Palaeogeography, Palaeoclimatology, Palaeoecology 534 (2019) 109288

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Palaeoecology and palaeoclimatic context of Romanian Carpathian MIS 3 cave bears using stable isotopes ($\delta^{13}C$ and $\delta^{18}O$)

Marius Robu[a,*], Jonathan Wynn[b], Cristina Montana Puşcaş[c,d], Ioana Nicoleta Meleg[a], Jeremy E. Martin[e], Silviu Constantin[f,g]

[a] *"Emil Racoviţă" Institute of Speleology, Romanian Academy, Calea 13 Septembrie 13, 050711 Bucharest, Romania*
[b] *Division of Earth Sciences, National Science Foundation, Alexandria, VA, USA*
[c] *Terra Analitic, Bulevardul Tudor Vladimirescu 32, 510095 Alba Iulia, Romania*
[d] *School of Geosciences, University of South Florida, 4202 East Fowler Avenue, NES107, Tampa, FL 33620, USA*
[e] *Université de Lyon, ENS de Lyon, Université Lyon 1, CNRS, UMR 5276 Laboratoire de Géologie de Lyon: Terre, Planète, Environnement, F-69342 Lyon, France*
[f] *"Emil Racoviţă" Institute of Speleology, Romanian Academy, Center for Geochronology & Paleoclimate, Frumoasă 31, 010986 Bucharest, Romania*
[g] *Centro Nacional de Investigación sobre la Evolucion Humana, CENIEH, Passeo Sierra de Atapuerca 3, 09002 Burgos, Spain*

A R T I C L E I N F O

Keywords:
Geochemistry
Dentine
Serial sampling
Intra-tooth variation
Ursus spelaeus

A B S T R A C T

Millimeter-scale growth rings in canine dentine of MIS 3 cave bears have been interpreted as annual growth bands produced, in part, by seasonal variation in growth rate. We present new intra-tooth stable carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotope profiles in dentine hydroxylapatite of early forming permanent teeth, from three famous Late Pleistocene cave bear sites from Romanian Carpathians. We measured $\delta^{13}C$ and $\delta^{18}O$ of the CO_3 fraction of dentine hydroxylapatite from samples covering a profile across the root, representing a general line from juvenile period to adulthood. Carbon isotopes measured in dentine samples – from the first to the last to be deposited – of the same individual, record an increase in $\delta^{13}C$ values throughout immature life of bears as has been shown previously, with lower precision, using age categories. For the first time, based on $\delta^{13}C$ data analysis, the weaning process in cave bears was identified. The $\delta^{18}O$ values show substantial variations related, most probably, to seasonal growth of the dentine. Finally, the CO_3 of dentine apatite extracted from cave bear canines proves to be reliable for geochemical analyses, reflecting physiology, behavior and palaeoclimatic conditions.

1. Introduction

The discovery of measurable natural variation in the stable isotopic composition of vertebrate fossil remains brought palaeontologists a valuable tool for studying fossil mammals from ancient marine and terrestrial communities (e.g. Longinelli, 1984; Clementz, 2012; Matthews et al., 2016; Martin et al., 2017). Carbon and oxygen isotopic abundances (reflected in $\delta^{13}C$ and $\delta^{18}O$ values) measured from fossil vertebrate teeth have been used for a long time to decipher the dietary habits and ecology of extinct species (Sullivan and Krueger, 1981; Krueger and Sullivan, 1984; Ambrose and Norr, 1993; Longinelli, 1984; Koch et al., 1989; Bocherens et al., 1996; Reinhard et al., 1996). Carbon isotopic abundances in carbonate hydroxylapatite [Ca_{10} (PO_4, CO_3)$_6$ (OH_2)] reflect the average of the whole diet components (amino acids, carbohydrates and lipids). The oxygen isotopic abundances recorded from the same tissue reflect the variation in the $\delta^{18}O$ value of body fluids controlled mainly by the isotopic composition of the ingested water. As the ingested water tracks local precipitations, $\delta^{18}O$ values obtained from dentine are used to reconstruct palaeoclimatic conditions and sources of water used by animals (Longinelli, 1984; Koch et al., 1989; Reinhard et al., 1996; Dotsika et al., 2011; Bocherens et al., 2011; Clementz, 2012; Krajcarz and Krajcarz, 2014; Krajcarz et al., 2014).

The permanent canine teeth of adult bears are useful for tracing age-related changes, mostly due to their large size, internal architecture and resilience to weathering. The chronological age of individuals can be accurately determined (Debeljak, 1996) from the annual layers of dentine or cementum, emphasized when odontogenesis is slowed during the annual period of denning (nutritional stress). Although the cementum layers record a longer history of the bear's life, dentine layers are better suited for geochemical analyses as they are thicker and can provide sufficient sampling material. It has been shown that the annual canine dentine layers in adult individuals may vary between five and eight, with the first five layers belonging to the primary dentine, and the others to the secondary dentine. Each dentine layer consists of a

* Corresponding author.
E-mail address: marius.robu@iser.ro (M. Robu).

https://doi.org/10.1016/j.palaeo.2019.109288
Received 1 March 2019; Received in revised form 19 July 2019; Accepted 22 July 2019
Available online 25 July 2019
0031-0182/

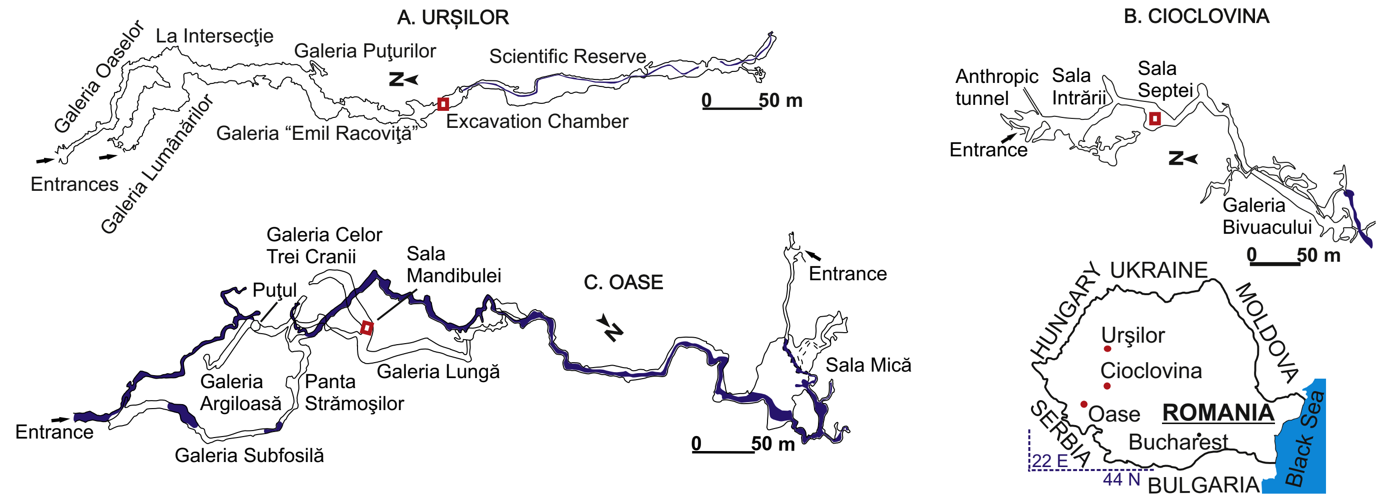

Fig. 1. The studied Romanian MIS 3 cave bears sites: A – Urşilor Cave, B – Cioclovina Cave, C – Oase Cave. (Cave maps redrawn after Vălenas (1979), Onac et al. (2011), and Constantin et al. (2013).)

thick, light-stained inner zone, deposited during the annual period of activity, and a very thin, dark-stained outer zone related to the period of denning (Rausch, 1961, 1967, 1969; Mundy and Fuller, 1964; Stoneberg and Jonkel, 1966; Sauer, 1966; Sauer et al., 1966; Koch et al., 1989). Knowing that the cyclicity of dentine growth layers in bear canines ends when adulthood is reached (Rausch, 1969), one can trace back both the ecological conditions and the climatic evolution by using a geochemical approach (e.g., using $\delta^{13}C$ and $\delta^{18}O$ values).

