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Oxygen isotope compositions of phosphate from arvicoline teeth and Quaternary climatic changes, Gigny, French Jura

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Abstract

Oxygen isotope compositions of biogenic phosphates from mammals are widely used as proxies of the isotopic compositions of meteoric waters that are roughly linearly related to the air temperature at high- and mid-latitudes. An oxygen isotope fractionation equation was determined by using present-day European arvicoline (rodents) tooth phosphate: $\delta^{18}O_p = 20.98(\pm 0.59) + 0.572(\pm 0.065)\ \delta^{18}O_w$. This fractionation equation was applied to the Late Pleistocene karstic sequence of Gigny, French Jura. Comparison between the oxygen isotope compositions of arvicoline tooth phosphate and Greenland ice core records suggests to reconsider the previously established hypothetical chronology of the sequence. According to the $\delta^{18}O$ value of meteoric water–mean air temperature relationships, the $\delta^{18}O$ value of arvicoline teeth records variations in mean air temperatures that range from 0° to 15°C.
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Keywords: Oxygen isotope; Phosphate; Arvicolinae; Pleistocene; Climate

Introduction

Many paleobiological studies have investigated causal factors between climate changes and biotic patterns (e.g., Clyde and Gingerich, 1998; Cornette et al., 2002; Vrba et al., 1989). One of the most popular marine proxies—the $\delta^{18}O$ of foraminifera—was commonly used to evaluate the impact of marine thermal variations on biotic changes. However, in addition to the poor correlations available between the marine and terrestrial domains, marine proxies of climate change cannot really constitute reliable indicators of terrestrial climate variables that structure the ecosystems (Alroy et al., 2000). Pleistocene climates are characterized by millennial-scale oscillations (Dansgaard/Oeschger [D–O] events) superimposed on the orbitally driven glacial–interglacial cycles (Dansgaard et al., 1993). These oscillations are expected to have impacts on biotic patterns (Roy et al., 1996), but uncertainties in the correlations between marine and terrestrial sedimentary sequences preclude the use of the marine record to quantify terrestrial biotic responses. Therefore, new proxies are required to estimate the impact of Quaternary climate changes on terrestrial fauna.

Oxygen isotope compositions of apatite in mammalian teeth and bones are now widely used to estimate the $\delta^{18}O$ of meteoric water (Longinelli, 1984). Moreover, at mid- to high-latitudes, the average weighted $\delta^{18}O$ of meteoric water is closely related to the mean annual air temperature (Dansgaard, 1964; Fricke and O'Neil, 1999; Von Grafenstein et al., 1996; Yurtsever and Gat, 1981). In most cases, phosphate oxygen isotope studies have focused on large mammal remains (e.g., Ayliffe and Chivas, 1990; Ayliffe et al., 1992; Bryant et al., 1994; Fricke et al., 1998; Genoni et al., 1998; Huertas et al., 1995; Luz et al., 1990), but the use of more abundant small mammals leads to sampling with a higher time resolution (Lindars et al.,

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2001). Previous studies of small mammals mainly focused on laboratory or wild specimens of murine species (D'Angela and Longinelli, 1990; Lindars et al., 2001; Luz and Kolodny, 1985; Luz et al., 1984). We emphasize that the Quaternary sediments are relatively poor in murine remains in the Northern Hemisphere. Arvicolines (voles and lemming), which constitute a rodent group, diversified about 5.5 myr ago (Repenning et al., 1990) with a present-day Holarctic repartition. Arvicoline teeth are highly abundant in the Plio-Pleistocene sediments of the Northern Hemisphere and are likely the most abundant mammal fossils in Quaternary sequences. Therefore, the oxygen isotope compositions of phosphate from arvicoline teeth could be potentially used to identify Plio-Quaternary climate changes and their consequences on the terrestrial biodiversity.

The aim of this paper is to (i) empirically determine a fractionation equation that relates the δ^{18}O of local meteoritic waters to the composition of tooth phosphate in present-day arvicolines; (ii) select the most adequate relationship between the oxygen isotope composition of meteoric water and air temperature based on the present-day arvicoline and climatic databases; (iii) apply our fractionation equation to Late Pleistocene arvicoline tooth phosphate for identifying possible cold and warm climate events.

Materials and methods

Taxonomic and geographical sampling of present-day fauna

Arvicolines have molars with a continuous growth mode as incisors. Mineralization and abrasion of teeth occur throughout the individual's life; therefore, their δ^{18}O value record the time period just before the animal's death. Thus, in the case of adult specimens, problems of intrajaw heterogeneity and metabolic fractionation effects before weaning, encountered with low-crowned molars of murines (Lindars et al., 2001), are probably nonexistent with arvicolines and can be neglected to a first approximation. Similar growth modes for molars and incisors allow the sampling of both tooth types. Because the life expectancy of arvicolines is about 6 months, seasonal effects can introduce biases in the oxygen isotope record of tooth phosphate. However, arvicoline species show outdoor activity greater from spring to fall than during winter (Le Louan and Quéré, 2003). Population size increases during spring and reaches a maximum during late summer then declines (Le Louan and Quéré, 2003). On the other hand, raptor populations at mid- and high latitudes show seasonal numerical response (breeding density, natality, migration, yearling dispersions) to spring and summer abundances of voles (e.g., Norrdahl and Korpimäki, 2002; Salamolard et al., 2000). Consequently, the probability of catchments by owls, responsible for fossil pellets accumulation, is high during summer. However, it is noteworthy that a similar bias will be recorded in an oxygen isotope fractionation equation established with present-day arvicoline species. Indeed, most individuals were trapped during spring and summer, or come from owl pellets.

Teeth were sampled in 12 European localities (Table 1), each of them being in the vicinity (within one latitudinal degree) of the "International Atomic Energy Agency and World Meteorological Organization" (IAEA/WMO, 2001) survey stations. For two additional localities (Torre del Greco and Basque Country) far enough from any IAEA/WMO station to estimate the isotopic composition of water ingested by the arvicolines, water from ponds has been sampled during either July or November 2002 for oxygen isotope analysis (Table 1).

Teeth belong to species of three genera (*Clethrionomys*, *Microtus*, and *Lemmus*) or one subgenus of *Microtus* (*Terricola*). Many sampled species are among the most abundant in the European Late Pleistocene fauna. The small size of fossil teeth did not allow us to separately analyze enamel from the dentine, therefore, oxygen isotope compositions of phosphate were obtained on bulk teeth. Twenty-eight present-day samples have been analyzed for their oxygen isotope compositions (Table 1). Samples represent either several teeth coming from one individual (15 individuals from six localities), or a pool of several teeth from different individuals of the same species (seven samples; 29 individuals from four localities). The remaining six samples correspond to the mixing of several isolated teeth that come from several individuals of the same species (Table 1).

