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What does the oxygen isotope composition of rodent teeth record?

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ABSTRACT

Oxygen isotope compositions of tooth phosphate ($\delta^{18}O_p$) were measured in 107 samples defined on the basis of teeth obtained from 375 specimens of extant rodents. These rodents were sampled from pellets collected in Europe from 38°N (Portugal) to 65°N (Finland) with most samples coming from sites located in France and Spain. Large oxygen isotopic variability in $\delta^{18}O_p$ is observed both at the intra- and inter-species scale within pellets from a given location. This isotopic variability is partly explained by heterochrony in tooth formation related to the short time of mineralization for all rodent species as well as the duration of mineralization that is species-dependent. Consequently, tooth phosphate of rodents records a short seasonal interval in the oxygen isotope compositions of meteoric waters ($\delta^{18}O_{mw}$). In addition, inter-species isotopic variability observed in the same pellets suggests behavioural differences implying distinct isotopic compositions for species living in the same location. At the scale of Europe, a robust linear oxygen isotope fractionation equation was determined for Muroidea between the midrange $\delta^{18}O_p$ values and $\delta^{18}O_{mw}$ values: $\delta^{18}O_p = 1.21(\pm 0.20)\delta^{18}O_{mw} + 24.76(\pm 2.70)$ with $R^2 = 0.79$ ($n = 9$; $p < 0.0001$).

1. Introduction

The Quaternary is characterized by a succession of alternating glacial and interglacial stages leading to climatic changes that have deeply modified the floral and faunal associations (e.g. Anderson et al., 2007). At high-latitude, the oxygen isotope composition of ice provides a continuous and high-resolution temporal record of the continental climate (e.g. Dansgaard et al., 1993). At lower latitudes, continental sedimentary deposits only provide discontinuous temporal and spatial records associated with difficulties in the absolute dating of fossils or their host sediments. Most continental climate proxies are based on pollen, insect or mammal associations. Different methods are applied to reconstruct climate modes; they are based either on the analysis of faunal associations in relation to their preferential extant ecological niches (Delpech et al., 1983, 2000; Chaline et al., 1995; Griggo, 1996; Jeannet, 2010), or on faunal communities (e.g. Legendre, 1986, 1989; Montuire and Marcolini, 2002), or on diversity and species richness (Montuire et al., 1997, 2006; Hernández Fernández, 2001; Legendre et al., 2005; van Dam, 2006; Hernández Fernández et al., 2007; Cuenca-Bescós et al., 2011). These different approaches generally involve the study of small mammals because of their high sensitivity to environmental parameters and climatic changes.

Longinelli's (1973, 1984) pioneer study demonstrated that the stable oxygen isotope composition of phosphatic tissues is a valuable proxy for investigating terrestrial climatic conditions. The oxygen isotope composition of biogenic phosphate ($\delta^{18}O_p$) depends on both body temperature and oxygen isotope composition of body water ($\delta^{18}O_{bw}$), itself related to the composition of ingested water most commonly of meteoric origin (Longinelli and Nuti, 1973; Kolodny et al., 1983; Luz et al., 1984). Indeed, most previous studies assumed that the oxygen isotope composition of vertebrate's body water reflects the oxygen isotope composition of meteoric water ($\delta^{18}O_{mw}$) depending on physiological parameters such as the general metabolism. These interdependent relationships allow the use of taxon-dependent oxygen isotope fractionation equations relating $\delta^{18}O_p$ to $\delta^{18}O_{mw}$. At mid- and high-latitudes, the mean annual $\delta^{18}O_{mw}$ is linearly related to the mean annual air temperature at the global scale (Dansgaard, 1964; Rozanski et al., 1993). Many oxygen isotope studies were performed on bones and teeth of large mammal fossils (e.g. Koch et al., 1989; Fricke et al., 1998; Tütken et al., 2007; Bernard et al., 2009; Chritz et al., 2009) as well as to small mammal fossils to estimate successfully past air temperatures (e.g. Lindars et al., 2001;

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Grimes et al., 2003, 2004; Navarro et al., 2004; Passey and Cerling, 2006; Tütken et al., 2006; Feranec et al., 2010; Héran et al., 2010; Gehler et al., 2011). Compared to large mammals, their small counterparts are characterized by a restricted habitat and mostly lack long-distance migratory behaviour, thus incorporating in their skeletal tissues a reliable record of their local environment. Moreover, the high abundance of small mammal remains in Quaternary sedimentary deposits potentially allows a high-temporal resolution of climate changes in the continental domain.

Grimes et al. (2008) questioned whether or not "small is beautiful?" before concluding that the oxygen isotope composition of small mammals constitutes a valuable proxy when it is interpreted in association with $\delta^{18}O_p$ values obtained from other vertebrate or invertebrate fossils. Grimes et al. (2008) dealt mainly with the use of small mammals for the reconstruction of Tertiary climates, and detailed a list of limitations implying a restricted use of small mammals alone to estimate Quaternary air temperatures. They emphasized problems such as the ^{18}O-enrichment of the ingested water relative to meteoric waters, variation in body temperature and a possible diagenetic alteration. In addition, we underline that 4 oxygen isotope fractionation equations relating $\delta^{18}O_{mw}$ to $\delta^{18}O_p$ of rodents have been proposed so far (Luz et al., 1984; Luz and Kolodny, 1985; D'Angela and Longinelli, 1990; Longinelli et al., 2003; Navarro et al., 2004). These linear equations are characterized by significant differences in their intercepts and slopes, which can lead to drastic differences in $\delta^{18}O_{mw}$ estimates and interpretations in terms of past climatic reconstructions (Héran et al., 2010; Fabre et al., 2011). Distinct oxygen isotope fractionation equations may result from biases caused by the use of restricted datasets, different species, the skeleton parts (bones, molars or incisors), and the more or less precise knowledge of the oxygen isotope composition of meteoric waters ingested by the rodents.