For animals that have an omnivorous or a carnivorous diet, the carbon isotope analysis of organic tissues of tooth dentine provides information reflective of the protein portion (collagen) of an individual's diet (Sullivan and Krueger, 1981; Krueger and Sullivan, 1984; Ambrose and Norr, 1993; Harrison and Katzenberg, 2003), whereas stable isotope values from bone, dentine, and enamel apatite carbonate largely reflect the whole diet (i.e., proteins, carbohydrates, and lipids; Ambrose and Norr, 1993; Harrison and Katzenberg, 2003). In general, apatite is more ^{13}C-enriched compared to collagen (by +9.6–14‰; DeNiro and Epstein, 1978a, 1978b; Sullivan and Krueger, 1981; Krueger and Sullivan, 1984; Lee-Thorp and Van Der Merwe, 1987; Lee-Thorp and Sponheimer, 2005; Fahy et al., 2015), their relationship being affected by the trophic level. The utility of bone/tooth apatite for stable carbon isotope analysis in palaeodietary studies stems from the fact that diagenesis of biogenic carbonates in the mineral over time is unexpectedly limited, and that chemical pretreatment further removes the effects of diagenetic alteration of the biogenic signal (Lee-Thorp et al., 1989). Therefore, palaeodietary inferences could be carried out using this method for dentine apatite of fossil remains up to $\sim 10^5$ years old (Clementz, 2012). Thus, apatite $\delta^{13}C$ measurements should not be regarded as an alternative to $\delta^{13}C$ collagen measurements, but may provide additional useful information about dietary trends.

Late Pleistocene cave bear fossils are the most abundant remains to be found in the caves of Europe, this extinct species being one of the best studied in Quaternary palaeontology. Nonetheless, there are still many debates within the scientific community regarding the diet, physiology and behavior of these ursids. Previous studies have focused on cave bear physiology (e.g. Nelson et al., 1998; Bocherens, 2015; Robu et al., 2018) using $\delta^{13}C$ values from bone collagen and have shown that the isotopic profiles of the four age groups (neonates, juveniles, sub-adults and adults) provide patterns of transfer of stable isotope signatures throughout the immature life of bears.

Sequential sampling of dentine within a single tooth can provide information on dietary and habitat changes over the course of an individual development from juvenile period to adulthood as well as seasonal variations in these ecological parameters later in the animal's life. Previous studies of fossil proboscideans – elephants and their extinct relatives (Koch et al., 1989; Fox and Fisher, 2004; Hoppe et al., 1999; Rountrey et al., 2007; Clementz, 2012) highlighted how serial sampling of both tooth enamel and dentine can be used to answer different questions about the ecology and life history of these animals. Koch et al. (1989) analyzing the $\delta^{18}O$ values from dentine layers, have shown that CO_3 fraction of apatite retains a signal in molars (proboscideans and bears), reflecting seasonal changes in the composition of drinking water.

The Romanian Carpathians host numerous, complex, and rich Late Pleistocene cave bear sites, suitable for palaeoecological and palaeoclimatological investigations. Three already famous Late Pleistocene cave bear sites from Romanian Carpathians were chosen for this study – the Urşilor, Oase and Cioclovina caves – known to the international scientific community for their impressive fossil bonebeds, human and faunal remains, and for their taphonomic and palaeoichnologic features (e.g. Richards et al., 2008; Robu et al., 2018). Analyzing both $\delta^{13}C$ and $\delta^{18}O$, retrieved from dentine apatite serial samples, has not been applied systematically to any MIS 3 species as yet. Therefore, studying the carbon and oxygen transfer signatures throughout the first years of life, using data from apatite of each individual, will bring a better understanding of MIS 3 cave bear palaeoecology and a better resolution of variations in diet and physiology during tooth growth.

2. Materials and methods

2.1. Carpathian site-specific samples

The Carpathian cave bear specimens derive from excavations in three extensive karst systems: Urşilor Cave, Peştera Cioclovina Uscată, and Peştera cu Oase (Fig. 1). Urşilor Cave (further on: Urşilor) is situated in the northwestern part of the Romanian Carpathians (the Apuseni Mountains). The analyzed cave bear material was sampled from the palaeontological excavation, situated within the Scientific Reserve (lower level of the cave). The analyzed cave bears were AMS ^{14}C dated between *c.* 47 and 39 cal kyr BP (Constantin et al., 2014; Fig. 1A).

The Peştera Cioclovina Uscată (*Dry Cioclovina Cave*; further on: Cioclovina) (Fig. 1B) is located in the northwestern part of the Southern Carpathians (the Şureanu Mountains) (Soficaru et al., 2007; Onac et al., 2011). Results of AMS ^{14}C dating indicate that the cave bears inhabited the cave between *c.* 44.2 and 31.4 cal kyr BP (Soficaru et al., 2007; Meleg et al., 2018; this study).

The Peştera cu Oase (*Ponor Plopa Cave*; further on: Oase) is situated in the southwestern part of the Southern Carpathians (the Anina Mountains) (Fig. 1C). The analyzed cave bear samples were excavated from the upper level of the cave (Sala Mandibulei and Panta Strămoşilor). The cave bears of the bone assemblage were dated between *c.* 50 and 40.4 cal kyr BP (Higham and Wild, 2013; this study).

2.2. Cave bear samples

Teeth of the analyzed cave bears were identified by their morphology (according to Torres et al., 1978; Tsoukala and Grandal-D'Anglande, 2002). DNA analyses have not been completed for all studied sites, although some populations were attributed to *U. ingressus* either on mtDNA or nuclear DNA basis or dental and metacarpal morphology (Richards et al., 2008; Robu, 2016; Meleg et al., 2018).

A number of 18 fused cave bear lower canines ($N = 18$) were analyzed to obtain carbon and oxygen isotopic composition from the structural carbonate of their dentine. The canines were selected from the analyzed sites ($N = 9$ females and $N = 9$ males; Table S1), with six canines being sampled from each collection/cave site. All canines were cut transversally, at the midheight of the canine root, where the maximum width occurred, in order to get as many samples as possible from the oldest to the youngest dentine (first and last to be deposited, respectively). Hydroxylapatite samples ($N = 112$) were drilled macroscopically, with a Dremel Stylus tool, from series of holes aligned parallel to incremental dentine (Fig. 2); the powder from each row of holes formed a single sample (*c.* 2 mg). We obtained five to nine non-overlapping samples within dentine tissue. The majority of canines ($N = 12$) had not a clear delimitation between the dentine layers (i.e. some of them were completely white in section) and therefore it was impossible to assign them to light/dark layers. Therefore, for reasons of sampling technique limitation we assume that the profiles from studied canines did not followed exactly the summer - fall/winter intervals but allowed us to identify the variations of both analyzed parameters, i.e. carbon and oxygen isotopes. The samples were analyzed following the method described by Koch et al. (1997).

The isotopic ratios are expressed as $\delta^{13}C$ and $\delta^{18}O$ values according to calculation: $\delta^{A}X = (R_{sample} / R_{standard} - 1) \times 1000$, where X is an element (C or O), A is the atomic mass number and R is the isotopic ratio $^{13}C/^{12}C$ or $^{18}O/^{16}O$. Values are reported in relation to Vienna-PDB (VPDB) standard, with $\delta^{18}O$ values being converted to VSMOW using the formula $\delta^{18}O_{VSMOW} = 1.03091 \times \delta^{18}O_{VPDB} + 30.91$ (Skrzypek et al., 2011). The laboratory standards used were NBS18 ($\delta^{13}C = -5.0‰$ and $\delta^{18}O = -23.1‰$) and NewCar (a sample of the Carrara Marble with $\delta^{13}C = +4.04‰$ and $\delta^{18}O = -3.38‰$). Both $\delta^{13}C$ and $\delta^{18}O$ values were measured using a Delta V+ (Thermo-Finnigan, Bremen, Germany) isotope ratio mass spectrometer (IRMS), in continuous flow mode (Fry et al., 1992) coupled to a Gasbench II preparation device (Thermo-Finnigan, Bremen, Germany) in the Department of Geology, University of South Florida.

2.3. Dating method

Ten cave bear samples ($N = 10$) derived from the analyzed canines were AMS ^{14}C dated at Poznan Radiocarbon Laboratory (Poland; Table S1). Collagen extraction was performed using the method described by Pietrowska and Goslar (2002) and the extracted collagen was then purified on Elkay 8 mm filters, and ultrafiltered on Vivaspin 15 MWCO 30 kD filters (Bronk Ramsey et al., 2004). The content of ^{14}C in carbon samples was measured following the protocol described by Goslar et al. (2004).