Sampling of La Baume de Gigny (Jura, France)

"La Baume de Gigny" is a highly studied Quaternary karstic sequence of the French Jura (for a synthesis, see Campy et al., 1989b). Three upper levels have been dated using ^{14}C (Table 2; Evin, 1989) between 14,450 cal yr B.P. (IV) and 33,400 cal yr B.P. (VIII). The first deposit (XX) after the speleothem arises nearly 60,000 yr ago based on migration of *Lagurus lagurus* (Campy and Chaline, 1993). The Lower complex (below the speleothem) was not sampled. Chaline and Brochet (1989) subdivided the Middle and Upper complex into 37 levels (i.e., sedimentary) or sublevels (i.e., micromammal sampling). One level (VII) could not be sampled. For 31 levels, six right lower M_1 (first lower molar) from one species have been sampled. One (levels V and IX) or two (level XI) supplementary arvicoline species were also analyzed for three levels from the Gigny sequence (Table 3). This tooth is the most reliable among fossil remains for identifying individual specimens from the same species. For the five remaining levels, characterized by poor fossil abundance, all the sampled teeth are incisors; consequently, the determination at the species level was

Table 1
Oxygen isotope compositions of present-day European arvicoline teeth and local meteoric waters

Geographic location	Species	Individuals	Tooth	$\delta^{18}O_p$	IAEA[+] station	$\delta^{18}O_w$[++]
Malaga (Spain)	*Microtus* (*Terricola*) *duodecimcostatus*	na*	molars	18.0	Gibraltar	−4.8
Malaga (Spain)	*Microtus* (*Terricola*) *duodecimcostatus*	2	molars	19.2	Gibraltar	−4.8
Malaga (Spain)	*Microtus* (*Terricola*) *duodecimcostatus*	4	molars	19.4	Gibraltar	−4.8
Güvenç (Ankara, Turkey)	*Microtus* sp.	1	molars	15.7	Ankara	−7.6
Güvenç (Ankara, Turkey)	*Microtus* sp.	2	molars	15.6	Ankara	−7.6
Tombolo (Toscana, Italy)	*Microtus* (*Terricola*) *savii*	1	molars	15.7	Pisa	−8.1***
Tombolo (Toscana, Italy)	*Microtus* (*Terricola*) *savii*	1	molars	15.1	Pisa	−8.1***
Tombolo (Toscana, Italy)	*Microtus* (*Terricola*) *savii*	1	molars	16.0	Pisa	−8.1***
Torre del Greco (Napoli, Italy)	*Microtus* (*Terricola*) *savii*	1	molars	17.6	Pond**	−6.8
Torre del Greco (Napoli, Italy)	*Microtus* (*Terricola*) *savii*	1	molars	18.8	Pond**	−6.8
Torre del Greco (Napoli, Italy)	*Microtus* (*Terricola*) *savii*	1	molars	18.8	Pond**	−6.8
Tortorici (Messina, Italy)	*Microtus* (*Terricola*) *savii*	na	molars	17.2	Palermo	−6.7
Roccapalumba (Palermo, Italy)	*Microtus* (*Terricola*) *savii*	na	molars	17.9	Palermo	−5.8
Fontasala (Trapani, Italy)	*Microtus* (*Terricola*) *savii*	na	molars	17.9	Palermo	−5.3
Bossy s/Frangy (Upper-Savoy, France)[a]	*Microtus arvalis*	1	molars	16.6	Thonon les bains	−9.6
Bossy s/Frangy (Upper-Savoy, France)[a]	*Clethrionomys glareolus*	1	molars	13.8	Thonon les bains	−9.6
Bossy s/Frangy (Upper-Savoy, France)[a]	*Clethrionomys glareolus*	1	molars	15.0	Thonon les bains	−9.6
Basque country (France)	*Microtus* (*Terricola*) *lusitanicus*	1	molars	17.0	Pond**	−5.9
Basque country (France)	*Microtus* (*Terricola*) *lusitanicus*	1	molars	17.4	Pond**	−5.9
Offenbach (Hessen, Germany)	*Microtus arvalis*	na	molars	14.3	Wasserkuppe Rhoen	−9.6
Osterburg (Saxonia Anhalt, Germany)	*Microtus arvalis*	na	molars	17.6	Berlin	−8.4
Finse in Ulvik (Hordaland county, Norway)[b]	*Microtus agrestis*	5	molars	14.8	Lista	−10.7
Finse in Ulvik (Hordaland county, Norway)[b]	*Clethrionomys glareolus*	4	molars	15.2	Lista	−10.7
Latnjajaure Field Station (northern Swedish Lapland, Sweden)[c]	*Microtus agrestis*	4	incisors	13.1	Abisko	−14.8
Latnjajaure Field Station (northern Swedish Lapland, Sweden)[c]	*Lemmus lemmus*	8	incisors	11.9	Abisko	−14.8
Finnish Lapland[d]	*Clethrionomys glareolus*	1	molars	13.1	Lapptrask	−13.9
Finnish Lapland[d]	*Clethrionomys glareolus*	1	molars	12.4	Lapptrask	−13.9
Finnish Lapland[d]	*Clethrionomys glareolus*	1	molars	12.9	Lapptrask	−13.9

Note. [+] International Atomic Energy Agency (IAEA/WMO, 2001).

[++] Annual mean weighted oxygen isotope compositions of meteoric waters corrected from altitude variations between the sampling location and the IAEA/WMO station.

[a] MHNG 1234.013 (trapped in March 1972)-1234.028-1234.029 (trapped in October 1972). MHNG refers to the collection of the "Museum d'Histoire Naturelle de Genève" (Switzerland).

[b] B4637-4638-4639-4645-4556-4662-4663-4665-4666 (trapped during summer 1981). B refers to the collection of the University of Bergen (Norway).

[c] Trapped in August 2001 from ecology project "Tundra Landscape Dynamics" of University of Göteborg (Sweden).

[d] Trapped in June 2002 by H. Hettonen (Vantaa Research Centre).

* Number of individuals unavailable (sample of isolated teeth coming from owl pellets).

** Isotopic composition measured from the nearest pond during either July 2002 or November 2002.

*** Mean isotopic composition calculated from the nearest years (1974, 1975) to the sampling year of teeth (1973). Other available data (1994–1995) have a strongly different value of $\delta^{18}O$ (−5.6).

not possible. As for present-day samples, bulk teeth were also used for the oxygen isotope analysis. The mixing of six fossil individuals of the same species from one level allows to partly reduce seasonal and time-averaging biases.

