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Proboscidean isotopic compositions provide insight into ancient humans and their environments

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ABSTRACT

Isotopic analyses of proboscidean remains (e.g., mammoth, mastodon, gompothere, elephant) can provide significant insights into past environmental conditions and animal behaviour. Because they are associated with humans over a broad geographical and temporal scale, proboscidean remains can also be used to understand the activities and environmental contexts of ancient humans. This paper reviews the isotopic literature on proboscideans, including (1) bulk tissue approaches to understanding past climate, vegetation patterns, and migrations, (2) serial sampling approaches to understanding seasonal variations, and (3) direct uses of proboscidean isotopic compositions to investigate human lifeways, including Neandertal and Upper Paleolithic humans in Europe and Paleoindian/Clovis people in North America.

1. Introduction

It is not hyperbole to state that proboscideans (e.g., mammoths, mastodons, gomphotheres, elephants) have been of interest to humans since the dawn of our species. Hominin associations with proboscideans date back at least 1.8 million years, and include *Homo erectus* and *Deinotherium*/*Elephas* in Africa (Domínguez-Rodrigo et al., 2014; Surovell et al., 2005), *Homo neanderthalensis*/*heidelbergensis* and *Elephas*/*Palaeoloxodon*/*Mammuthus* in Europe (Bocherens, 2011; Boschian and Sacca, 2010; Onoratini et al., 2012; Yravedra et al., 2014), and *Homo floresiensis* and dwarf *Stegodon* in Indonesia (Aiello, 2010; Brumm et al., 2010). Anatomically modern humans have a long history of association with proboscideans over a vast temporal and geographical range (Gaudzinski et al., 2005), including Upper Paleolithic Europe and Asia (Germonpre et al., 2008; Kuzmin, 2010; Pitulko and Nikolskiy, 2012; Svoboda et al., 2011; Zhang et al., 2010), pre-Clovis and Clovis-era North America (Grayson and Meltzer, 2002; Sánchez et al., 2009; Surovell and Waguespack, 2008; Waters et al., 2011) and modern Africa and Asia (Hoare, 2000; Sukumar, 1989; 2008). Premodern and modern humans hunted and scavenged proboscideans for food (Agam and Barkai, 2016; Byers and Ugan, 2005; Demay et al., 2012; Grayson and Meltzer, 2002; Mussi and Villa, 2008; Nikolskiy and Pitulko, 2013), utilized skeletal remains for tools and housing materials (Boschian and Saccà, 2015; Demay et al., 2012; Haynes and Hemmings, 1968; Nikolskiy and Pitulko, 2013; Onoratini et al., 2012; Saunders et al., 1990; Zutovski and Barkai, 2016), and depicted proboscideans in art (Braun and Palombo, 2012; Conard, 2003; Pettitt, 2008; Purdy et al., 2011) (Fig. 1). Proboscideans closely resemble humans in a variety of physical, social and behavioural characteristics (e.g., large brains, long gestation, extended maternal care, close family bonds, complex social hierarchies, mourning the dead, showing altruism, expressing empathy), which may have contributed to heightened significance of proboscideans to human cultures in both ancient and modern times (Lev and Barkai, 2016). Human hunting has been implicated in the extinction of some proboscidean taxa (Haynes, 2002a; Koch and Barnosky, 2006), though the extent of human impacts remains contentious (Grayson, 2007; Kuzmin, 2010; Nogués-Bravo et al., 2008; Stuart, 2005; Ugan and Byers, 2008). Over the last 4000 years, captive elephants have been used for military purposes, transportation, labor (e.g., logging), cultural festivities, and entertainment (Sukumar, 2008). Hunting elephants (especially for ivory) has played a major role in elephant population decline, and has been the focus of considerable public attention and conservation efforts (Bouché et al., 2011; Wittemyer et al., 2011). Human-elephant conflict (e.g., crop raiding and human retaliation) also

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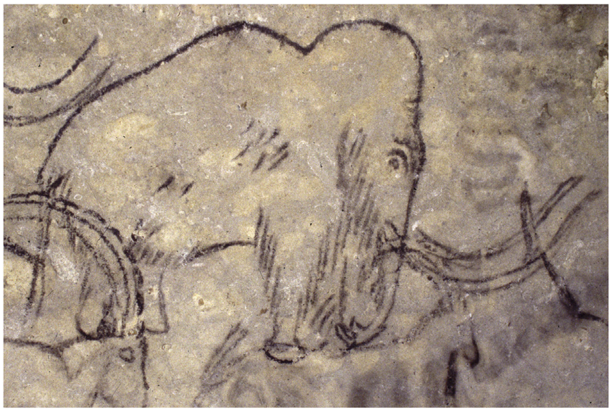

Fig. 1. Paleolithic depiction of a mammoth from Rouffignac Cave, France. Photograph courtesy of Frédéric Plassard, copyright *Grotte de Rouffignac*.

remains a concern in parts of Asia and Africa today (Sukumar, 2008).

Given the incredible temporal duration and geographical scope of associations between humans and proboscideans, analysis of proboscidean remains associated with or contemporaneous with human groups has the potential to provide insights into many aspects of human life. Stable isotope analysis, in particular, can potentially be used to reconstruct past environments and aspects of human subsistence activities. An advantage of using animal remains instead of more traditional proxies for environmental reconstruction (e.g., sedimentary or ice-core records) is that the former tend to record changes over finer time scales (e.g., seasonal variations in temperature, rainfall, and vegetation types), which better reflect the lived experiences of humans. Furthermore, animal remains can be collected from the same geographic areas that humans occupied, and in some cases animal remains are directly associated with human activities, allowing them to provide direct evidence for environmental conditions at those locations. In contrast, ice and sediment cores used to make paleoclimatic inferences are often located considerable distances from human-occupied regions.

