conditions during the Early and early Middle Pleistocene inferred from large mammal communities, and implications for hominin dispersal in Europe. *Quaternary Science Reviews* 30, 1368–1395. Special Issue: Ecological scenarios for human evolution during the Early and early Middle Pleistocene in the western Palaearctic.
- Kalb, J.E., Mebrate, A., 1993. Fossil Elephantoids from the Hominid-Bearing Awash Group, Middle Awash Valley, Afar Depression, Ethiopia. *Transactions of the American Philosophical Society* 83, i–xv, 1–114.
- Koufos, G.D., 1993. Late Pliocene carnivores from western Macedonia (Greece). *Paläontologische Zeitschrift* 67, 357–376.
- Krissek, L.A., 1995. Late Cenozoic ice-rafting records from Leg 145 sites in the North Pacific: Late Miocene onset, Late Pliocene intensification, and Pliocene-Pleistocene events. In: Rea, D.K., Basov, I.A., Scholl, D.W., Allan, J.F. (Eds.), *Proceedings of the Ocean Drilling Program. Scientific Results, North Pacific Transect, Covering Leg 145 of the cruises of the Drilling Vessel Joides Resolution, Yokohama, Japan, to Victoria, Canada, Sites 881–887 20 July–20 September 1992. Ocean Drilling Program Texas, A&M University*, vol. 145, p. 179–194.
- Kuzmina, I.E., 1971. Formirovanie teriofauny severnogo Urala v pozdnem antropogene. *Trudy Zoologicheskogo Instituta AN SSSR* 49, 44–122 (in Russian).
- Lazarev, P.A., 2008. *Krupnye mlekopitayushchie antropogena Yakutii*. Nauka, Novosibirsk (in Russian).
- Lisiecki, L.E., Raymo, M.E., 2005. A Pliocene-Pleistocene stack of 57 globally distributed benthic $\delta^{18}\text{O}$ records. *Paleoceanography* 20, PA1003. <http://dx.doi.org/10.1029/2004PA001071>.
- Lister, A.M., 1996. Evolution and taxonomy of Eurasian mammoths. In: Shoshani, J., Tassy, P. (Eds.), *The Proboscidea. Evolution and Palaeoecology of Elephants and Their Relatives*. Oxford University Press, Oxford, New York, Tokyo, pp. 203–213.
- Lister, A.M., 2004. The impact of Quaternary Ice Ages on mammalian evolution. *Philosophical Transactions of the Royal Society B* 359, 221–241.
- Lister, A.M., Sher, A.V., 2001. The Origin and Evolution of the Woolly Mammoth. *Science* 294, 1094–1097.
- Lister, A.M., Stuart, A.J., 2010. The West Runton mammoth (*Mammuthus trogontherii*) and its evolutionary significance. *Quaternary International* 228, 180–209.
- Lister, A.M., van Essen, H., 2003. *Mammuthus rumanus* (Ștefănescu), the earliest mammoth in Europe. In: Petculescu, A., Știucă, E. (Eds.), *Advances in Vertebrate Paleontology "Hen to Panta"*. Romanian Academy. Speleological Institute "Emil Racoviță", Bucharest, pp. 47–52.
- Lister, A.M., Sher, A.V., van Essen, H., Wei, G., 2005. The pattern and process of mammoth evolution in Eurasia. *Quaternary International* 126–128, 49–64.
- Lister, A.M., Dimitrijević, V., Marković, Z., Knežević, S., Mol, D., 2012. A skeleton of 'steppe' mammoth (*Mammuthus trogontherii* (Pohlig)) from Drmno, near Kostolac, Serbia. *Quaternary International* 276–277, 129–144.
- Liu, T.-S., Li, X.-G., 1989. Mammoths in China. In: Martin, P.S., Klein, R.G. (Eds.), *Quaternary Extinctions. A Prehistoric Revolution*. The University of Arizona Press, Tucson, AZ, pp. 517–527.
- Maglio, V.J., 1973. Origin and Evolution of the Elephantidae. *Transactions of the American Philosophical Society*, N. S. 63, 1–149.
- Markov, G.N., 2010. *Mammuthus rumanus*, early mammoth evolution, and migration out of Africa. In: Lacombat, F., Mol, D. (Dir.), *The Vth International Conference on mammoths and their relatives*. Quaternaire, Hors-série 3, 25–26.