Table 2
Radiocarbon ages and calibrated ages for Gigny

Sample	Lab[a]	^{14}C age[b]	$\pm\sigma$	Calibrated age[c]	$\pm\sigma$
IV	Ly1798	12,370	460	14,450	630
IV	Ly1702	13,620	480	16,160	650
V	Ly1703	22,430	500	25,760	430
VIII	Ly789	28,500	1400	32,200	1400
VIII	Ly566	29,500	1400	33,400	1500

Note. [a] Laboratory number.

[b] Radiocarbon age (^{14}C yr B.P.) after Evin (1989).

[c] Calibrated age (cal yr B.P.) using CALPAL 2001 curve of the CALPAL_A software (Weninger et al., 2002).

Analytical methods

Phosphate was isolated from arvicoline teeth as Ag_3PO_4 following the protocol derived from the method proposed by Crowson et al. (1991) and slightly modified by Lécuyer et al. (1993). $^{18}O/^{16}O$ ratios were measured by reducing silver phosphate to CO_2 using graphite reagent (Lécuyer et al., 1998; O'Neil et al., 1994). Samples of Ag_3PO_4 were mixed with pure graphite powder in proportions of 0.8 mg of C to 15 mg of Ag_3PO_4. They were weighed into tin reaction capsules and loaded into quartz tubes and degassed for 30 min at 80°C in vacuum. The sample was then heated at 1100°C for 1 min to promote the redox

Table 3
Oxygen isotope compositions of arvicoline teeth from La Baume de Gigny (Jura, France) and estimates of water compositions and air temperatures

Levels	Species	Teeth	$\delta^{18}O_p$	$\delta^{18}O_w$	T	95% CI
IV	*M. malei*	LR M_1	15.3	−10.0	7.7	5.5–9.7
V	*M. malei*	LR M_1	14.6	−11.2	5.7	3.3–7.7
	M. arvalis	LR M_1	15.5	−9.6	8.4	6.4–10.4
			15.0[a]	−10.4	7.0	4.9–8.9
VI	*M. arvalis*	LR M_1	15.0	−10.5	6.9	4.7–8.8
VI	*M. arvalis*	LR M_1	13.3	−13.5	1.7	−1.3–4.1
VI	*M. arvalis*	LR M_1	13.8	−12.5	3.4	0.7–5.6
VI	*M. arvalis*	LR M_1	14.0	−12.2	3.8	1.1–6.1
VI	Arvicolinae	incisors	14.9	−10.6	6.6	4.3–8.6
VI	Arvicolinae	incisors	14.7	−11.0	6.1	3.8–8.1
VII						
VIII	Arvicolinae	incisors	15.1	−10.3	7.1	5.0–9.1
IX	Arvicolinae	incisors	15.6	−9.5	8.6	6.6–10.6
IX	*M. malei*	LR M_1	17.2	−6.6	13.7	11.6–15.9
	M. arvalis	LR M_1	16.3	−8.2	10.9	8.9–12.9
			16.8[a]	−7.3	12.3	10.4–14.5
X	*M. malei*	LR M_1	15.9	−8.9	9.6	7.6–11.5
XI	*M. malei*	LR M_1	16.6	−7.7	11.7	9.8–13.7
	M. arvalis	LR M_1	16.6	−7.6	11.8	9.8–13.8
	M. gregalis	LR M_1	17.6	−5.9	14.7	12.7–17.1
			16.9[a]	−7.1	12.7	10.8–14.9
XII	*M. malei*	LR M_1	14.2	−11.8	4.5	2.0–6.6
XIII	*M. malei*	LR M_1	15.1	−10.3	7.1	4.9–9.1
XIII	*M. malei*	LR M_1	14.8	−10.8	6.3	4.0–8.2
XIVa top	Arvicolinae	incisors	13.9	−12.5	3.5	0.7–5.7
XIVa bottom	*M. agrestis*	LR M_1	15.6	−9.4	8.7	6.7–10.7
XIVb	*M. agrestis*	LR M_1	16.0	−8.7	10.0	8.0–12.0
XV	*M. agrestis*	LR M_1	15.8	−9.1	9.3	7.3–11.2
XV	*M. agrestis*	LR M_1	14.8	−10.9	6.23	3.9–8.2
XV	*M. agrestis*	LR M_1	14.0	−12.2	4.0	1.3–6.1
XV bottom	*M. agrestis*	LR M_1	13.4	−13.3	1.9	−1.1–4.4
XVIa top	*M. agrestis*	LR M_1	14.3	−11.7	4.7	2.2–6.8
XVIa bottom	*M. arvalis*	LR M_1	13.0	−14.0	0.9	−2.3–3.4
XVIb top	*M. arvalis*	LR M_1	12.9	−14.2	0.5	−2.8–3.1
XVIb top	*M. arvalis*	LR M_1	14.9	−10.6	6.6	4.4–8.6
XVIb bottom	*M. arvalis*	LR M_1	14.3	−11.7	4.7	2.2–6.8
XVIb bottom	*M. arvalis*	LR M_1	13.2	−13.6	1.5	−1.7–4.0
XVII top	*M. arvalis*	LR M_1	13.2	−13.6	1.5	−1.6–3.9
XVII bottom	*M. arvalis*	LR M_1	15.5	−9.6	8.4	6.3–10.3
XIXa	*M. arvalis*	LR M_1	15.6	−9.3	8.8	6.9–10.8
XIXb	*M. arvalis*	LR M_1	14.8	−10.8	6.3	4.0–8.3
XIXc	*M. arvalis*	LR M_1	13.5	−13.2	2.2	−0.7–4.6
XIXc	*M. arvalis*	LR M_1	14.9	−10.7	6.6	4.3–8.5
XX	*M. arvalis*	LR M_1	15.7	−9.3	9.0	6.9–10.9

Note. The abbreviation *M.* is for the genus *Microtus.* LR M_1 corresponds to the first right lower molar. Temperature was estimated according to Von Grafenstein et al.'s (1996) equation.