2.4. Statistical analyses

Statistical analyses were performed using the software PAST (Paleontological Statistics), version 3.20 (Hammer et al., 2001) and R (R Core Team, 2018). Hierarchical clustering was used to explore relationship patterns of $\delta^{18}O$ and $\delta^{13}C$ variability among the studied samples. Euclidean distances were used to calculate a similarity matrix based on the average values of $\delta^{18}O$ and $\delta^{13}C$ for 18 canines from Urşilor, Oase and Cioclovina caves, and Ward's method was selected to define the distance between identified classes. The optimum number of clusters has been assessed by computing the silhouette information using the R package *cluster* (Maechler et al., 2019). To visualize the similarity among studied samples, non-metric multidimensional scaling and minimum-spanning tree linking samples were computed based on average values of $\delta^{18}O$, $\delta^{13}C$ and median ^{14}C date for 18 canines from Urşilor, Oase and Cioclovina caves. Given that the absolute ages have a different unit and scale compared to the $\delta^{18}O$, $\delta^{13}C$ values, normalization has been used to rescale the data. Correlation tests were performed to verify the strength of relationship between intra-tooth $\delta^{13}C$ and $\delta^{18}O$ values. Shapiro-Wilk test was used to test the normality of data. Further, for normally distributed data Pearson correlation method was used, and for data not normally distributed Spearman rho method was used. For the correlation analyses, R packages stats (R Core Team, 2018) and ggplot2 (Wickham, 2009) were used.

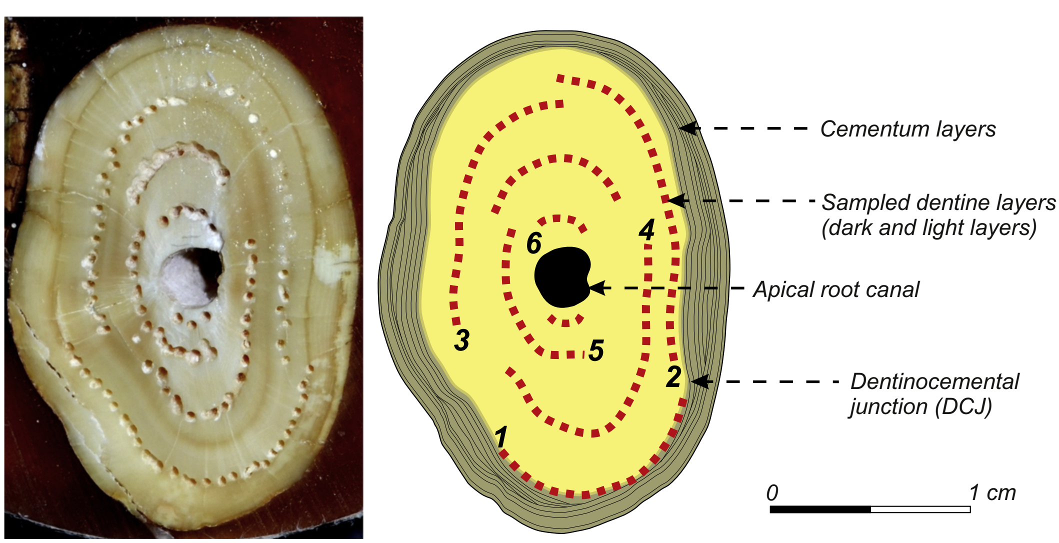

Fig. 2. Sampling methodology within a cross-section of a cave bear canine. Dentine samples 1 ➔ 6 were sampled for stable isotope analysis; the 1st sample is the earliest dentine to form while the 6st is the last.

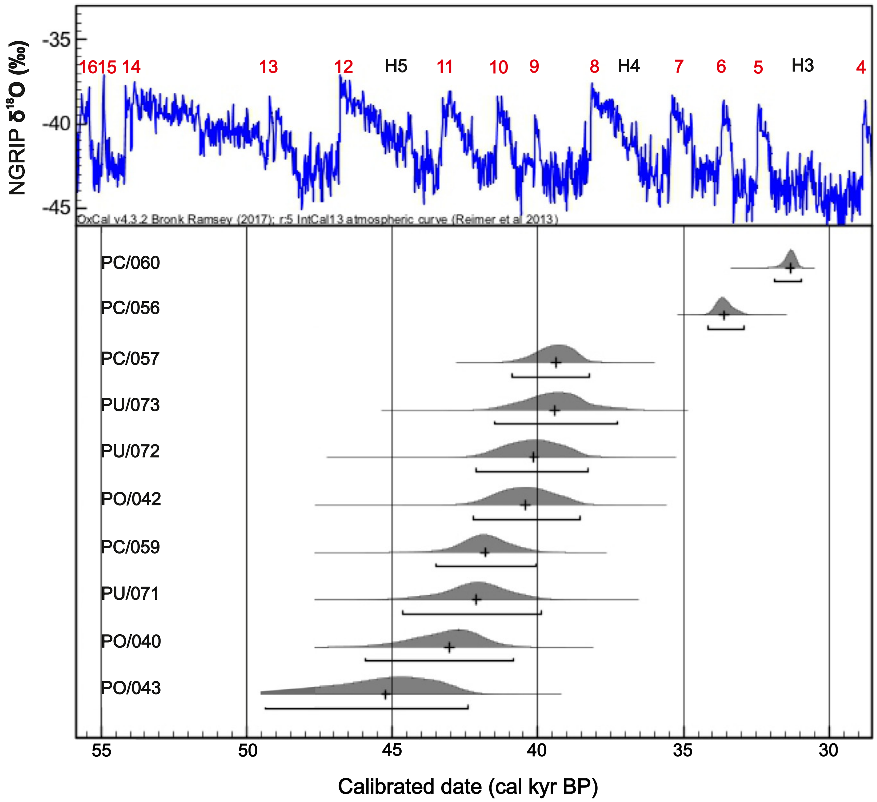

Fig. 3. Calibrated ^{14}C AMS ages of the cave bear samples ($N = 10$).

3. Results

The results of radiocarbon dating are given in Table S1 ($N = 10$ samples). All ages were calibrated using the OxCal 4.3.2 program (Bronk Ramsey, 2017) and the IntCal13 calibration curve (Reimer et al., 2013). Radiocarbon ages (Fig. 3) of the 10 cave bear bone samples collected from the analyzed sites range between *c.* 45 and 31 cal kyr BP (median values) for both surface and excavated finds. The majority of the dated samples of bears belong to 45–39 cal kyr BP interval – known for its faunal richness across caves from both the Carpathians and the rest of Eurasia – and to a last pulsation of this species, around 31 cal kyr BP ($N = 2$; from Cioclovina Cave) at a time believed to be close to its extinction (Pacher and Stuart, 2009).

3.1. δ^{13}C values

The obtained δ^{13}C values of all 112 dentine apatite samples range from −17.5 to −9‰ (average of all samples −12.8‰; Fig. 4A–C). All δ^{13}C profiles are recording an increment of carbon values throughout the deposition of cave bear dentine until adulthood. Urşilor samples ($N = 36$) have extreme values between −16.7 and −9.2‰, Oase samples ($N = 38$) spread between −14.9 and −9.0‰ and, Cioclovina samples ($N = 38$) spread between −17.5 and −9.9‰.

Comparing the δ^{13}C values of the oldest dentine samples of the analyzed canines (precluding adulthood in bears), with the average of the δ^{13}C collagen values obtained for the same site (e.g. Robu et al., 2013, 2018), we found that the lowest $\Delta\delta^{13}C_{collagen\text{-}apatite}$ difference ($\delta^{13}C_{collagen} - \delta^{13}C_{apatite}$) was recorded for Cioclovina, +7.9‰ ($\delta^{13}C_{collagen} = -21.1$ and $\delta^{13}C_{apatite} = -13.2$‰), while the Urşilor bears had a $\Delta\delta^{13}C_{collagen\text{-}apatite}$ value of +9.6‰ ($\delta^{13}C_{collagen} = -21.6$ and $\delta^{13}C_{apatite} = -12.0$‰). The highest average difference recorded in the Oase individuals between the two parameters $\Delta\delta^{13}C_{collagen\text{-}apatite}$ was +11.3‰ ($\delta^{13}C_{collagen} = -21.4$ and $\delta^{13}C_{apatite} = -10.1$‰, respectively).

