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Proboscideans and paleoenvironments of the Pleistocene Great Lakes: landscape, vegetation, and stable isotopes

Jessica Z. Metcalfe [a,*], Fred J. Longstaffe [a], Greg Hodgins [b,c]

[a] Department of Earth Sciences, The University of Western Ontario, London, ON N6A 5B7, Canada
[b] NSF Arizona AMS Laboratory, Department of Physics, The University of Arizona, Tucson, AZ 85721-0081, USA
[c] School of Anthropology, The University of Arizona, Tucson, AZ 85721-0081, USA

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ABSTRACT

In this study, we review the history of proboscideans in the Great Lakes region (Ontario and western New York) in the context of local glacial and vegetational histories. Further, we investigate mammoth (*Mammuthus*) and mastodon (*Mammut*) environmental niche partitioning using stable isotope analysis of bone and dentin collagen ($\delta^{13}C_{col}$, $\delta^{15}N_{col}$) and structural carbonate in tooth enamel bioapatite ($\delta^{13}C_{sc}$, $\delta^{18}O_{sc}$), and demonstrate that stable isotopes can be used to identify non-locals among museum specimens with no contextual records. New radiocarbon dates suggest that Ontario mastodons lived in tundra-like environments as well as their more common spruce forest habitat. Local Ontario/New York mammoths and mastodons consumed 100% C_3-plant diets and drank low-^{18}O waters, consistent with colder-than-modern climates and proximity to glacial meltwater sources. Mammoths and mastodons occupied distinct environmental niches, characterized by different oxygen- and nitrogen-isotope compositions and geographical locations. This suggests that direct competition for resources was not a major factor in their local extinction. We suggest that both mammoths and mastodons obtained water from sources formed primarily from precipitation rather than glacial meltwater. We describe how high $\delta^{15}N$ values in mammoths could have been caused by a combination of preferences for dry environments, consumption of low-nutrient forage (particularly stems and stalks), coprophagy, geophagy, and dung fertilization. We argue that low $\delta^{15}N$ values in mastodons could have been caused by consumption of trees and shrubs (including nitrogen-fixing taxa) and a preference for recently deglaciated landscapes and/or spruce environments. Finally, we raise the possibility that mastodons contributed to the spruce-pine transition by browsing directly on spruce trees.

1. Introduction

Mammoths (*Mammuthus*) and mastodons (*Mammut*) were once widespread in North America, but became extinct throughout most of the continent at the end of the Pleistocene (ca 11,000–10,000 BP) (Agenbroad, 2005; Waters and Stafford, 2007). The cause of their extinction has been the subject of controversy (see Haynes, 2009 for review), as it coincides with both the onset of the Younger Dryas chronozone and the appearance of Clovis hunters in North America (Haynes, 2002; Haynes, 2008). Although consensus has not been reached, it is now evident that megafaunal extinction processes differed among regions and taxa (e.g., Guthrie, 2003, 2006; Shapiro et al., 2004; Buck and Bard, 2007; Ugan and Byers, 2007; Campos et al., 2010; Kuzmin, 2010; Vegas-Vilarrúbia et al., 2011; Macdonald et al., 2012).

Typically, woolly mammoths (*Mammuthus primigenius*) inhabited steppe-tundra environments (e.g., Harington and Ashworth, 1986; Nielsen et al., 1988) and American mastodons (*Mammut americanum*) inhabited open spruce forests (Dreimanis, 1967; Zazula et al., 2006). Mammoths have been classified as grazers, and mastodons as browsers, based on dental and other morphological adaptations (Harington and Ashworth, 1986; G. Haynes, 1991), tooth enamel isotopic compositions (MacFadden and Cerling, 1996; Koch et al., 1998; DeSantis et al., 2009), enamel microwear (Green et al., 2005), dung and gut contents (Ukraintseva et al., 1996; Newsom and Mihlbachler, 2006), and associated pollen and plant macrofossil assemblages (Dreimanis, 1967, 1968;

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[*] Corresponding author. Present address: Department of Anthropology, The University of British Columbia, 6303 NW Marine Dr., Vancouver, BC V6T 1Z1, Canada. Tel.: +1 604 984 8881.
E-mail addresses: jess_metcalfe@hotmail.com, jessica.metcalfe@ubc.ca (J.Z. Metcalfe).

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Harington et al., 1993; Guthrie, 2001). However, these and other studies also indicate that mammoths and mastodons, like their modern elephant relatives, were capable of significant dietary flexibility (e.g., Lepper et al., 1991; Mead et al., 1986; Newsom and Mihlbachler, 2006; Owen-Smith, 1988; Sukumar, 1989, 2003; van Geel et al., 2008). At least one woolly mammoth in Illinois appears to have inhabited a wet, forested environment, contrary to the characteristic habitat of this species (Saunders et al., 2010). Columbian mammoths (*Mammuthus columbi*) in Colorado utilized several environmental zones, as evidenced by grasses, conifers and possibly oak phytoliths in their tooth calculus (Cummings and Albert, 2007). Mastodon tooth calculus contained abundant grass phytoliths, despite the usual classification of mastodons as browsers (Gobetz and Bozarth, 2001). The degree to which mammoth and mastodon environmental niches overlapped is important, since competition for resources would have increased susceptibility to regional extirpation during late Pleistocene environmental changes (Saunders et al., 2010).