[a] Mean value for the considered horizons.

reaction. The CO_2 produced during this reaction was directly trapped in liquid nitrogen to avoid any kind of isotopic reaction with quartz at high temperature. CO_2 was then analyzed with a Finnigan DeltaE™ mass spectrometer at the University of Lyon. Isotopic compositions are quoted in the standard δ notation relative to V-SMOW. The reproducibility of measurements carried out on tooth enamel samples was better than 0.3‰ (1σ). Silver phosphate precipitated from standard NBS120c (natural Miocene phosphorite from Florida) was repeatedly analyzed ($\delta^{18}O = 21.61 \pm 0.26$‰; $n = 19$) along with the silver phosphate samples derived from the arvicoline tooth collection (Tables 1 and 3). These results are close to those obtained from a similar analytical procedure (21.75 ± 0.19‰: Lécuyer et al., 1998); or from other chemical methods or techniques of extraction such as Ag_3PO_4–BrF_5 (21.7 ± 0.2‰: Lécuyer et al., 1993), $BiPO_4$ (21.4 ± 0.4‰: Bryant et al., 1994), or direct laser-fluorination (21.3 ± 0.4‰: Lindars et al., 2001).

Aliquots of 3 ml of pond water from Napoli area and Basque country have been isotopically equilibrated in a pyrex reactor with 20 µmol of CO_2 of known oxygen isotope composition at 25°C for 48 h. Using the oxygen isotope fractionation factor determined by O'Neil and Adami (1969) at 25°C, the $\delta^{18}O$ of the water sample is deduced from the $\delta^{18}O$ of the isotopically equilibrated CO_2 that was analyzed with a Finnigan DeltaE™ mass spectrometer at the University of Lyon. Measurement error is less than 0.1‰.

Results

Oxygen isotope data

Stable isotope compositions of phosphate from present-day arvicoline teeth and local meteoric waters are summarized in Table 1. Isotopic values of phosphate ($\delta^{18}O_p$) from the present study range between 11.9‰ and 19.4‰ and $\delta^{18}O$ of waters ($\delta^{18}O_w$) between −14.8‰ and −4.8‰. $\delta^{18}O_w$ was corrected for altitude effects following a gradient of −0.003‰ m^{-1} (Siegenthaler and Oeschger, 1980). The mean of the average pairwise differences in $\delta^{18}O_p$ between analytical samples within one locality is 0.81‰ when samples correspond to one individual, and 0.66‰ when samples correspond to the pool of several individuals.

Arvicoline teeth from Gigny have $\delta^{18}O_p$ values that range from 12.9‰ to 17.6‰ (Table 4). Large variations in $\delta^{18}O_p$ (Fig. 1) with time are observed at the sublevel scale (e.g., VI, XV, XVIb, XVII) or between major sedimentary discontinuities (e.g., XIVb–XIVa, XX–XIXb). The average difference between multiple $\delta^{18}O_p$ measurements from the same level is 1‰ (except one null difference). This estimate is relatively comparable to those observed in the present-day data set. Therefore, we conclude that the sampling of several individuals provides a rather robust average estimate of $\delta^{18}O_p$ at the level scale in the Gigny sequence.

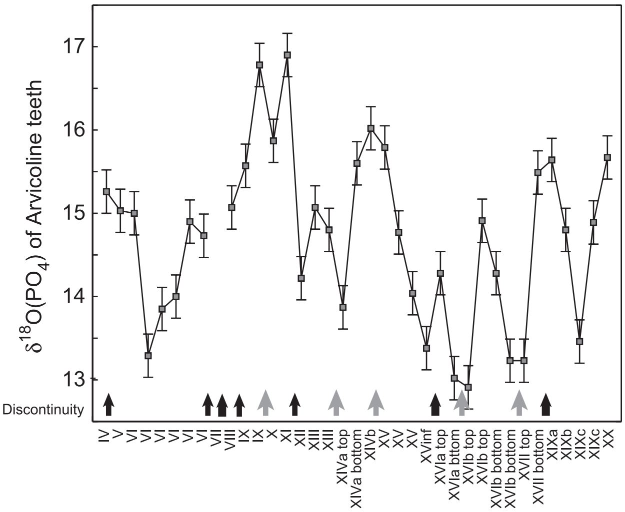

Figure 1. Oxygen isotope compositions of PO_4^{3-} from arvicoline teeth throughout the Gigny sequence. Error bars represent ±1σ analytical errors. Black arrows locate sedimentary discontinuities based on the extent of weathering defined by the thickness of the dissolution cortex of limestone fragments (Campy and Chaline, 1993). Gray arrows locate discontinuities based on the truncation of the lithological unit (Campy and Chaline, 1993).

Determination of the arvicoline–water oxygen isotope fractionation equation

Average isotopic compositions were used to compute the linear fit between the $\delta^{18}O_p$ of present-day arvicoline

Table 4
Present-day air temperatures and model estimates from oxygen isotope compositions of arvicoline tooth phosphate

Sample	Meteorological data[a]			Dansgaard's model			Yurtsever and Gat's model			Von Grafenstein et al's model		
	T^b	January	July	T^b	95% CI	p*	T^b	95% CI	p*	T^b	95% CI	p*
Malaga	18.3	12.1	25.1	14.4	12.3–17.0	0.004	24.8	20.5–30.1	0.01	18.7	16.2–21.9	0.75
Güvenç	10.6	−0.2	21.0	6.2	4.5–7.8	<0.001	7.9	4.5–11.3	0.12	8.9	6.9–10.8	0.09
Tombolo	13.9	6.0	22.6	6.1	4.3–7.6	<0.001	7.7	4.2–10.9	<0.001	8.8	6.7–10.7	<0.001
Torre del Greco	15.8	7.7	24.7	13.2	11.3–15.5	0.02	22.3	18.4–27.1	0.006	17.3	15.0–20.1	0.23
Tortorici	15.5	9.1	23.3	10.1	8.4–11.9	<0.001	16.0	12.6–19.8	0.91	13.6	11.7–15.8	0.04
Roccapalumba	17.9	11.6	25.3	11.9	10.1–14.0	0.002	19.7	16.0–24.1	0.04	15.8	13.6–18.3	0.80
Fontasala	17.6	11.6	24.7	11.8	10.0–14.0	<0.001	19.6	15.9–24.0	0.40	15.7	13.6–18.3	0.07
Bossy s/Frangy[+]	10.1	1.6	19.5	4.9	3.0–6.5	<0.001	5.2	1.5–8.6	0.009	7.3	5.2–9.3	0.01
Basque country	14.3	8.2	20.6	10.1	8.4–11.9	<0.001	15.6	12.6–19.8	0.36	13.6	11.6–15.8	0.50
Offenbach	5.4	−2.8	13.9	2.6	1.0–4.4	0.009	0.7	−3.7–4.3	0.02	4.7	2.1–6.8	0.54
Osterburg	9.2	−0.1	18.5	11.1	9.3–13.1	0.05	18.0	14.5–22.2	<0.001	14.8	12.7–17.2	<0.001
Finse in Ulvik	−0.9	−7.7	5.7	4.6	2.7–6.2	<0.001	4.7	0.8–8.1	0.004	7.0	4.8–9.0	<0.001
Latnjajaure Field Station[++]	−2.3	−8.3	7.8	−1.9	−4.8–0.5	0.75	−8.6	−14.7– −3.8	0.03	−0.7	−4.3–2.1	0.32
Finnish Lapland	0.2	−13.2	14.4	−1.0	−3.7–1.1	0.31	−6.8	−12.4– −2.4	0.01	0.3	−2.9–2.9	0.94
Min |deviation|				0.4			0.2			0.1		
Max |deviation|				7.8			8.8			7.9		
Mean |deviation|				4.0			4.8			2.3		

