



Megafaunal split ends: microscopical characterisation of hair structure and function in extinct woolly mammoth and woolly rhino



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ABSTRACT

The large extinct megafaunal species of the Late Pleistocene, *Mammuthus primigenius* (woolly mammoth) and *Coelodonta antiquitatis* (woolly rhino) are renowned for their pelage. Despite this, very little research has been conducted on the form and function of hair from these iconic species. Using permafrost preserved hair samples from seven extinct megafaunal remains, this study presents an in-depth microscopical characterisation of preservation, taphonomy, microbial damage, pigmentation and morphological features of more than 420 hairs. The presence of unique structural features in hairs, from two extinct megafauna species, such as multiple medullae and unparallelled stiffness suggests evolution of traits that may have been critical for their survival in the harsh arctic environment. Lastly, despite popular depictions of red-haired and/or uniformly coloured mammoths, a closer examination of pigmentation reveals that mammoth coats may have exhibited a mottled/variegated appearance and that their 'true' colours were not the vivid red/orange colour often depicted in reconstructions. Insights gained from microscopical examination of hundreds of extinct megafauna hairs demonstrate the value of extracting as much morphological data as possible from ancient hairs prior to destructive sampling for molecular analyses.

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1. Introduction

Mammalian hair predominantly consists of the protein keratin, which due to its chemical structure is highly durable. This resilience is responsible for the survival and preservation of hair for millennia in remains that have been exposed to diverse and extreme conditions such as freezing, burial and mummification. Hair preserved in archaeological and palaeontological contexts is now sought after as a source of "pure" preserved ancient DNA (Gilbert et al., 2008; Rasmussen et al., 2011); however there is much to be gained from the morphological analysis of hair before it is destructively sampled.

Mammalian hair is essentially composed of three layers consisting of the outermost cuticle, an inner cortex and a central core or medulla (Fig. 1). Close inspection of animal pelts reveals the presence of three distinct types of hair: overhairs, guard hairs and

underhairs. Overhairs are the most prominent and coarsest of hairs on the pelage (coat) and are commonly circular in cross-sectional shape. Guard hairs are less coarse and shorter than overhairs; guard hairs exhibit an array of medullae morphologies, scale patterns and cross-sectional shapes that are usually diagnostic for a particular taxon (Teerink, 1991). The underhairs are shorter and much finer; they range from being wavy, lightly curled to tightly curled and commonly show circular cross-sections. In most mammalian hairs there is a gradation from one hair 'type' to another. This gradation is not abrupt as shown by the presence of 'transitional' hair types, which bear 'hybrid' features.

All mammalian hair shares similar chemical and physical composition and structure. Cross-sectional shapes, medullae morphologies and scale pattern not only differentiate human hair from animal but may also assist in differentiating animal hairs that originate from different taxa. Furthermore, mammalian hairs exhibit intra- and interspecies variance in profile and morphological characteristics depending on the somatic origin (body area that hair originates from) (Brunner and Coman, 1974; Teerink, 1991). While many extant taxa have been studied with regards to hair form and function, for obvious reasons, extinct species have received much less attention.

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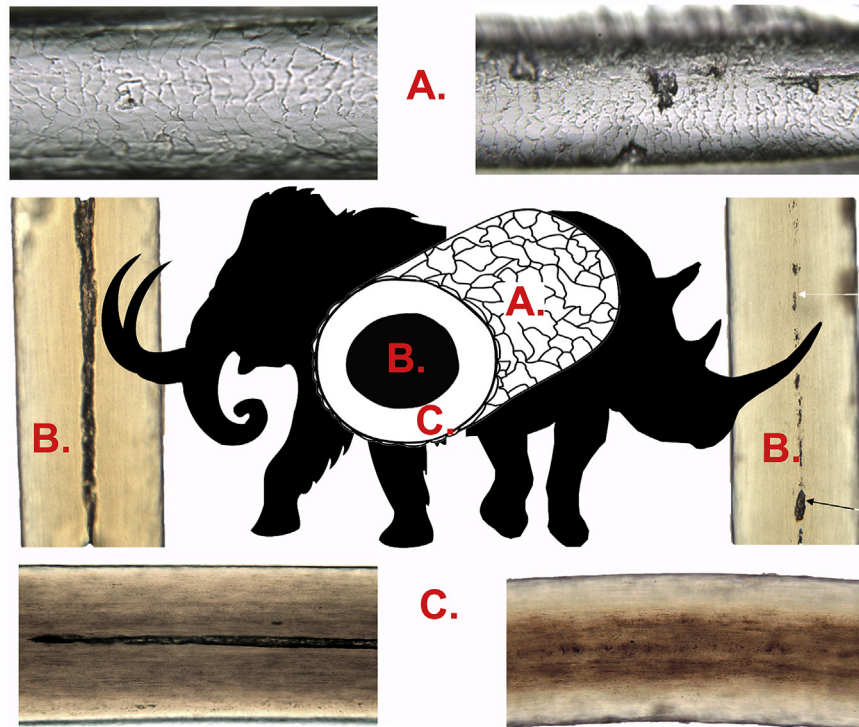