- McDonald, J.N., Ray, C.E., Harington, C.R., 1991. Taxonomy and Zoogeography of the Musk Ox Genus *Praeovibos* Staudinger, 1908. In: Purdue, J.R., Klippel, W.E., Styles, B.W. (Eds.), *Beavers, Bobwhites, and Blue-Points: Tributes to the Career of Paul W. Parmalee*. Illinois State Museum Scientific Papers 23 (The University of Tennessee, Department of Anthropology Report of Investigations 52), pp. 285–314.
- Melles, M., Brigham-Grette, J., Minyuk, P.S., Nowaczyk, N.R., Wennrich, V., DeConto, R.M., Anderson, P.A., Andreev, A.A., Coletti, A., Cook, T.L., Haltia-Hovi, E., Kukkonen, M., Lozhkin, A.V., Rosén, P., Tarasov, P., Vogel, H., Wagner, B., 2012. 2.8 Million Years of Arctic Climate Change from Lake El'gygytyn, NE Russia. *Science* 337, 315–320.
- Moigne, A.-M., Palombo, M.R., Belda, V., Heriech-Briki, D., Kacimi, S., Lacombat, F., de Lumley, M.-A., Moutoussamy, J., Rivals, F., Quilès, J., Testu, A., 2006. Les faunes de grands mammifères de la Caune de l'Arago (Tautavel) dans le cadre biochronologique des faunes du Pléistocène moyen italien. *L'Anthropologie* 110, 788–831.
- Mol, D., Tikhonov, A., van der Plicht, J., Kahlke, R.-D., Debruyne, R., van Geel, B., van Reenen, G., Pals, J.P., de Marliave, C., Reumer, J.W.F., 2006. Results of the CER-POLEX/Mammuthus Expeditions on the Taimyr Peninsula, Arctic Siberia, Russian Federation. *Quaternary International* 142–143, 186–202.
- Molnar, P., 2005. Mio-Pliocene growth of the Tibetan Plateau and evolution of East Asian climate. *Palaeontologia Electronica* 8. http://palaeo-electronica.org/paleo/2005_1/molnar2/issue1_05.htm.
- Morgan, G.S., Lucas, G.G., Estep, J.W., 1998. Association of *Cuvieronius*, *Stegomastodon*, and *Mammuthus* (Mammalia: Proboscidea) in the Early Irvingtonian of New Mexico. *Journal of Vertebrate Paleontology* 18, 65A.
- Nikitin, V.P., 2006. *Paleokarpologiya i stratigrafiya paleogena i neogena Aziatskoj Rossii*. Akademicheskoye izdatel'stvo "Geo", Novosibirsk (in Russian).
- Obada, T.F., 2010. The remarks on the systematic attribution of the most ancient Elephantinae Gray, 1821 (Mammalia, Proboscidea) of Europe. In: Lazarev, P., Boeskorov, G., Maschenko, E. (Eds.), *Proceedings of the IV International Mammoth Conference*. Institut prikladnoj ekologii Severa AN RS (Ya), Yakutsk, pp. 80–106.
- Pei, W.-C., 1957. The zoogeographical divisions of Quaternary mammalian faunas in China. *Vertebrata Palasiatica* 1, 9–24.
- Pereladov, V.T., Shpanskiy, A.V., 1997. Pervye nakhodki sherstistogo nosoroga na Vostochnoj Chukotke. In: *Voprosy Geologii i Paleontologii Sibiri*. Izdatel'stvo Tomskogo Gosuniversiteta, Tomsk, pp. 94–98 (in Russian).
- Péwé, T.L., Hopkins, D.M., 1967. Mammal Remains of Pre-Wisconsin Age in Alaska. In: Hopkins, D.M. (Ed.), *The Bering Land Bridge*. Stanford University Press, Stanford, CAL, pp. 267–270.
- Qiu, Z., 2000. Nihewan fauna and Q/N boundary in China. *Quaternary Sciences* 20, 142–154.
- Qiu, Z., Deng, T., Wang, B., 2004. Early Pleistocene Mammalian Fauna from Longdan, Dongxiang, Gansu, China. *Palaeontologia Sinica* 191, N. S. C 27, 11–198, pl. 1–XXXIV.
- Rădulescu, C., Samson, P., 1985. Pliocene and Pleistocene mammalian biostratigraphy in southeastern Transylvania (Romania). *Travaux de l'Institut de Spéologie «Emile Racovitza»* 24, 85–95.
- Ramstein, G., Fluteau, F., Besse, J., Joussaume, S., 1997. Effect of orogeny, plate motion and land-sea distribution on Eurasian climate change over the past 30 million years. *Nature* 386, 788–795.