Note. [a] Data from the NOAA, National Climatic Data Center; Global Climate Perspectives System database. (http://ingrid.ldeo.columbia.edu/SOURCES/.NOAA/.NCDC/) except [+]from IAEA-WMO GNIP database (IAEA/WMO, 2001), and [++]from the Latnjajaure Field Station.

[b] *T* correspond to air temperatures (°C) corrected for the altitude effect using a gradient of 0.007° m^{-1}.

* Two-tailed probabilities estimated from the comparison of observed values with the distribution of temperatures obtained from 10,000 parametric bootstrap simulations.

teeth and the weighted $\delta^{18}O_w$ (Fig. 2). The least-squares fit yields the following equation:

$$\delta^{18}O_p = 21.356 + 0.617\delta^{18}O_w \quad (1)$$

with $R^2 = 0.86$ ($p < 0.0001$). However, this equation does not take into account the interannual variation in the composition of the meteoric water (i.e., its standard deviation). In the same way, the standard deviation obtained from replicates ($n = 19$) of the phosphate standard NBS120c can be used as an estimate of the standard error of mean $\delta^{18}O_p$. For taking into account the analytical error, a least-squares fitting procedure was performed using a parametric bootstrap simulation (Efron and Tibshirani, 1993). A new data set of mean compositions of both $\delta^{18}O_p$ and $\delta^{18}O_w$ was simulated using bivariate normal distribution for each station. In each sampling site, the covariance between $\delta^{18}O_p$ and $\delta^{18}O_w$ is unknown and both values were therefore considered independently. This choice overestimated standard errors on regression coefficients and is more conservative than in the case for which an assumption is made about the covariance. Least-squares regression is then repeated, yielding values for the slope and the intercept. A total of 10,000 simulations was performed, leading to the following equation:

$$\delta^{18}O_p = 20.98(\pm 0.59) + 0.572(\pm 0.065)\delta^{18}O_w \quad (2)$$

which differs slightly from Eq. (1). Slope and intercept are not independent and simulations yield a covariance of 0.0359. Eq. (2) is considered more conservative than Eq. (1) for estimating past $\delta^{18}O_w$ because natural variability and analytical errors have been considered.

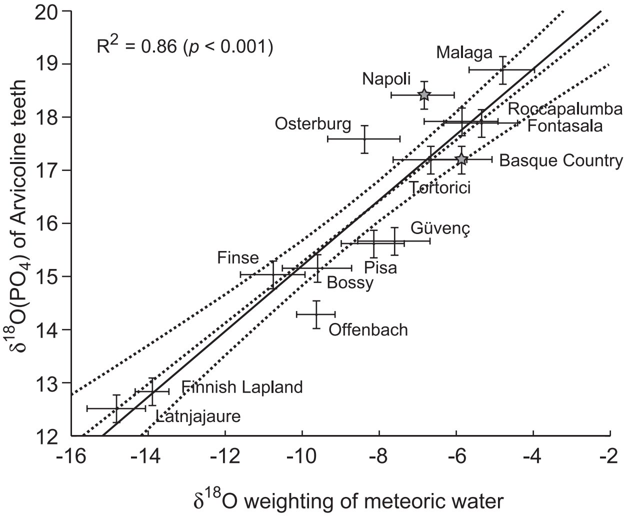

Figure 2. Mean oxygen isotope compositions of PO_4^{3-} from present-day arvicoline teeth as a function of the mean annual weighted oxygen isotope compositions of local meteoric waters. Vertical error bars correspond to the analytical error associated with $\delta^{18}O_p$ values. Horizontal error bars correspond to the standard deviation associated with the mean annual $\delta^{18}O$ of meteoric waters. The black plain line corresponds to the least squares linear fit of data (Eq. 1). The black dotted lines corresponds to the mean least squares linear fit and the 95% confidence lines obtained from 10,000 parametric bootstrap simulations (Eq. 2). Stars indicate the two arvicoline tooth samples for which local pond waters have been analyzed for their oxygen isotope compositions.

The slope of our Eq. (2) determined for arvicolines is comparable to that previously obtained by Luz and Kolodny (1985) on laboratory rats (slope = 0.49, p = 0.09). One-tailed probabilities of the observed coefficient values are estimated from the comparison with the parametric bootstrap samples of the arvicoline coefficients. It is noteworthy that the intercept is significantly lower in the case of rats (intercept = 17.88, $p < 0.0001$) studied by Luz and Kolodny (1985) than in the case of our wild arvicolines. Our equation may also be compared (Fig. 3) to that determined on wild European mices by D'Angela and Longinelli (1990) for which the intercepts are similar (p = 0.15) but the slope (slope = 0.79) of the latter is significantly higher (p = 0.001). These differences could result from different metabolic activities and diets among these subfamilies of rodents but also from uncertainties related to the compositions of ingested waters derived from food and free water in the case of wild animals.