Fig. 5 shows the variation of δ^{13}C values between sexes among the studied Carpathian populations: for females, it appears that the highest average is recorded for the Oase and Urşilor females (−11.9‰, and −12.0‰, respectively), and the lowest for Cioclovina, −14.6‰ (Fig. 5A). For males, the highest average value was measured in the Oase bears: −11.9‰, and lowest values in Urşilor (−13.9‰) and Cioclovina (−13.7‰) (Fig. 5B). Both graphs suggest differences among sexes within all three cave bear sites: for Urşilor, females show δ^{13}C values enriched by +1.9‰ when compared with males, while for Oase and Cioclovina, the situation is opposite, males have enriched δ^{13}C values by +0.5 and +0.9‰, respectively.

3.2. δ^{18}O values

The obtained δ^{18}O values of the 112 dentine apatite samples range from 16.4 to 29.5‰ (average of all samples 23.1‰; Fig. 4D–F) and are in agreement with data obtained elsewhere for MIS 3 cave bears (e.g. Krajcarz et al., 2014). All δ^{18}O profiles show high variability throughout the deposition of cave bear dentine until adulthood. Urşilor samples ($N = 36$) have extreme values ranging between 19.3 and 29.5‰ (average 23.4‰), Oase ($N = 38$), range between 16.4 and 25.8‰ (average 23.1‰) and Cioclovina ($N = 38$), range between 17.9 and 26.6‰ (average 22.7‰).

The intra-tooth δ^{18}O variability of the analyzed bears ranges from 1 to 8.2‰. Among the three caves, Oase has the highest intra-tooth variability for all δ^{18}O profiles, while Cioclovina has the lowest. Nonetheless, all sites have bears with both types of δ^{18}O profiles, suggesting intra-cave variability, Cioclovina having the widest range (21.5–25.5‰) and Oase the narrowest (22.6–24‰) (Fig. 6).

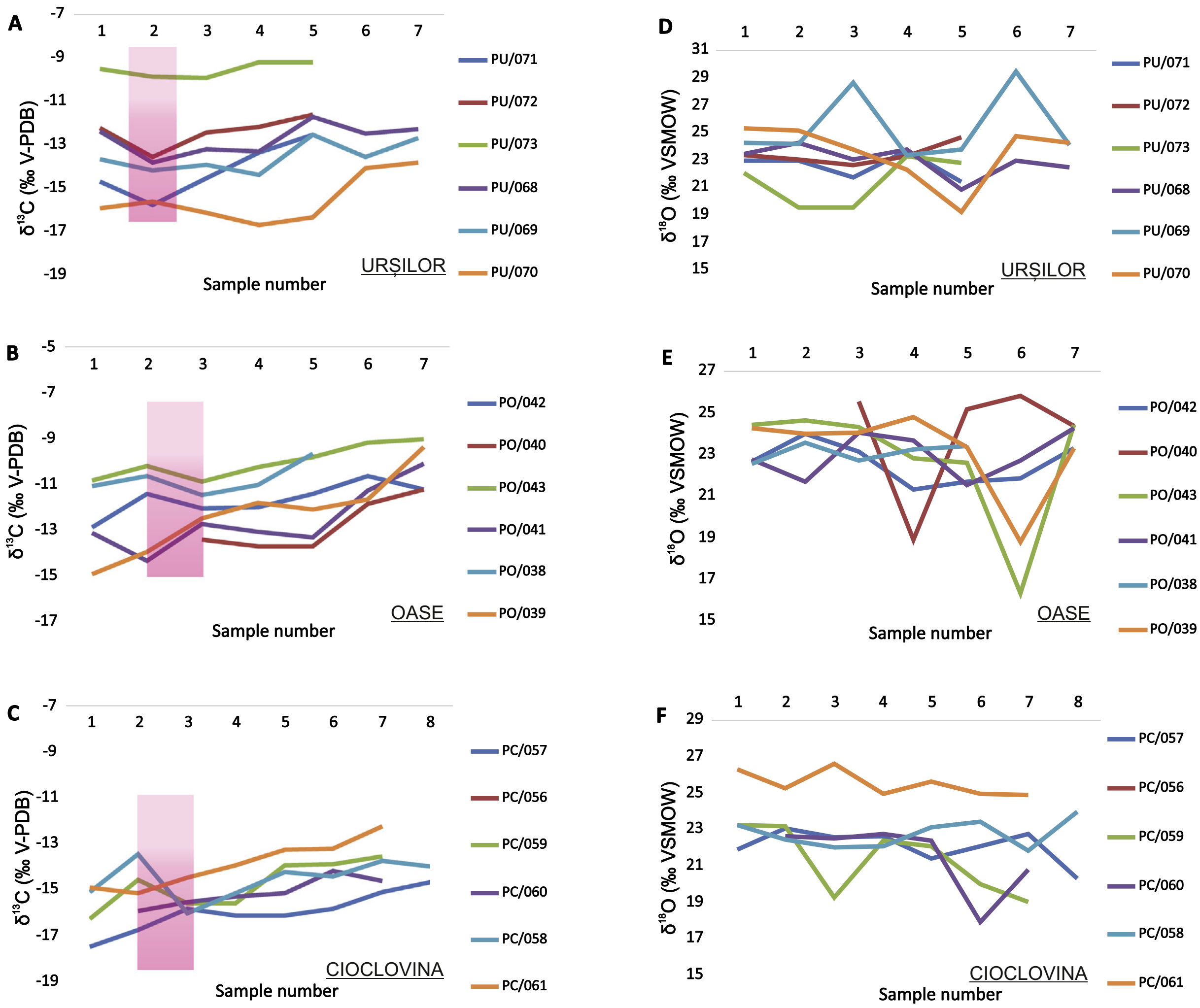

Fig. 4. $\delta^{13}C$ and $\delta^{18}O$ data obtained from the dentine samples of MIS 3 cave bears from analyzed sites (six canines analyzed/each site). A–C: $\delta^{13}C$ results from Urşilor (*N* = 36), Oase (*N* = 38) and Cioclovina caves (*N* = 38), respectively; D–E: $\delta^{18}O$ results from Urşilor (*N* = 36), Oase (*N* = 38) and Cioclovina caves (*N* = 38), respectively. X axis 1 ➔ 8: dentine samples from earliest to latest samples. Pink bands indicate the inferred weaning period. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

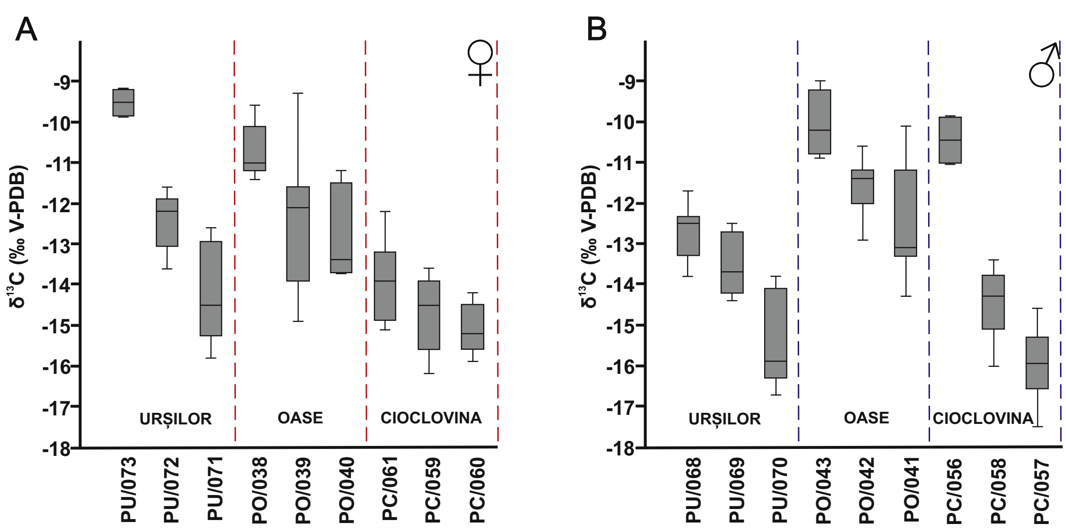

Fig. 5. Boxplots of $\delta^{13}C$ data from Urşilor, Oase and Cioclovina caves. A: females (*N* = 9 canines, 52 samples); B: males (*N* = 9 canines, 60 samples). For each locality analyzed samples were sorted from high to low to better visualize the range of $\delta^{13}C$ values.