- Randi, E., Mucci, N., Pierpaoli, M., Douzery, E., 1998. New phylogenetic perspectives on the Cervidae (Artiodactyla) are provided by the mitochondrial cytochrome b gene. *Proceedings of the Royal Society London B* 265, 793–801.
- Raufuss, I., von Koenigswald, W., 1999. New remains of Pleistocene *Ovibos moschatus* from Germany and its geographic and stratigraphic occurrence in Europe. *Geologie en Mijnbouw* 78, 383–394.
- Raymo, M.E., Nisancioglu, K., 2003. The 41 kyr world: Milankovitch's other unsolved mystery. *Paleoceanography* 18, 1011. <http://dx.doi.org/10.1029/2002PA000791>.
- Ruddiman, W.F., Kutzbach, J.E., 1989. Forcing of Late Cenozoic Northern Hemisphere Climate by Plateau Uplift in Southern Asia and the American West. *Journal of Geophysical Research* 94, 18,379–18,391.
- Sala, B., 1983. Les faunes ongulés de Badanj et leurs indications paléoclimatiques. In: Colloque International "La position taxonomique et chronologique des industries à pointes à dos autour de la Méditerranée européenne", Siena, 3–6 Novembre 1983. Tipografia Senese, Siena, pp. 341–345.
- Savinevskiy, A.B., Ptashinskiy, A.V., 1999. The hunting catch of ancient sea-mammal hunters of Kamchatka. In: Poyarkov, N.D. (Ed.), *The biology and conservation of the birds of Kamchatka*. 1. Dialog, Moscow, pp. 109–111 (in Russian, with English summary).
- Schreve, D., 2001. Differentiation of the British late Middle Pleistocene interglacials: the evidence from mammalian biostratigraphy. *Quaternary Science Reviews* 20, 1693–1705.
- Shchelinsky, V.E., Dodonov, A.E., Baigusheva, V.S., Kulakov, S.A., Simakova, A.N., Tesakov, A.S., Titov, V.V., 2010. Early Palaeolithic sites on the Taman Peninsula (Southern Azov Sea region, Russia): Bogatyri/Sinyaya Balka and Rodniki. *Quaternary International* 223–224, 28–35.
- Sher, A.V., 1971. *Mlekopitayushchie i stratigrafiya Pleistozena krajnego severovostoka SSSR i Severnoj Ameriki*. Nauka, Moskva (in Russian).
- Sher, A.V., 1986. On the History of Mammal Fauna of Beringida. *Quartärpaläontologie* 6, 185–193.
- Sher, A.V., 1987. Olyorian land mammal age of Northeastern Siberia. *Palaeontographia Italica* 74, 97–112.
- Sher, A., 1992. Beringian fauna and early Quaternary mammalian dispersal in Eurasia: ecological aspects. In: Von Koenigswald, W., Werdelin, L. (Eds.), *Mammalian Migration and Dispersal Events in the European Quaternary*. Courier Forschungsinstitut Senckenberg, 153, pp. 125–133.
- Sher, A.V., Weinstock, J., Baryshnikov, G.F., Davydov, S.P., Boeskorov, G.G., Zazhigin, V.S., Nikolskiy, P.A., 2011. The first record of "spelaeoid" bears in Arctic Siberia. *Quaternary Science Reviews* 30, 2238–2249.
- Sher, A.V., Kaplina, T.N., Giterman, R.E., Lozhkin, A.V., Arkhangelov, A.A., Kiselyov, S.V., Kouznetsov, Yu.V., Virina, E.I., Zazhigin, V.S., 1979. Late Cenozoic of the Kolyma Lowland. In: Sher, A.V., Kaplina, T.N. (Eds.), *Tour XI Guide-Book, XIV Pacific Science Congress, USSR, Khabarovsk August 1979*. Academy of Sciences of the USSR, Moscow, pp. 1–115 (in Russian and English).
- Shichi, K., Kawamuro, K., Takahara, H., Hase, Y., Maki, T., Miyoshi, N., 2007. Climate and vegetation changes around Lake Baikal during the last 350,000 years. *Palaeogeography, Palaeoclimatology, Palaeoecology* 248, 357–375.
- Soergel, W., 1939. Unter welchen klimatischen Verhältnissen lebten zur Bildungszeit der altdiluvialen Kiese von Süßenborn *Rangifer*, *Ovibos* und *Elephas trogontherii* in Mittel- und Norddeutschland? *Zeitschrift der Deutschen Geologischen Gesellschaft* 91, 828–835.
- Soergel, W., 1940. Der Klimacharakter des Mammut. *Paläontologische Zeitschrift* 22, 29–55.