An explanation can be obtained from the comparison of our empirical data with those derived from fractionation equations computed by using the box model developed by Langlois et al. (2003). Values of physiological parameters and initial oxygen isotope compositions assigned to the reservoirs are the same as in the "Rodent" case study that was presented in Langlois et al. (2003) and Kohn (1996). The only differences are the oxygen isotope composition of food was either (i) a function of the oxygen isotope composition of surface waters assuming an enrichment of 6‰ for food water and a composition of solid food equal to the weighted sum of the compositions of each food component according to Schmidt et al.'s (2001) equations, or (ii) as in the "Rodent" case, fixed to 0.08‰ for the food water and to 18.71‰ for the organic matter (Kohn, 1996). In the first case (i), the modeled fractionation equation yields $\delta^{18}O_p = 0.6021\delta^{18}O_w + 21.21$, which has a slope and an intercept similar to those of our estimated fractionation equation ($p_{\text{slope}} = 0.31$, $p_{\text{intercept}} = 0.34$). In the second case, box modeling provides the fractionation equation $\delta^{18}O_p = 0.37\delta^{18}O_w + 18.9$, which has a slope and an intercept significantly lower ($p_{\text{slope}} = 0.0002$, $p_{\text{intercept}} < 0.0001$) than those of our estimated fractionation equation. Modeling reveals that $\delta^{18}O_p$ are primarily controlled by the food composition, which in the case of wild individuals (mice and arvicolines), is basically related to the $\delta^{18}O$ of surface waters. Change in the initial ^{18}O-enrichment of food water (50% lower) yields a slope ($\delta^{18}O_p = 0.72\delta^{18}O_w + 20.2$) close to that observed for the mice's equation. Therefore, the difference of slopes between wild mice and arvicolines fractionation equations can be likely related to differences in species-dependent diet behaviors. The equation established with isotopic data from laboratory rats significantly differs from the latter because food composition is fixed as dry pellets

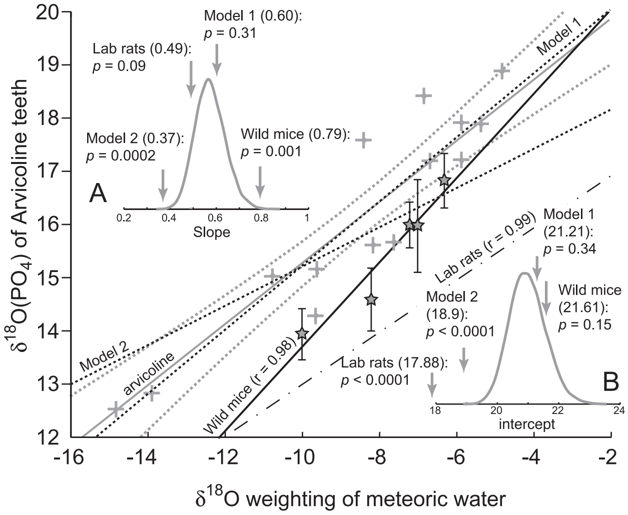

Figure 3. Comparison of $\delta^{18}O_p$ of European arvicoline teeth with the results of previous published oxygen isotope compositions of rodents. Stars correspond to the mean oxygen isotope compositions of European murine bones (*Apodemus*) from D'Angela and Longinelli (1990). Black plain line corresponds to the least squares fit of *Apodemus* bone data. Whereas the slope of *Apodemus* bones is significantly different from the slope of arvicoline teeth, *Apodemus* data are relatively close to arvicoline data and are included in the error field deduced from the linear regression of our data. The black dashed line corresponds to Luz and Koldony's (1985) equation that was determined with laboratory rats. Black dotted lines correspond to equations obtained using the box model of Langlois et al. (2003). Insets show kernel density estimates of the parametric bootstrap samples of the slope (A) and the intercept (B) of arvicoline data compared to other empirical (mice and rats) or theoretical (models 1 and 2) values (one-tailed probabilities).

(Luz and Kolodny, 1985), and thus resembles more the "Rodent" case. In conclusion, we propose that our empirical equation is valid to estimate mean $\delta^{18}O$ values of surface waters from the $\delta^{18}O$ of phosphate of arvicoline species.

Discussion

The water $\delta^{18}O$–air temperature relationship

Since Dansgaard's (1964) work, various relationships between air temperature and $\delta^{18}O$ values of meteoric waters have been determined (e.g., Von Grafenstein et al., 1996; Yurtsever and Gat, 1981), and we observe that these various equations lead to sizable differences in the estimates of air temperatures. Moreover, errors associated with both the isotopic measurement of phosphate and the determination of coefficients of the phosphate–water fractionation equation are never considered when estimating past water composition or air temperature. A parametric bootstrap simulation (Efron and Tibshirani, 1993) was performed (10,000 iterations) to calculate water compositions and air temperatures with a 95% confidence interval. A new set of values for $\delta^{18}O_p$ and regression coefficients was simulated using a trivariate normal distribution with a null covariance between $\delta^{18}O_p$ and coefficients (slope and intercept). The oxygen isotope compositions of meteoric waters were then estimated using Eq. (2), and air temperatures calculated using the water–air temperature relationships (Dansgaard, 1964; Von Grafenstein et al., 1996; Yurtsever and Gat, 1981).

To test our model equation, isotopic temperatures inferred from arvicoline data are compared to meteorological data (Table 4). Statistical results presented in Table 4 lead to conclude that Von Grafenstein et al.'s (1996) equation provides the most reliable results. This conclusion is mainly supported by the minimal average absolute deviations between observed and estimated temperatures.

The global accuracy of our model equation can be evaluated by comparing with a *t* test the least squares fit between observed and estimated air temperatures to a theoretical line of equality between them (Fig. 4). Using Von Grafenstein et al.'s (1996) equation, the slope of the regression line between observed and estimated air temperatures does not differ from 1, whereas in the case of Dansgaard's equation, the slope is significantly lower than 1, and large CI (confidence intervals) are obtained when using Yurtsever and Gat's equation. Therefore, we conclude that Von Grafenstein et al.'s (1996) equation should provide the most reliable air temperature estimates inferred from arvicoline oxygen isotope data. Calculated air temperatures from phosphate $\delta^{18}O$ well match present-day observed temperatures, thus validating this isotopic equation as a proxy of mean annual air temperatures.

The $\delta^{18}O$ record in Late Pleistocene arvicoline teeth from Gigny, France

The home ranges of a rodent as well as that of their predators (mainly owls), which are responsible for localized accumulation deposits of prey remains, are relatively restricted. These ecological aspects induce variations in the $\delta^{18}O$ of the rodent teeth assemblage, which records local climate changes.

We cannot exclude that some processes of diagenetic alteration could have disturbed the pristine $\delta^{18}O$ of the studied arvicoline teeth. Well-preserved and unbroken teeth have been systematically selected for isotopic measurements. Based on the phosphate chemical yields measured during the wet chemistry procedure, clustered P_2O_5 contents from 35% to 40% indicate that the original stoichiometry of arvicoline tooth apatite was preserved in the karstic environment of the Gigny cave.

The $\delta^{18}O$ of past meteoric waters, estimated from arvicoline phosphate values by using the method explained above, vary between −14.2‰ and −5.9‰ (Table 3). Such values correspond to present-day climatic conditions that spread from Finnish Lapland to southern Italy.