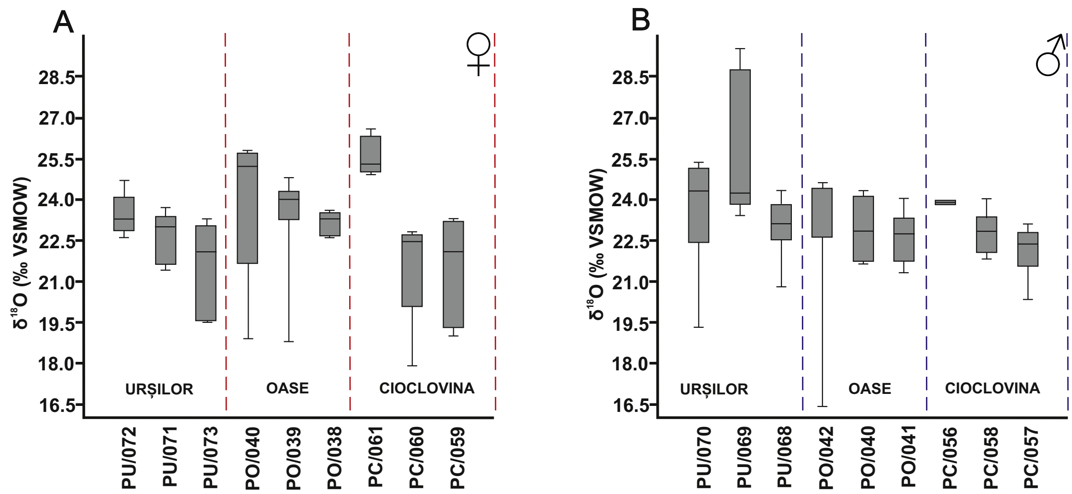

Fig. 6. Boxplots of $\delta^{18}O$ data from Urşilor, Oase and Cioclovina caves. A: females (N = 9 canines, 52 samples); B: males (N = 9 canines, 60 samples). For each locality analyzed samples were sorted from low to high to better visualize the range of $\delta^{18}O$ values.

4. Discussion

4.1. Physiology and behavior using $\delta^{13}C$ data

The large range of $\delta^{13}C$ values measured for the MIS 3 Carpathian cave bears span the dietary range, from herbivores to carnivores, taking into account the values for dentine apatite published so far (e.g. Bocherens et al., 1994). While few data obtained from dentine apatite for Pleistocene bears (adults) were recorded around −16.0 to −14.0‰ (Bocherens et al., 1994), our mean values of the $\delta^{13}C$ show a large inter-cave variation (−16.0 to −9.0‰, for the last sample of the analyzed specimens), with values typical for both carnivores (−12.6 to −12.1‰ as depicted for lions and wolfs) and herbivores (−11.4 to −10.1‰ for horses, artiodactyls, *Capra*, etc.; Bocherens et al., 1994; Fig. 7). The large variation in $\delta^{13}C$ values of the Romanian Carpathian cave bears may indicate ecological differences, linked to different dietary and/or habitat preferences as previously shown by Robu et al. (2013, 2018). On the other hand, the differences in $\delta^{13}C$ values among sexes could be due to either random and size sampling (only three males and females analyzed/site), different intra-cave dietary habits or could be due to a combination of both.

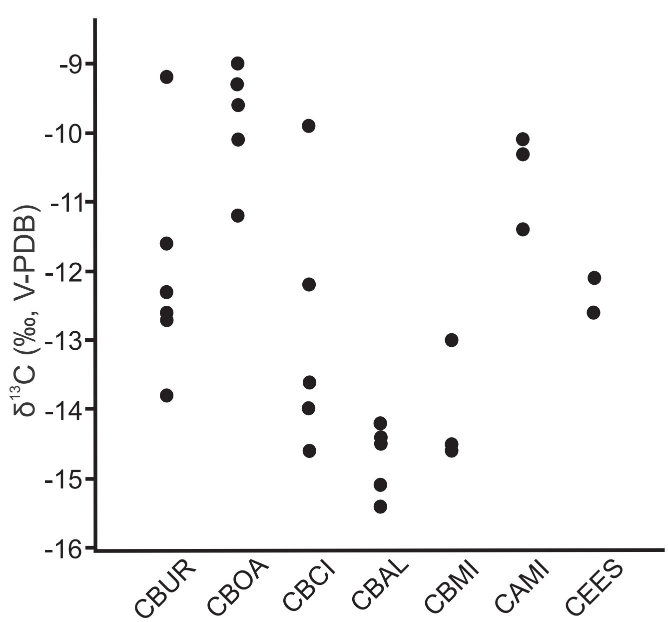

Fig. 7. Jitter plot of $\delta^{13}C$ values from dentine apatite from various MIS 3 mammals across Europe. Cave bears: CBUR – Urşilor (N = 6); CBOA – Oase (N = 6); CBCI – Cioclovina (N = 6); CBAL – Aldéne (N = 5); CBMI – Mialet (N = 4). Herbivores: CAMI – Mialet (N = 3); CEES – Escale (N = 2).
(Data for Aldéne, Mialet and Escale from Bocherens et al. (1994).)

The $\delta^{13}C$ records of studied cave bears show a similar pattern among them, in which $\delta^{13}C$ values are increasing from juveniles to adults, in accordance to previous research (e.g. Nelson et al., 1998; Robu et al., 2018), indicating a change of diet across time (Fig. 4A–C). For all studied cave bears, a negative shift of $\delta^{13}C$ profiles was recorded for the second (mainly at Urşilor) or the third (mainly at Oase and Cioclovina caves) dentine samples, roughly corresponding with the first years of life, presumably 1–2 years old for the analyzed specimens. Apparently, the "second dentine sample drop" profile is present as well at Oase and Cioclovina caves, while the "third dentine sample drop" profile was recorded at Urşilor as well, to a lesser extent. Although it seems that these records are site-characteristic, in fact, it may be a matter of random sampling and it is very likely for the $\delta^{13}C$ negative shifts to be related to the weaning completion in cave bears, a critical period for the future adults, reflected in low lipids and energy input in their diet. It was shown in some studies that the positive trend in $\delta^{13}C$ associated with weaning could be the result of decreasing proportion of lipids in the diet brought by the transition from high to low dependence on milk (e.g. Hobson and Sease, 1998). Thus, when fat represents an important component in the animal diet, carbonate $\delta^{13}C$ should have more negative values than when fat is less important (Rountrey et al., 2007). In one of the sister species of cave bears, the modern brown bear, *Ursus arctos*, it was documented that the weaning period takes place during the first or second year of life, while the separation of cubs from their mothers occurs at 1–3 (occasionally 4) years of age (McLellan, 1994; Dahle and Swenson, 2003; Bjørn and Swenson, 2003), a fact supported as well by our results. The same $\delta^{13}C$ variation related to the weaning process has been reported for human canines retrieved from archaeological context, by Sandberg et al. (2014).

4.2. Palaeoclimatic context using $\delta^{18}O$ data

The similarity of $\delta^{18}O$ patterns between our fossil data and the data on bears published by Koch et al. (1989), in both amplitude and relation to serial dentine samples, indicate that the isotopic signal recorded in our fossil samples has no diagenetic influence. Although the dentine layers were only partially identified (as light and dark bands), as a general remark we could assume that the lower and the higher values of the $\delta^{18}O$ profiles may reveal the isotopic signature of the seasonal variation of the tooth growth (Fig. 4D–F). The δ^{18}O values of dentine retrieved from the structural carbonate for the MIS 3 Carpathian cave bears are in agreement with the results published elsewhere on dental enamel apatite (e.g. Bocherens et al., 1994; Krajcarz et al., 2014). The intra-tooth amplitude of isotopic variation of δ^{18}O is in the same range (1–8.2‰) as the one observed for the Younger Dryas North American mammoths and bears (Koch et al., 1989).

At cave-level, low δ^{18}O variations have been recorded (Cioclovina – 4.2‰, Urşilor – 3.9‰, Oase – 2.6‰), a similar pattern when compared with MIS 3–4 cave bears from Biśnik Cave from Poland (3.9‰; Krajcarz and Krajcarz, 2014). No sex-related differences in δ^{18}O values among the analyzed cave bears were recorded, with high and low variation patterns being obtained for both females and males.