- Sotnikova, M.V., 1978. Novye dannye o khishchnykh mlekopitayushchikh verkhnego pliotse na u nizhego plejstotsena na territorii severo-vostoka SSSR. *Byulleten' Komissii po Izucheniyu Chetvertichnogo Perioda* 48, 22–30 (in Russian).
- Sotnikova, M.V., 1982. K istorii roda *Gulo* v Evrazii. *Trudy Zoologicheskogo Instituta AN SSSR* 111, 65–73 (in Russian).
- Sotnikova, M.V., 1988. Assotsiatsiya melkikh volk – ksenotsion v pozdnem eopleistotsene – rannem pleistotsene Zentralnoj Azii. *Byulleten' Komissii po Izucheniyu Chetvertichnogo Perioda* 57, 78–89 (in Russian).
- Spassov, N., 1999. The Mammalian Megafauna from the Late Villafranchian Localities Varshets and Slivnitsa (Bulgaria) and the Biochronology of the

- Villafranchian in S.-E. Europe. Ph.D. Thesis, National Museum of Natural History Sofia, Bulgarian Academy of Sciences, Bulgaria (in Bulgarian).
- Spassov, N., 2000. Biochronology and zoogeographic affinities of the Villafranchian faunas of Bulgaria and South Europe. *Historia naturalis bulgarica* 12, 89–128.
- Staudinger, W., 1908. *Praeovibos priscus*, nov. gen. et nov. sp., ein Vertreter einer *Ovibos* nahestehenden Gattung aus dem Pleistocän Thüringens. *Centralblatt für Mineralogie, Geologie und Paläontologie* 1908, 481–496.
- Storer, J.E., 2002. Advances in the ice age biostratigraphy of Eastern Beringia. In: Dougherty, B.J., McCracken, A.D. (Eds.), *Abstracts and Short Papers from the Canadian Paleontology Conference 2002*. Geological Survey of Canada, Ottawa, p. 46.
- Storer, J.E., 2003. The Eastern Beringian vole *Microtus deceitensis* (Rodentia, Muridae, Arvicolinae) in Late Pliocene and Early Pleistocene faunas of Alaska and Yukon. *Quaternary Research* 60, 84–93.
- Storer, J.E., 2004. A new species of *Mustela* (Mammalia; Carnivora; Mustelidae) from the Fort Selkirk fauna (Early Pleistocene) of Yukon Territory, Canada. *Paludicola* 4, 151–155.
- Thierens, M., Pirllet, H., Colin, C., Latruwe, K., Vanhaecke, F., Lee, J.R., Stuut, J.-B., Titschack, J., Huvenne, V.A.I., Dorschel, B., Wheeler, A.J., Henriot, J.-P., 2011. Ice-rafting from the British-Irish ice sheet since the earliest Pleistocene (2.6 million years ago): implications for long-term mid-latitude ice-sheet growth in the North Atlantic region. *Quaternary Science Reviews* 44, 229–240.
- Tong, H., 2010a. Proboscidean fossil records in Nihewan Basin, North China. In: Lacombe, F., Mol, D. (Dir.), *The Vth International Conference on mammoths and their relatives*. Quaternaire, Hors-série 3, 173–174.
- Tong, H., 2010b. New materials of *Mammuthus trogontherii* (Proboscidea, Mammalia) of Late Pleistocene age from Yuxian, Hebei. *Quaternary Sciences* 30, 307–318 (in Chinese, with English abstract).
- Turner, E., With Contributions from Boenigk, W., Frechen, M., van Kolfschoten, M., Schnepf, E., Sefkov, E., Steensma, K., 1997. Ariendorf. Quaternary deposits and Palaeolithic excavations in the Karl Schneider gravel pit. *Jahrbuch des Römisch-Germanischen Zentralmuseums Mainz* 44, 3–191, pl. 1–8.
- Van Essen, H., 2003. Tooth morphology of *Mammuthus meridionalis* from the southern bight of the North Sea and from several localities in the Netherlands. In: Reumer, J.W.F., De Vos, J., Mol, D. (Eds.), *Advances in Mammoth Research, Proceedings of the Second International Mammoth Conference, Rotterdam, May 16–20 1999*. Deinsea 9, pp. 453–511.
- Van Essen, H., 2011. Tracing Transitions. An overview of the evolution and migrations of the genus *Mammuthus* Brookes, 1828 (Mammalia, Proboscidea). Ph.D. Thesis Universiteit Leiden, The Netherlands.
- Vangengejm, E.A., Erbaeva, M.A., Sotnikova, M.V., 1990. Pleistocene Mammals from Zasulino, Western Transbaikalia. *Quartärpaläontologie* 8, 257–264.