According to Von Grafenstein et al.'s (1996) equation, paleotemperatures (Table 3) fluctuated between 0.5°C

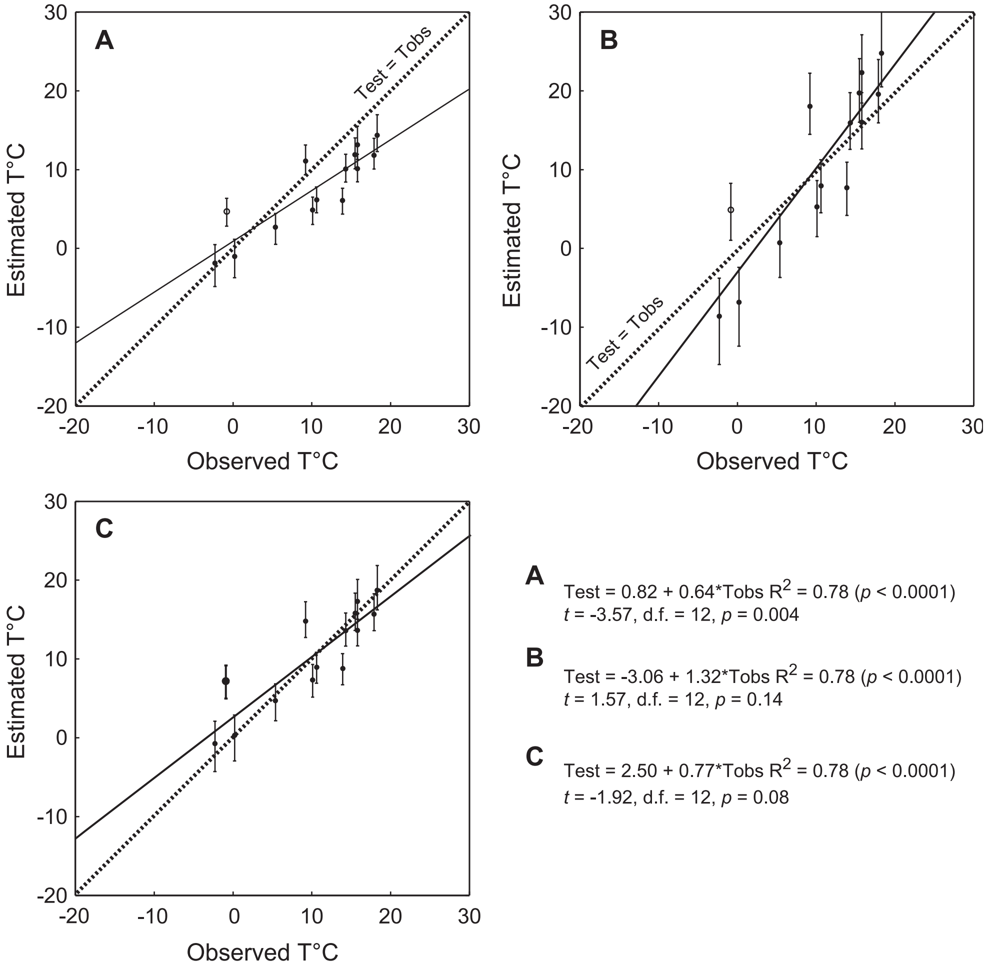

Figure 4. Relationship between observed and estimated air temperatures according to three published "δ^{18}O of water–air temperature" relationships: (A) Dansgaard (1964); (B) Yurtsever and Gat (1981); (C) Von Grafenstein et al. (1996). The dotted black line illustrates the equality between observed and estimated air temperatures. Error bars represent the 95% confidence interval associated with estimated temperatures derived from 10,000 bootstrap simulations. The black plain line represents the least squares fit of all data.

(level XVIb top) and 14.7°C (level XI) with an average confidence interval of 4.4°C. The evolution of air temperatures reveals a first cooling period from level XX to level XVIa with three interstadial events, a warmer phase from XV to IX with a cooling event between XIVa top and XII, then a second cooling period, which appeared in level VI, followed by higher temperatures throughout late levels VI to IV.

Comparison between Gigny $\delta^{18}O_p$ and Greenland $\delta^{18}O$ ice core records

The δ^{18}O time series of the GISP2 Greenland ice core (Grootes et al., 1993) provides a high-frequency record of the Pleistocene climate. We can contrast the recorded local climate changes in the $\delta^{18}O_p$ values of Gigny arvicoline teeth and the alternating cold and warm periods recorded in the Greenland ice core (Fig. 5).

Based on two ^{14}C dates (Evin, 1989), the deposit of level IV occurred between the end of the stade 1 and the interstade 1 (Fig. 5), and the deposit of level V corresponds to the beginning of the stade 2. The stade 2 cooling event corresponds to the advance of the glacier front during the LGM in the Jura area (Buoncristiani et al., 2002), likely responsible for the erosive hiatus between levels V and IV by activating the karstic network (Campy and Chaline, 1993). Another radiocarbon age obtained for level VIII indicates a deposit between the interstades 7 and 4. Thus, the cooling event identified in Gigny sequence (level VI) on the basis of $\delta^{18}O_p$ decreasing from +15‰ to +13.5‰ should have taken place during one of the cooling events 3–6. In any case, the age of this Gigny cooling event previously identified on the basis of a synthetic interpretation of faunal, pollen, and sedimentary data (Campy et al., 1989a) is older than previously estimated; that is, the end of marine oxygen isotope stage (MIS) 3 instead of MIS 2.

Because older levels were not dated, nor did they provide "infinite" ages according to Evin (1989), a calibration with the Greenland ice record is difficult to