With some exceptions it appears that analyzed bears, during the first two dentine samples (the first years of life) have similar δ^{18}O values suggesting a low mobility whereas starting with the third dentine sample, the values may show significant shifts, sometimes up to 6‰. This pattern may indicate a growing mobility and could be related with the δ^{13}C data that show a significant change in bears physiology during the first years of life. Modern brown bears, one of the closest relative to the MIS 3 cave bears, have a home-range size according to some studies (Krofel et al., 2010, 2012) between 300 and 1600 km, with an average of 600–700 km. It is therefore plausible that during the feeding and mating period, bears could drink water with different δ^{18}O value than usual, a notion reflected in the δ^{18}O isotopic record. Thus, the high variations could be a reflection of a broader territorial range, for both females and males. On the other hand, the large intra-species δ^{18}O variations seen in cave bears could be related as well to the fact that a large part of their body water was obtained from plant sources (e.g., fruits) in the context of the unstable climate of MIS 3. Both males and females show high variability of δ^{18}O intra-tooth values. However, it must be kept in mind as well that during the period between 30 and 50 kyr BP many short-term climatic changes have occurred and the δ^{18}O signal could be biased (Shackleton and Hall, 2001; Van Meerbeeck et al., 2009; Bocherens et al., 2011; Bocherens, 2015).

4.3. Palaeoclimatic and palaeoecologic inferences using δ^{13}C and δ^{18}O data

Bocherens et al. (2011) suggested that warmer time periods led to more positive δ^{18}O values retrieved from cave bear tissues, due to temperature effects on δ^{18}O values of meteoric water. Therefore, values > 22‰ would correspond to warmer periods, values < 21.3‰ would correspond to a colder period, and those between 21.3 and 22‰ may indicate intermediate climatic periods. Moreover, the landscape inference may be possible, following Bocherens' (2015) scheme for the relation between δ^{13}C values and vegetation cover. We explored whether climatic episodes based on δ^{18}O signature relate to inferred landscape from δ^{13}C signature to further depict a pattern in our dataset. The clustering shows a heterogeneous pattern, regardless of sites (Fig. 8). Based on the average δ^{13}C and δ^{18}O values of Romanian bears, two main clusters are depicted: a first one with high δ^{13}C values (−13.9 to −9.5‰), and a second with low δ^{13}C values (−16 to −14.2‰). For most of the samples in cluster one, high δ^{13}C values correspond to high δ^{18}O, suggesting a warmer climate associated with more open forests. Within cluster 2, three samples from Cioclovina (PC/59, PC/57, and PC/060) form a distinct cluster, revealing cooler conditions in the area in three different time periods (~42, 40 and 31 ka BP, respectively).

Corroborating the δ^{13}C and δ^{18}O values with the absolute age of bears (Fig. 9), it appears that the highest variability is observed in Cioclovina, and is related to at least three distinct time periods when the cave was occupied. The analysis shows a similarity between Urşilor and Oase, with two clusters emerging: (i) one dated at around 45–43 cal kyr BP, from Oase, with two individuals and (ii) a second one, from Oase and Urşilor, with four individuals, dated at 42–39 cal kyr BP. Within the aforementioned cluster, two individuals, a male (PO/42) and a female (PU/072), from Oase and Urşilor, respectively, show similar data in terms of age and δ^{13}C and δ^{18}O variation, suggesting a similar environment and physiology for the cave bears of the two sites (separated by *c.* 200 km).

For six canine samples from Oase and Cioclovina we were able to partially identify the typology of several sampled dentine layers (i.e. dark or light layers) and to relate them with the isotopic data we obtained. Fig. 10 shows intra-tooth comparisons of the δ^{13}C and δ^{18}O profiles for the six analyzed samples. Except PO/041 (and to a lesser extent PC/061) – with an obvious relation between the two parameters along the entire profile (both parameters fluctuate in a similar manner) – for the other four samples, δ^{13}C and δ^{18}O have a certain relation only for short sequences. The light dentin layers, attributed to the spring-summer season do not always have the higher δ^{18}O values when compared with the dark layers, (attributed to the cold season) and vice versa. The same situation was recorded for the δ^{13}C profiles, with no relation between the type of dentin layer and the carbon isotopic values. Nonetheless, for three of the analyzed canines (PO/041, PC/058, PC/061), a dramatic decrease of both δ^{13}C and δ^{18}O values (the weaning period) was recorded at the first part of the profiles, corresponding with the 1st or 2nd dark (D) dentine layers (1st-2nd year of life). As such, correlation tests were ran for 17 canines (except PC/056: only two dentine samples) for testing if a relation between the δ^{13}C and δ^{18}O intra-tooth profiles occurred. Although for some samples a relation between the trend of the values of both δ^{13}C and δ^{18}O profiles was noticed, the tests did not provide statistically significant correlations (e.g. PO/041: R = 0.61; p = 0.150; Table S2). Instead, for three samples with no clear delimitation between the dentine layers (e.g. PU/073: R = 0.98; p = 0.02) the relation between δ^{13}C and δ^{18}O was statistically significant. However, the general correlation between δ^{13}C and δ^{18}O data obtained for analyzed canines had no significant correlation at all (R = 0.09; p = 0.306) and indicates no dependence among carbon and oxygen isotopes retrieved from canine dentine, throughout the juvenile period to adulthood for studied bears.

5. Conclusions

Based on δ^{13}C data profiles, our study shows that the weaning process in cave bears can be identified and attributed to the first and second dentine samples (presumably 1–2 years old). Serial dentine samples display large intra-tooth δ^{18}O variation of up to 8.2‰, reflecting seasonal variations in the δ^{18}O of meteoric water and a variable mobility of bears, regardless of sex. There is no correlation between intra-tooth δ^{13}C and δ^{18}O variability retrieved from canine dentine throughout the juvenile period to adulthood for cave bears. This study shows that bear ontogeny – when analyzing the dentine profiles – encompasses the juvenile period and adulthood, thus providing more data of δ^{13}C and δ^{18}O for a single individual and palaeoecological insights than before. Corroborating the δ^{13}C and δ^{18}O values with radiocarbon data may lead to correlations with past climatic and habitat changes during the lifetime of the cave bears. The CO_3 component of dentine apatite retrieved from cave bear canines proves to be a reliable proxy for reconstructing physiology behavior and palaeoclimatic conditions.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2019.109288.

Acknowledgments

Thirty years ago, Paul L. Koch, Daniel C. Fisher and David Dettman published in *Geology* (1989) a study where they highlighted, for the first time, how dentine serial sampling of bear's canine can reveal palaeoecological and palaeoenvironmental insights from the past. Their study was an inspiration to us and therefore, this paper is dedicated to them. The authors are indebted to the Apuseni Mountains Natural Park Administration and to Prof. Dr. B.P. Onac (School of Geosciences, University of South Florida, USA) for their field assistance and scientific support. Authors show their appreciation as well for the two

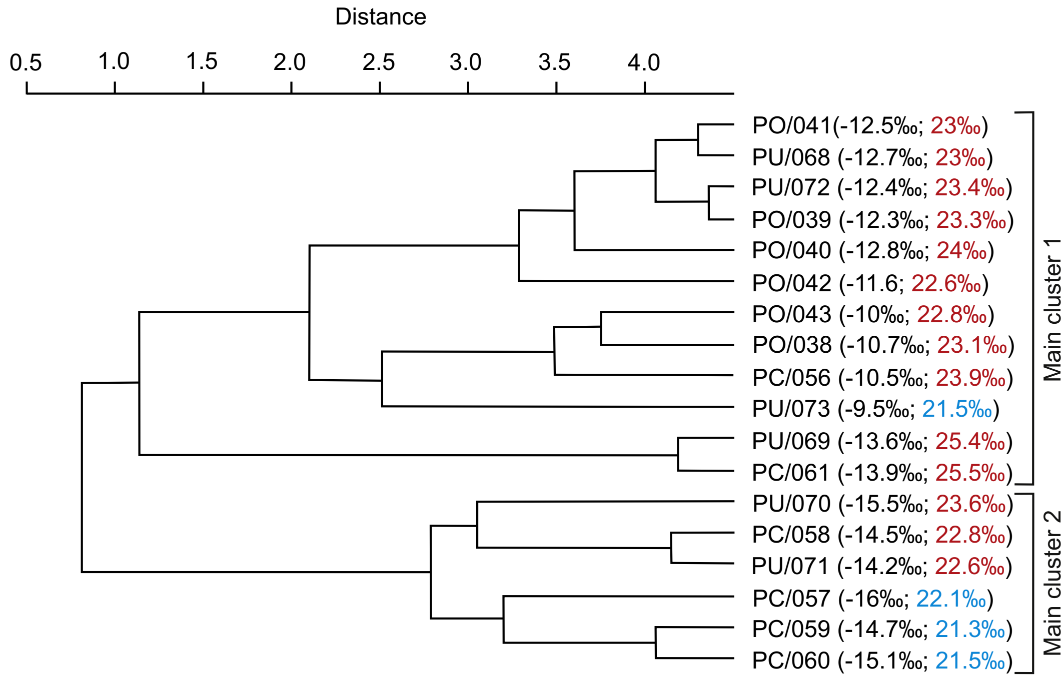

Fig. 8. Hierarchical clustering of average values of $\delta^{18}O$ and $\delta^{13}C$ of all dentine samples of each analyzed canine (N = 18) data from Urşilor, Oase and Cioclovina caves. Between brackets, with red $\delta^{18}O$ values indicating warm periods, and with blue $\delta^{18}O$ values indicating cooler periods; $\delta^{13}C$ values are given in black. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