The aim of this study is to explore the environmental meaning of the oxygen isotope composition of phosphate from rodent teeth. Therefore we provide a new set of 107 data sampled from 375 extant rodents collected in Europe from 38°N (Portugal) to 65°N (Finland). The dataset is used to propose a new oxygen isotope fractionation equation between phosphate and ambient water for the Muroidea superfamily (Rodentia). Finally, the origin of isotopic variability in tooth composition, observed at the intra-species and inter-species scale, is discussed as a potential record of continental climate seasonality.

2. Materials and methods

2.1. Extant rodents

Oxygen isotope ratios were measured in 107 samples defined on the basis of teeth obtained from 375 specimens of extant rodents, either from a single tooth or up to 14 teeth which have been pooled to constitute a single isotope analysis (Tables 1 and 2). For each site, a minimum number of teeth were collected whenever possible according to the recommendations made by several authors in order to infer the local water $\delta^{18}O$ values (e.g., Clementz and Koch, 2001; Navarro et al., 2004; Fox-Dobbs et al., 2007). Teeth were mainly extracted from owl's pellets that ensure tooth concentration before their potential incorporation into sedimentary deposits. Twenty-six rodents from 8 pellets were analyzed in order to test the intra- and inter-species variability whereas the remaining samples represent for each locality a pool of several teeth from one or several specimens belonging to the same species. As a whole, teeth belong to 11 extant species of the Muroidea superfamily, mainly arvicolids, which are the wood mouse (*Apodemus sylvaticus*), the southern water vole (*Arvicola sapidus*), the water vole (*A. terrestris*), the snow vole (*Chionomys nivalis*), the Cabrera's vole (*Iberomys cabrerae*), the common vole (*Microtus* (*Microtus*) *arvalis*), the field vole (*M.* (*M.*) *agrestis*), the Mediterranean pine vole (*Microtus* (*Terricola*) *duodecimcostatus*), the Lusitanian pine vole (*M.* (*T.*) *lusitanicus*), the common pine vole (*M.* (*T.*) *subterraneus*), and the bank vole (*Myodes glareolus*). It is noteworthy that all these studied extant rodent species have been commonly recovered from excavations of Pleistocene deposits.

Rodents were extracted from preserved modern pellets (under the roof of bell-towers, in barns, and at the base of trees) sampled from 79 European localities (Fig. 1), distributed over a latitudinal gradient ranging from 38°N (Portugal) to 65°N (Finland). Under mid-latitude climate conditions, pellets are preserved a few months to a few years depending on their location and exposition to weather conditions. Samples that come from France and Spain were collected at various elevations (from ≈ 0 m to 1500 m) and distances (from ≈ 0 km to 500 km) from coastlines, thus belonging to several microclimatic modes such as the temperate maritime, continental and mountain ones.

$\delta^{18}O_p$ values of rodents that were used to establish former oxygen isotope fractionation equations were not taken into account in this study because the oxygen isotope measurements of phosphate were based on different analytical methods and standard values (Luz and Kolodny, 1985; D'Angela and Longinelli, 1990; Longinelli et al., 2003), or various methods to infer the $\delta^{18}O_{mw}$ values (Navarro et al., 2004).

2.2. Estimates of the oxygen isotope composition of meteoric waters

Each sample location was georeferenced with elevation, latitude and longitude coordinates (Tables 1 and 2). Minimum and maximum values of the monthly oxygen isotope compositions of meteoric waters ($\delta^{18}O_{mw}$), as well as the mean annual $\delta^{18}O_{mw}$, were calculated (Tables 1 and 2) by using an algorithm developed by Bowen and Wilkinson (2002), and refined by Bowen and Revenaugh (2003). The dataset was derived from the International Energy Association/World Meteorological Organization Global Network for Isotopes in Precipitation by using the Online Isotopes in Precipitation Calculator (Bowen et al., 2005; Bowen, 2010).

2.3. Estimates of air temperatures

Mean annual air temperatures along with both minimum and maximum monthly air temperatures were calculated for each studied locality by using the software New Local Climate Estimator (LocClim v1.11) (Grieser et al., 2006). These climatic parameters were obtained through the interpolation of 10 meteorological stations located in the closest vicinity to the studied locality. Two methods were used depending on the geographic position of the studied site relative to the location of the meteorological stations. The Kriging method was used for a studied site surrounded by several distant (≥ 50 km) meteorological stations whereas the Nearest Neighbors method was preferred for stations that are very close (≈ 10 km to 20 km) to the studied rodent site.

2.4. Regression of data

Reduced major axis (RMA) regression was used to examine the relationship between the $\delta^{18}O_p$ and the $\delta^{18}O_{mw}$. An intrinsic property of the RMA method implies that the slope of the regression $y=f(x)$ is the reciprocal of the slope of $x=f(y)$. This procedure is appropriate for the analysis of an oxygen isotope fractionation equation because variations in both independent (x)