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Digesting the data - Effects of predator ingestion on the oxygen isotopic signature of micro-mammal teeth

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ABSTRACT

Biogenic minerals such as dental apatite have become commonly analysed archives preserving geochemical indicators of past environmental conditions and palaeoecologies. However, post-mortem, biogenic minerals are modified due to the alteration/replacement of labile components, and recent moves to utilise micro-mammal tooth $\delta^{18}O$ signatures for refined Cenozoic terrestrial palaeoclimate reconstructions has lacked consideration of the chemical effects of predator digestion.

Here, the physical and chemical condition of laboratory-raised mouse (*Mus musculus*) teeth have been investigated in conjunction with their bulk phosphate and tissue-specific $\delta^{18}O$ values prior, and subsequent, to ingestion and excretion by various predator species (owls, mammals and a reptile). Substantial variability (up to 2‰) in the $\delta^{18}O$ values of both undigested teeth and those ingested by specific predators suggests significant natural heterogeneity of individual prey $\delta^{18}O$. Statistically distinct, lower $\delta^{18}O$ values (~0.7‰) are apparent in teeth ingested by barn owls compared to undigested controls as a result of the chemically and enzymatically active digestive and waste-pellet environments. Overall, dentine tissues preserve lower $\delta^{18}O$ values than enamel, while the greatest modification of oxygen isotope signals is exhibited in the basal enamel of ingested teeth as a result of its incompletely mineralised state. However, recognition of ^{18}O-depletion in chemically purified phosphate analyses demonstrates that modification of original $\delta^{18}O$ values is not restricted to labile oxygen-bearing carbonate and organic phases.

The style and magnitude of digestive-alteration varies with predator species and no correlation was identified between specific physical or minor/trace-element (patterns or concentrations) modification of ingested teeth and disruption of their primary oxygen isotope values. Therefore, there is a current lack of any screening tool for oxygen isotope disruption as a result of predation. These results point to the need for careful application of the micro-mammal oxygen isotope palaeoenvironmental proxy in future studies.

1. Introduction

In recent decades, significant steps towards quantification of absolute past environmental conditions have been made, utilising advances in the analysis and interpretation of stable isotopic data (e.g., Bemis et al., 1998; Clementz, 2012; Ghosh et al., 2006; Kingston et al., 1994; Koch, 1998; McCrea, 1950; Urey, 1947). Subsequent to the discovery that oxygen isotopic ratios in mammalian phosphatic tissues can be related to temperature and the isotopic composition of the oxygen source (Longinelli, 1984), biogenic apatite-based terrestrial palaeoenvironmental reconstructions have proliferated (Bryant et al., 1996; Fricke et al., 1998; Fricke and O'Neil, 1996; Grimes et al., 2003; Héran et al., 2010; Kohn and Cerling, 2002; Levin et al., 2006; Luz and Kolodny, 1985; Pryor

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et al., 2014; Stephan, 2000). Importantly, many of the mammalian species analysed in these studies are extant or have modern relatives whose metabolic controls on oxygen isotope fractionation can be constrained through experimentation, while their characteristic thermo-regulation removes temperature as a significant variable affecting oxygen isotope ratios. This leaves primary oxygen isotope values to be interpreted solely in terms of the isotopic composition of the animal's main source of body water oxygen, which varies with ecology but is commonly related to vegetative and meteoric water after weaning. Importantly, the $\delta^{18}O$ values of meteoric water correlates to mean annual temperature and aridity (Fig. 1; Levin et al., 2006; Luz et al., 1990). The majority of studies analysing oxygen isotope ratios in mammalian mineralised tissues have focussed on large and abundant fossils due in part to the minimum analytical mass of material required, and there has therefore been significant focus on biogenic apatite from relatively large herbivorous mammals (Ayliffe et al., 1994; Lehmann et al., 2016; Martin et al., 2011; Pellegrini et al., 2011). However, advances in analytical techniques used to analyse phosphate oxygen isotopes, such as the development of precise chemical purification methods (O'Neil et al., 1994), a direct laser fluorination technique (Lindars et al., 2001) and in-situ ion-probe analysis (Aubert et al., 2012), combined with increased understanding of micro-mammal (body mass < 300 g; Andrews, 1990) metabolism and biomineralisation (Bryant et al., 1996; Kohn, 1996), have led to the proposal that micro-mammal teeth are an under-exploited source of palaeoenvironmental data for the Cenozoic (Grimes et al., 2003, 2008; Lindars et al., 2001). There are numerous potential advantages of using micro-mammal teeth for oxygen isotope analysis as opposed to teeth from macro-mammals, which include:

i. Micro-mammal remains typically offer a fine temporal resolution within sections due to their abundance, often as a result of accumulation at predatory nest sites (Andrews, 1990; Denys et al., 1997; Fernández-Jalvo et al., 2016; Grimes et al., 2008).
ii. Many individuals (e.g. rodents) are geographically restricted, have relatively short lifespans and continuously growing incisors, do not undertake significant migrations and therefore their tooth geochemistry is more representative of local conditions at the time of death (Andrews, 1990; Leichliter, 2011).
iii. Extant micro-mammal relatives can be easily studied in the laboratory in order to better constrain metabolic pathways and other ecological controls on the geochemistry of biomineralised tissues (Jeffrey et al., 2015; Luz and Kolodny, 1985; Luz et al., 1984; Navarro et al., 2004; Royer et al., 2013a).