Perhaps because they are so large and abundant, proboscidean bones, teeth, and tusks were among the first faunal remains used for paleoenvironmental reconstruction by stable isotope analysis (e.g., Ayliffe et al., 1992, 1994; Bocherens et al., 1994; Koch, 1989). Although isotopic studies of proboscideans have increased dramatically in recent years, relatively few have attempted to use the data to make inferences about human activities. This paper reviews previous isotopic (δ^{13}C, δ^{15}N, δ^{18}O, δ^{2}H, and ^{87}Sr/^{86}Sr) work on proboscideans, summarizing what we have learned about proboscideans, people, and their environments. Previous researchers have provided thorough reviews on the use of stable isotopes in skeletal remains for dietary and environmental reconstruction (e.g., Bocherens, 2011; Hedges et al., 2004; Koch, 1998; Koch et al., 1994; Kohn and Cerling, 2002; West et al., 2006), so comprehensive background information is not provided here. Instead, I describe insights gained from a large body of research on proboscidean tissues (including bone, tooth, tusk, and hair) that spans more than two decades. First, I review the use of bulk proboscidean tissue isotopic compositions for reconstructing past environments, considering isotopes of carbon, nitrogen, oxygen, and strontium in turn. The bulk sampling approach averages multiple seasons or years of growth (Fig. 2), providing information on more time-averaged (e.g., decadal) conditions in the past. Second, I describe isotopic studies employing serial-sampling of proboscidean tissues (i.e., tooth or tusk dentin, tooth enamel, and hair), which can provide insights into seasonal variations (Fig. 2). Third, I describe studies that have used the isotopic compositions of proboscidean remains that were directly associated or contemporaneous with humans to make inferences about human activities and human environments. These studies show that proboscidean isotopic compositions can provide considerable insight into environmental conditions, animal behaviour, and human activities at different temporal and geographical scales.

2. Bulk tissue approaches to paleoenvironmental inferences

Bulk tissue approaches utilize samples of bone, tusk, tooth, or hair that average several seasons of growth, providing time-averaged isotopic records that can be used to make inferences about general environmental conditions and/or diet over a period of years or decades.

2.1. Carbon isotopes

Carbon isotope compositions of herbivore remains (e.g., collagen (col) in bone, keratin in hair, structural carbonate (sc) in enamel or bone bioapatite) can provide information on the types of plants consumed (especially C_3 vs C_4), the environmental conditions of plant growth, and (possibly) animal physiology. A common approach in areas with significant C_4 plants is to use animal δ^{13}C values to distinguish between grazing (C_4 grass consumption) and browsing (C_3 tree and shrub consumption – but C_3 grasses could also contribute) and/or the relative proportions of C_3 and C_4 plants at a location or during a particular time period. Using tooth enamel $\delta^{13}C_{sc}$, Cerling et al. (1999) demonstrated that fossil elephants in Africa and Asia between 5 and 1 million years ago fed almost exclusively on grasses, whereas today they have highly flexible diets which can include large quantities of browse (e.g., Codron et al., 2012). For proboscideans and other herbivore taxa in Florida, there was a shift in enamel $\delta^{13}C_{sc}$ around 7 Ma (MacFadden and Cerling, 1996), indicating increased C_4 plant consumption in step with the global proliferation of C_4 plants (Cerling et al., 1993, 1997). The niche breadth and degree of niche partitioning of proboscideans and other taxa in Florida also changed with Plio-Pleistocene climatic variations (DeSantis et al., 2009). In South America, gomphothere diets varied with latitude: the greatest C_4 plant consumption occurred in equatorial regions, but considerable dietary variability occurred within taxa living at the same latitude (Sánchez et al., 2004). Carbon isotopes have also been used to estimate the dietary C_4 contents of modern elephants (e.g., Sukumar and Ramesh, 1992), Middle Pleistocene proboscideans in southern Europe (Palombo et al., 2005), mammoths and gomphotheres in Mexico (Mayte et al., 2016; Perez-Crespo et al., 2012, 2015) and mammoths and mastodons in the central, southern, and eastern United States (Baumann and Crowley, 2015; Feranec, 2004; Hoppe, 2004; Koch et al., 1998, 2004; MacFadden and Cerling, 1996; Tankersley et al., 2015). In lower latitude areas, mammoths tended to consume diets high in C_4 grasses, whereas mastodons consumed predominantly C_3 plants (i.e., trees and shrubs). However, some Columbian mammoths from southern Arizona and Mexico had δ^{13}C values that indicated significant proportions of trees and shrubs (or C_3 grasses) in the diet (Mayte et al., 2016; Metcalfe et al., 2011; Perez-Crespo et al., 2012). A plot of $\delta^{13}C_{sc}$ with latitude for North America shows that C_4 plants are present in the diets of mammoths south of about 45°N, but are completely lacking north of that latitude (Fig. 3). This is consistent with the approximate northern extent of modern C_4 plants (but note that longitudinal and altitudinal variations also occur, and that these have changed over time) (Leavitt et al., 2007; von Fischer et al.,