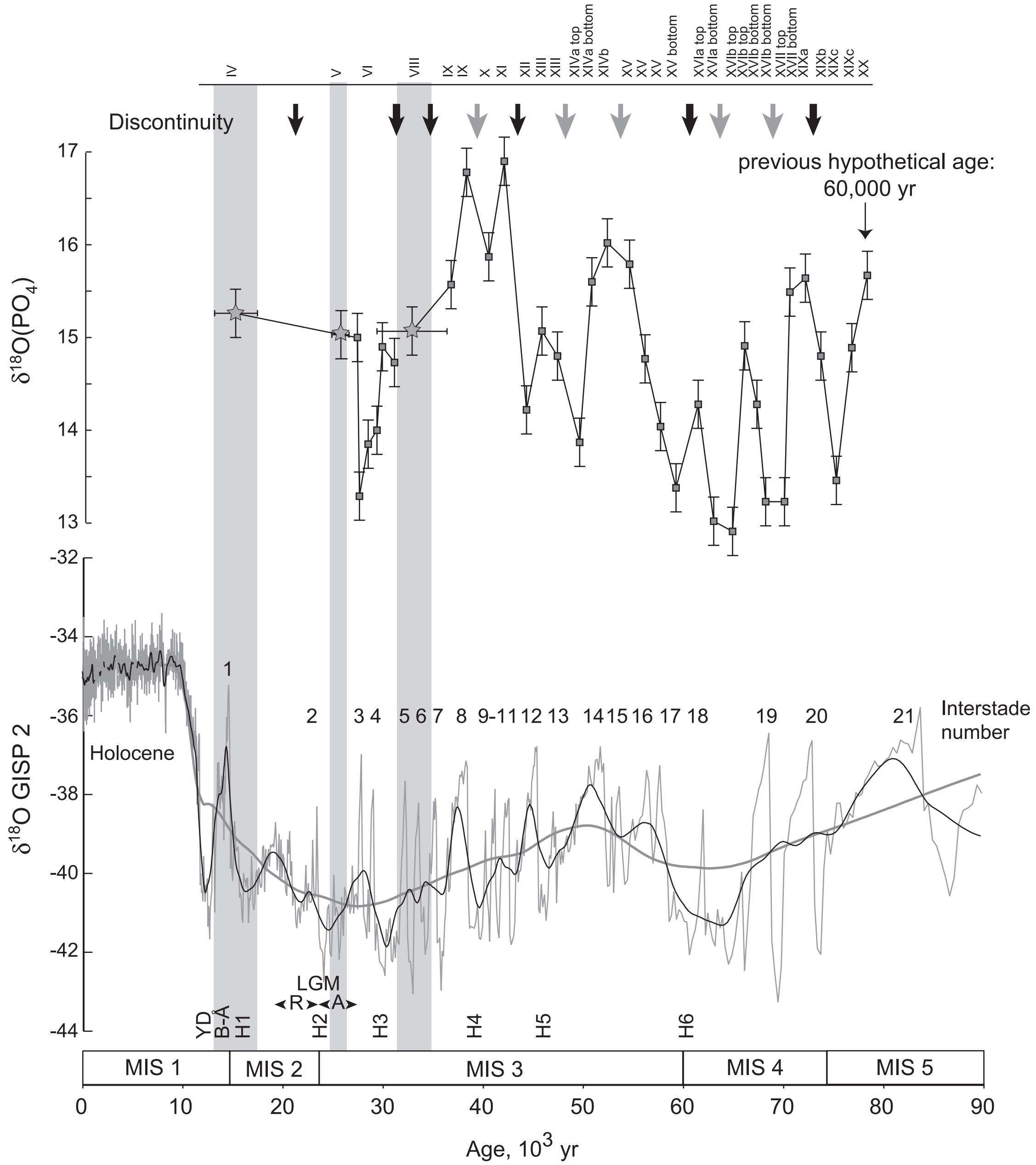

Figure 5. Comparison of δ^{18}O of PO_4^{3-} from arvicoline teeth in Gigny sequence with the δ^{18}O record of GISP 2 Greenland ice core (Grootes et al., 1993) during the last 90,000 yr. The upper part of Gigny sequence was either dilated or contracted for correlation of calibrated radiocarbon ages (star with 95% CI) with the time scale. Gray areas define age uncertainties. Other levels were plotted roughly uniformly with some spacing at the vicinity of a discontinuity. MIS: Marine Isotopic Stages; YD: Younger Dryas; B–Å: Bølling–Ålerød interstade; H#: Heinrich event; A and R: advance and retreat phases of the Jura glacier during the Last Glacial Maximum (Buoncristiani et al., 2002). The hypothetical age for the base of the sequence is after Campy and Chaline (1993). See Figure 1 for discontinuities.

establish given the highly sporadic karstic record. However, the hypothetical age of 60,000 yr based on faunal migration for level XX (Campy and Chaline, 1993) is not confirmed by the observed arvicoline $\delta^{18}O_p$ trend (Fig. 5). A MIS 4 age (between 60,000 and 74,000 yr ago) could correspond to the cooling trend (XX–XVIa) marked by minimal $\delta^{18}O_p$ values down to +13‰ recorded at Gigny. Comparison between the oxygen isotope compositions of arvicoline tooth phosphate and Greenland ice core records suggests to reconsider the previously established hypothetical chronology of the Gigny sequence.

Concluding remarks

The determination of an oxygen isotope fractionation equation between arvicoline tooth phosphate and local meteoric water provides potentially good estimates (along with minimized errors) of past water compositions and air temperatures. However, we emphasize that, basically, $\delta^{18}O_p$ values only model the oxygen isotope compositions of meteoric waters and are not robust proxies of air temperatures. Indeed, variations in the $\delta^{18}O$ values of rainfall may also be related to the seasonal variations of precipitation amounts. Thus, estimated air temperatures may be biased if precipitation is not equally distributed over the year. Therefore, only correlations between proxies of meteoric water compositions can be performed to test whether local isotopic records may have a regional or a global climatic significance.

The use of $\delta^{18}O_p$ of arvicoline teeth appears promising for identifying high-resolution continental climatic variations. However, taking into account the sporadic nature of the karstic record, the global, regional, or local significance of the climatic signal remains delicate to assess without a high-resolution chronology. Inferred $\delta^{18}O$ values of Late Pleistocene meteoric waters from Gigny cave (France) vary through time from −14‰ to −6‰ and agree with alternating warm and cold periods that could be compared to present-day climatic conditions prevailing from northern (Scandinavia) to southern (Mediterranean basin) Europe.

The comparison between GISP 2 and levels XX to XVIa suggests that the previously established chronology (Campy and Chaline, 1993; Chaline et al., 1995), and consequently, the timing of migration of *L. lagurus* in France should be considered with caution. The hypothesis that the MIS 4 stade is recorded at Gigny would imply a lesser erosive event than previously suggested; the glacier front being probably more distant, and the karstic network remained active without being affected by strong erosive phases.

Further studies could be devoted to intercalibrations of the $\delta^{18}O_p$ of arvicoline teeth as a proxy of continental climates with other proxies such as the structure of communities and transfer functions based on the species richness (e.g., Chaline et al., 1995; Montuire et al., 1997). Finally, we may consider that the measurement of oxygen isotope compositions of arvicoline teeth constitutes a promising approach for testing potential terrestrial biotic responses to high-resolution climatic fluctuations.

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