Though primary precipitation of bioapatite yields oxygen isotope values that may be used as an environmental proxy, post-mortem modification of tooth and bone geochemistry can prevent fossil material from acting as a useful palaeoclimatic archive. The surface structure or chemical composition of biogenic apatite may be modified by several biostratinomic (pre-burial) and fossil-diagenetic (post-burial) taphonomic agents; predation or scavenging, non-predatory animal modification (such as gnawing), lichens, algae and fungi, roots, weathering, soil corrosion, and reworking (Fernández–Jalvo et al., 2002). Studies have shown that the densely crystalline, highly mineralised and physically robust composition of tooth enamel is resistant to alteration, which makes it a suitable fossil media for geochemical, and specifically oxygen isotope, analyses (Ayliffe et al., 1994; Bryant et al., 1994; Fernández-Jalvo et al., 2014; Pellegrini et al., 2011; Roelofs et al., 2017). In particular, it has been determined that the phosphate component of enamel is more resistant to ex-vivo modification due to the stronger P-O bond relative to the C-O bond of carbonate (e.g., Grimes et al., 2008). However, a potential significant issue with the use of biomineralised micro-mammal tissues as oxygen isotope media is the fact that they typically accumulate as a result of ingestion and subsequent excretion by a predator (Andrews, 1990; Royer et al., 2013b). Although the physical effects of digestion on the preservation of the structure of teeth and bones have been extensively investigated (Crandall and Stahl, 1995; Denys et al., 1997; Fernandez-Jalvo and Andrews, 1992, 2016; Fernández-Jalvo et al., 2014; Fernández–Jalvo et al., 2002; Laudet and Selva, 2005), a significant oversight in the scientific literature is the potential predatory taphonomic disruption of the chemistry of biogenic apatite. Any disruption of biomineral $\delta^{18}O$ values will have significant implications for palaeoenvironmental reconstructions.

Digestion is a progressive process that primarily affects the most mineralised tissue, such as enamel, advancing from the tip to the centre of the element (Fernández-Jalvo et al., 2014). The degree of

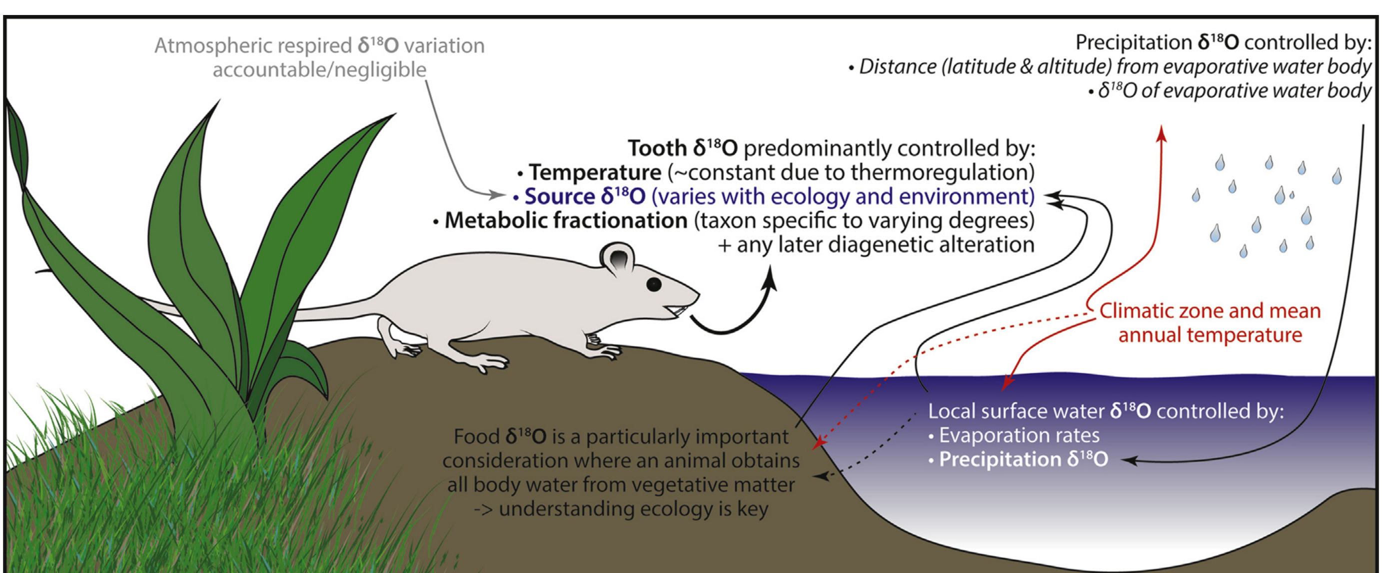

Fig. 1. Summary of the significant known controls on the $\delta^{18}O$ signature of micro-mammal teeth prior to this work.