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

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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 southwestward 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.

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

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[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.

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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 Caenozoic 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 preudomorphoses, 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 parallelled 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*, *Crocuta* and *Panthera*, in addition to different groups of horses (*Equus*) which undoubtedly originated in the Nearctic, also