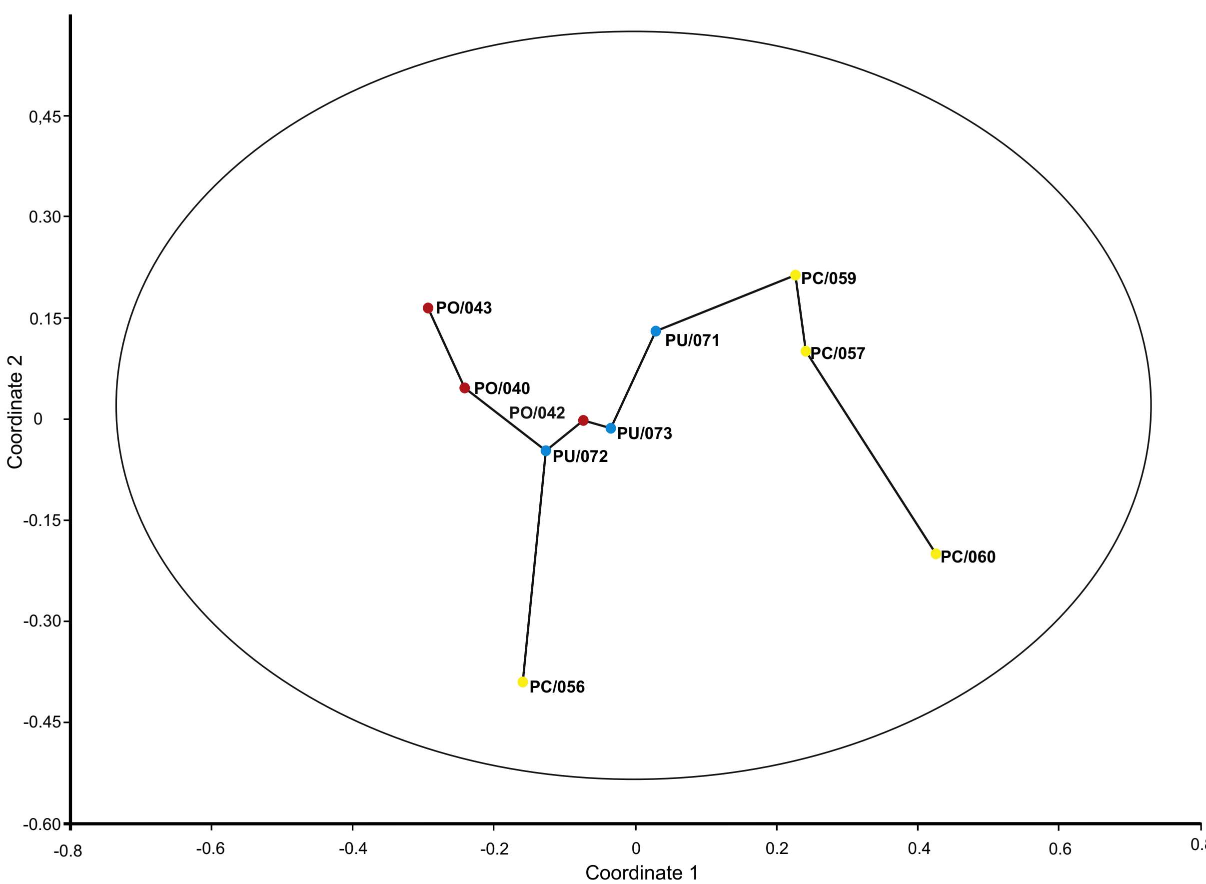

Fig. 9. Non-metric multidimensional scaling and minimum spanning tree in a two-dimensional visual representation constructed for the MIS 3 cave bears, from the analyzed sites, based on average values of $\delta^{13}C$, $\delta^{18}O$ data for each canine, and ^{14}C AMS data (N = 10) (first two coordinates represent 75% of the variance; stress = 0). Red dots – Oase, yellow dots – Cioclovina, blue dots – Urşilor. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

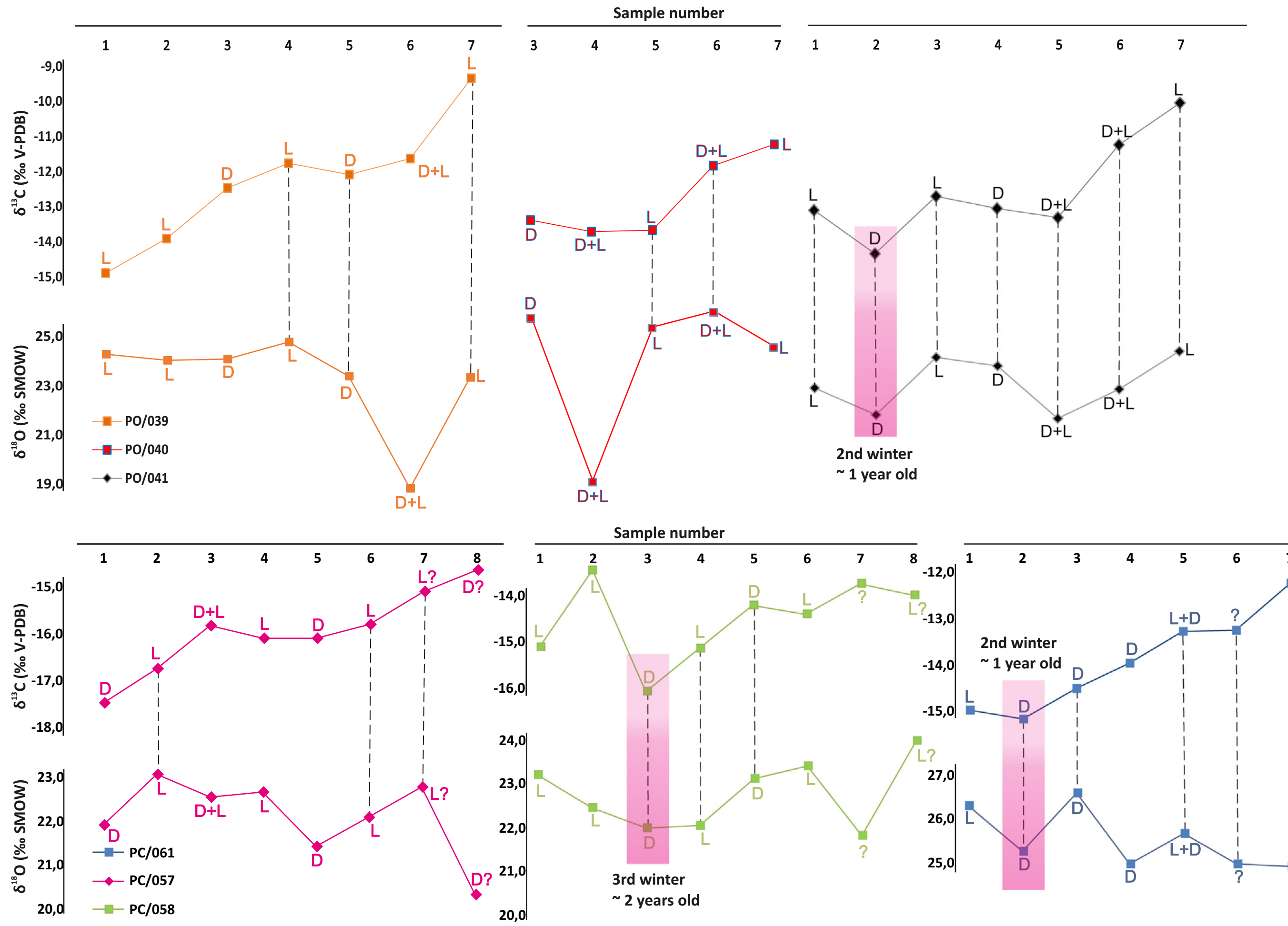

Fig. 10. δ^{13}C and δ^{18}O profiles for the cave bear canines with distinguishable dentin layers (D = dark layer; L = light layer; ? = unknown). Weaning period, as indicated with pink bands, was assigned only to those samples with visible δ^{13}C and δ^{18}O shifts. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

anonymous reviewers who improved significantly this paper. This work was financed by the Romanian National Authority for Scientific Research and Innovation, through grants PCE 197/2016, PCCF 16/2018 and EEA-Norway Grant #0126 (KARSTHIVES2).