Mammoths and mastodons were abundant north of the Erie basin (Dreimanis, 1967, 1968; McAndrews and Jackson, 1988), but most previous isotopic studies have focused on more southern regions (e.g., Fisher, 2009; Koch et al., 1989, 1998). Here, we investigate environmental niche partitioning of mammoths and mastodons north of the latitude of Lake Erie (i.e., in southern Ontario and western New York; Fig. 1), using the carbon-, nitrogen-, and oxygen-isotope compositions of bones and teeth. We explore similarities and differences in the isotopic compositions of mammoths and mastodons, which reflect their diet, drinking water, and metabolism. We present new radiocarbon dates for Ontario mastodons, and explore the use of stable isotope compositions to identify non-local individuals in museum collections. Ultimately, we aim to improve our understanding of the processes of environmental change and proboscidean extinction in the Great Lakes region.

1.1. Proboscidean chronology and glacial history

All dates and ages referred to in this paper are reported in conventional radiocarbon (^{14}C) years before present (BP), which is defined as AD 1950. The Great Lakes region contains an abundance of postglacial mammoth and mastodon remains that could provide important insights into late Pleistocene ecology and extinctions (Dreimanis, 1967, 1968; McAndrews and Jackson, 1988). Geological contexts and associated pollen records suggest that both mammoths and mastodons inhabited Ontario between about 12,500 and 10,000 BP (McAndrews and Jackson, 1988). For western New York state mastodons, radiocarbon dates on collagen range from 11,700 ± 40 BP (Feranec and Kozlowski, 2012) to 10,430 ± 60 BP (Laub, 2010). Most of the dates for Ontario mastodons were obtained using now outdated pretreatment methods and/or less reliable substrates such as wood or muck, so their chronology is less precisely known (McAndrews and Jackson, 1988). The only two direct radiocarbon dates for Ontario mammoths are 12,190 ± 40 BP (mean of three dates for the Muirkirk mammoth; Harington et al., 2012) and 10,790 ± 150 BP (Rostock mammoth; Pilny et al., 1987). Radiocarbon dates for three mammoths from western New York state range from 11,750 ± 65 BP to 10,350 ± 45 BP (Feranec and Kozlowski, 2012). There is no reliable evidence for survival of Ontario proboscideans into the Holocene (McAndrews and Jackson, 1988), though a relatively late date was obtained for a mastodon from northern Indiana (10,055 ± 40 BP) (Woodman and Athfield, 2009). Regardless of the timing of local extirpation, mammoths and mastodons appear to have inhabited the region during the same period of time.

Despite the contemporaneity of mammoths and mastodons in Ontario, their habitats were geographically distinct (McAndrews and Jackson, 1988). Mastodon remains are more abundant, and tend to be found either immediately north of modern Lake Erie or just south of Lake Ontario (Dreimanis, 1967; McAndrews and Jackson, 1988). In contrast, mammoth remains tend to be found on the western shores of Lake Ontario (McAndrews and Jackson, 1988). It is thought that these habitats corresponded to lower-lying wetlands and well-drained uplands, respectively (McAndrews and Jackson, 1988).

1.2. Erie basin lake levels

Fig. 2 depicts the lake-level changes described in this and the following section. The Laurentide Ice Sheet (LIS) permanently receded from the Erie basin after 14,000 BP (Lewis et al., 2012). The melting glacier formed lakes, which have different names depending on the time period. Around 14,000–13,400 BP, Lakes Maumee and Arkona formed from glacial meltwater directly adjacent to the ice sheet (Lewis et al., 1994, 2012). Around 13,200 BP the LIS had retreated to modern Georgian Bay and northern Lake Ontario, and low-level Lake Ypsilanti had formed in the Erie basin (Lewis et al., 1994, 2012). At this time most of southern Ontario, including parts of the Erie basin currently submerged by Lake Erie, was open to colonization by plants and animals (Morris et al., 1993). However, within about 200 years, a glacial advance closed the eastern Erie outlet and impounded meltwater in the basin, forming Lakes Whittlesey (13,000 BP) and Warren (12,800 BP) (Lewis et al., 1994, 2012), which submerged the entire Erie basin and parts of southern Ontario. By 12,000 BP, Early Lake Erie levels had again

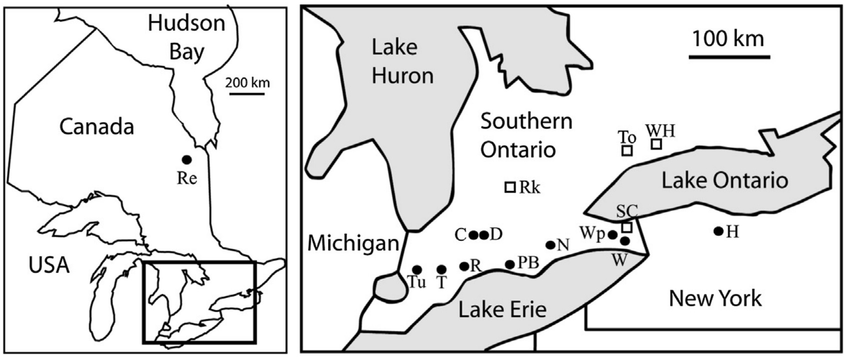

Fig. 1. The discovery locations of mastodon (closed circle) and mammoth (open square) specimens analysed in the present study. Inset box is enlarged in the second map. Re = Renison, Tu = Tupperville, T = Thamesville, R = Rodney, C = Caradoc, D = Delaware, PB = Port Burwell, N = Norfolk, Wp = Wellandport, W = Welland, SC = Saint Catharines, H = Hiscock, Rk = Rostock, To = Toronto, WH = West Hill.