- Vangengejm, E.A., Belyaeva, E.I., Garutt, V.E., Dmitrieva, E.I., Zazhigin, V.S., 1966. *Mlekopitayushchie eopleistotsena zapadnogo Zabaikal'ya*. Nauka, Moskva (in Russian).
- Velichko, A.A., Akhlestina, E.F., Borisova, O.K., Gribchenko, Yu.N., Zhidovinov, N.Ya., Zelikson, E.M., Iosifova, Yu.I., Klimanov, V.A., Morosova, T.D., Nechaev, V.P., Pisareva, V.V., Svelitskaya, T.V., Spasskaya, I.I., Udartsev, V.P., Faustova, M.A., Shik, S.M., 2005. East European Plain. In: Velichko, A.A., Nechaev, V.P. (Eds.), *Cenozoic Climatic and Environmental Changes in Russia*. The Geological Society of America, Special Paper 382, Boulder, Colorado, pp. 31–66.
- Vereshchagin, N.K., Baryshnikov, G.F., 1982. Paleoeology of the mammoth fauna in the Eurasian Arctic. In: Hopkins, D.M., Matthews Jr., J.V., Schweger, C.E., Young, S.B. (Eds.), *Palaeoecology of Beringia*. Academic Press, New York, pp. 267–279.
- Wang, Y., Deng, T., Biasatti, D., 2006. Ancient diets indicate significant uplift of southern Tibet after ca. 7 Ma. *Geology* 34, 309–312.
- We, G.B., Wang, Y., Jin, C.Z., 2010. New materials of the steppe mammoth from northern China, with discussion on the origin and evolutionary patterns of mammoths. In: Lacombe, F., Mol, D. (Dir.), *The Vth International Conference on mammoths and their relatives*. Quaternaire, Hors-série 3, p. 93.
- Wei, G., Taruno, H., Jin, C., Xie, F., 2003. The earliest specimens of the steppe mammoth, *Mammuthus trogontherii*, from the Early Pleistocene Nihewan Formation, North China. *Earth Science (Japan)* 57, 289–298.
- Wei, G.B., Taruno, H., Kawamura, Y., Jin, C.Z., 2006. Pliocene and Early Pleistocene Primitive Mammoths of Northern China: Their revised taxonomy, biostratigraphy and evolution. *Journal of Geosciences, Osaka City University* 49, 59–101.
- Wei, Q., 2009. Paleolithic sites of Nihewan. In: *International Symposium on Paleo-anthropology in Commemoration of the 80th Anniversary of the Discovery of the First Skull of Peking Man and the First Asian Conference on Quaternary Research*, Beijing, pp. 8–27.
- Westgate, J., Froese, D.G., 2003. Quartz Creek: Pliocene ice wedges/Quartz Creek tephra (63° 46' N, 139° 03' W.). In: Froese, D.G., Zazula, G.D. (Eds.), *3rd International Mammoth Conference. Field Guide to Quaternary research in the Klondike Goldfields. Occasional Papers in Earth Sciences* 6, pp. 62–63.
- Xue, X., 1991. Quaternary Mammalian Fossils and Fossil Human Beings. In: Zhang, Z., Shao, S., Tong, G., Cao, J. (Eds.), *The Quaternary of China*. China Ocean Press, Beijing, pp. 307–374.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, Rhythms, and Aberrations in Global Climate 65 Ma to Present. *Science* 292, 686–693.
- Zazula, G.D., Turner, D.G., Ward, B.C., Bond, J., 2011. Last interglacial western camel (*Camelops hesternus*) from eastern Beringia. *Quaternary Science Reviews* 30, 2355–2360.
- Zhang, Z.-Q., 2006. Chinese Late Neogene land mammal community and the environmental changes of East Asia. *Vertebrata Palasiatica* 44, 133–142 (in Chinese, with English summary).
- Zhegallo, V.I., Zazhigin, V.S., Kolosova, G.N., Malaeva, E.M., Murzaeva, V.E., Sotnikova, M.V., Vislobokova, I.A., Dmitrieva, E.D., Dubrovo, I.A., 1982. Nalaikha – opornyj razrez nizhnego pleistotsena Mongolii. In: Nikiforova, K.V. (Ed.), *Stratigrafiya i paleogeografiya antropogena*. Nauka, Moskva, pp. 124–143 (in Russian).
- Zhu, R., An, Z., Potts, R., Hoffman, K.A., 2003. Magnetostratigraphic dating of early humans in China. *Earth Science Reviews* 61, 341–359.