Fig. 1. Schematic diagram of a generic mammalian hair (centre) that consists of three major components. (A) The outermost cuticle, (B) the central core or medulla which may be continuous (left) or interrupted (right) and (C) cortex that contains pigment granules (melanins) which may be uniformly distributed across the hair shaft (left) or medially distributed (right).

The woolly mammoth (*Mammuthus primigenius*) is probably the most iconic and charismatic of all the extinct northern megafauna and is renowned for its size and hairy coat. Vast numbers of these animals roamed Eurasia and North America in the Pleistocene before becoming extinct on the mainland some 10,000 years ago. The species clung to existence until the last known individuals, comprising a dwarf island population on Wrangel Island, vanished some 4000 years ago (Vartanyan et al., 1993). The causes underlying the extinction of woolly mammoth still remain elusive – a complex interplay of climate and anthropogenic influences is currently proposed (Lorenzen et al., 2011). Despite becoming extinct a few thousand years ago a great deal is known about the woolly mammoth, and it is arguably one of the best-understood representatives of the extinct megafauna. Their relative abundance and wide geographic range increased the probability of discovering their remains; their demise and subsequent entombment in a natural freezer ensured exceptional preservation.

In contrast, the woolly rhinoceros (*Coelodonta antiquitatis*) is less well understood. This is probably due to the paucity of mummified remains (compared to woolly mammoth) that have been discovered, which may reflect the more restricted geographic distribution of this species (it was absent from large areas of the high Arctic, for example) and possibly lower population density, relative to that of the woolly mammoth.

The morphology of woolly mammoth and woolly rhinoceros bones, teeth and carcasses have been extensively studied and documented contributing a wealth of knowledge with regards to their natural history and adaptations to surviving cold temperatures (Boeskorov, 2004). Woolly mammoth were also among the first species to be investigated using PCR of ancient mitochondrial (Paabo et al., 1989) and nuclear DNA (Greenwood et al., 1999). The advent of next generation sequencing enabled researchers to

sequence short, fragmented strands of mammoth DNA using the elephant genome as a scaffold (Miller et al., 2008). Significantly, the substrate used for this genome was mammoth hair due to the high levels (relative to contaminating environmental sequences) of endogenous mammoth DNA compared to bone (Gilbert et al., 2008) (Gilbert et al., 2007). The survival of woolly mammoth hair entombed in permafrost for millennia is testament to the resilience of the biopolymer keratin to withstand harsh environmental conditions and insults. In contrast to the woolly mammoth's genome and skeletal morphology, hairs comprising the thick woolly coat, for which this species and (woolly rhino) are famously known, have received little detailed morphological examinations. The objective of the current study is to conduct detailed and comprehensive microscopical examination of hairs from these extinct megafauna in order to investigate possible relationships between hair structure and the environment these animals inhabited and study the effects of taphonomy.

2. Materials and methods

2.1. Materials

A total of six woolly mammoth (Jarkov, Yukagir, Dima, Fishhook, M25 and M26) and one woolly rhinoceros (Churapcha) hair samples were examined. The original geographic locations in which the remains of these megafauna were found and specimen details are presented in Fig. 2 and in more detail in other publications (Gilbert et al., 2007, 2008).

Adult African elephant (*Loxodonta africana*) hairs were obtained from the United States Fisheries and Wildlife Forensic Laboratory and Aalborg Zoo, Denmark. Adult Asian elephant (*Elephas maximus*) hairs were obtained from Copenhagen Zoo, Denmark. Somatic

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