References

Ambrose, S.H., Norr, L., 1993. Experimental evidence for the relationship of the carbon isotope ratios of whole diet and dietary protein to those of bone collagen and carbonate. In: Lambert, J.B., Grupe, G. (Eds.), Prehistoric Human Bone. Springer, Berlin Heidelberg, pp. 1–37.

Bjørn, D., Swenson, J.E., 2003. Family breakup in brown bears: are young forced to leave? J. Mammal. 84 (2), 536–540.

Bocherens, H., 2015. Isotopic tracking of large carnivore palaeoecology in the mammoth steppe. Quat. Sci. Rev. 117, 42–71.

Bocherens, H., Fizet, M., Mariotti, A., 1994. Diet, physiology and ecology of fossil mammals as inferred from stable carbon and nitrogen isotope biogeochemistry: implications for Pleistocene bears. Palaeogeograpy Palaeoclimatolology Palaeoecology 107, 213–225.

Bocherens, H., Koch, P.L., Mariotti, A., Geraads, D., Jaeger, J.J., 1996. Isotopic biogeochemistry (^{13}C, ^{18}O) of mammalian enamel from African Pleistocene hominid sites. Palaios 11, 306–318.

Bocherens, H., Stiller, M., Hobson, K.A., Pacher, M., Rabeder, G., Burns, J.A., Tutken, T., Hofreiter, M., 2011. Niche partitioning between two sympatric genetically distinct cave bears (*Ursus spelaeus* and *Ursus ingressus*) and brown bear (*Ursus arctos*) from Austria: isotopic evidence from fossil bones. Quat. Int. 245, 238–248.

Bronk Ramsey, C., 2017. Methods for summarizing radiocarbon datasets. Radiocarbon 59 (2), 1809–1833.

Bronk Ramsey, C., Higham, T., Bowles, A., Hedges, R., 2004. Improvements to the pre-treatment of bone at Oxford. Radiocarbon 46 (1), 155–163.

Clementz, M.T., 2012. New insight from old bones: stable isotope analysis of fossil mammals. J. Mammal. 93 (2), 368–380.

Constantin, S., Munteanu, C.M., Milota, Ş., Sarcină, L., Gherase, M., Rodrigo, R., Zilhão, J., 2013. The Ponor-Plopa Cave-system: description, sediments, and genesis. In: Constantin, S., Zilhão, J. (Eds.), Trinkaus, E. Oxford University Press, Life and Death at the Peştera cu Oase – A Setting for Modern Human Emergence in Europe, pp. 41–55.

Constantin, S., Robu, M., Munteanu, C.M., Petculescu, A., Vlaicu, M., Mirea, I., Kenesz, M., Drăguşin, V., Hoffman, D., Anechitei, V., Timar-Gabor, A., Roban, R.D., Panaiotu, C.G., 2014. Reconstructing the evolution of cave systems as a key to understanding the taphonomy of fossil accumulations: the case of Urşilor Cave (Western Carpathians, Romania). Quat. Int. 339–340, 25–40.

Dahle, B., Swenson, J.E., 2003. Home ranges in adult Scandinavian brown bears *Ursus arctos*: effect of population density, mass, sex, reproductive status and habitat type. J. Zool. 260, 329–335.

Debeljak, I., 1996. A simple preparation technique of cave bear teeth for age determination by cementum increments. Revue de Paleobiologie 15 (1), 105–108.

DeNiro, M.J., Epstein, S., 1978a. Influence of diet on the distribution of carbon isotopes in animals. Geochim. Cosmochim. Acta 42, 341–351.

DeNiro, M.J., Epstein, S., 1978b. Carbon isotopic evidence for different feeding patterns in two hyrax species occupying the same habitat. Science 201, 907–908.

Dotsika, E., Zisi, N., Tsoukala, E., Poutokis, D., Lykoudis, S.P., Giannakopoulos, A., 2011. Palaeoclimatic information from isotopic signatures of Late Pleistocene Ursus ingressus bone and teeth apatite (Loutra Arideas Cave, Macedonia, Greece). Quat. Int. 245 (2), 291–301.

Fahy, G.E., Boesch, C., Hublin, J.J., Richards, M.P., 2015. The effectiveness of using carbonate isotope measurements of body tissues to infer diet in human evolution: evidence from wild western chimpanzees (*Pan troglodytes verus*). J. Hum. Evol. 88, 70–78.

Fox, D.L., Fisher, D.C., 2004. Dietary reconstruction of Miocene Gomphotherium (Mammalia, Proboscidea) from the Great Plains region, USA, based on the carbon isotope composition of tusk and molar enamel. Palaeogeogr. Palaeoclimatol. Palaeoecol. 206, 311–335.

Fry, B., Brand, W., Mersch, F.J., Tholke, K., Garritt, R., 1992. Automated analysis systems for coupled δ^{13}C and δ^{15}N measurements. Anal. Chem. 64, 288–291.

Goslar, T., Czernik, J., Goslar, E., 2004. Low-energy ^{14}C AMS in Poznan radiocarbon

laboratory, Poland. Nuclear Instruments and Methods B 223–224, 5–11.
Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontol. Electron. 4 (1) (9 pp.).
Harrison, R.G., Katzenberg, M.A., 2003. Paleodiet studies using stable carbon isotopes from bone apatite and collagen: examples from Southern Ontario and San Nicolas Island, California. Journal of Anthropology and Archaeology 22 (3), 227–244.
Higham, T., Wild, E.M., 2013. Radiocarbon dating of the Peştera cu Oase faunal remains. In: Constantin, S., Zilhão, J. (Eds.), Trinkaus, E. Oxford University Press, Life and Death at the Peştera cu Oase – A Setting for Modern Human Emergence in Europe, pp. 77–85.
Hobson, K.A., Sease, J.L., 1998. Stable isotope analyses of tooth annuli reveal temporal dietary records: an example using Stellar sea lions. Marine Mammal Science 14 (1), 116–129.
Hoppe, K.A., Koch, P.L., Carlson, R.W., Webb, S.D., 1999. Tracking mammoths and mastodons: reconstruction of migratory behavior using strontium isotope ratios. Geology 27, 439–442.
Koch, P.L., Fisher, D.C., Dettman, D., 1989. Oxygen isotope variation in the tusks of extinct proboscideans: a measure of season of death and seasonality. Geology 17, 515–519.
Koch, P.L., Tuross, N., Fogel, M.L., 1997. The effects of sample treatment and diagenesis on the isotopic integrity of carbonate in biogenic hydroxylapatite. J. Archaeol. Sci. 24, 417–429.
Krajcarz, M.T., Krajcarz, M., 2014. The 200,000 year long record of stable isotopes ($\delta^{13}C$, $\delta^{18}O$) from cave bear (*Ursus spelaeus*) teeth from Biśnik Cave, Poland. Quat. Int. 339–340 (7), 119–130.
Krajcarz, M.T., Krajcarz, M., Marciszak, A., 2014. Paleoecology of bears from MIS 8–MIS 3 deposits of Biśnik Cave based on stable isotopes ($\delta^{13}C$, $\delta^{18}O$) and dental cementum analyses. Quat. Int. 326–327, 114–124.
Krofel, M., Filacorda, S., Jerina, K., 2010. Mating-related movements of male brown bears on the periphery of an expanding population. Ursus 21 (1), 23–29.
Krofel, M., Jonozovic, M., Jerina, K., 2012. Demography and mortality patterns of removed brown bears in a heavily exploited population. Ursus 23 (1), 91–103.
Krueger, H.W., Sullivan, C.H., 1984. Models for carbon isotope fractionation between diet and bone. In: Johnson, P.E. (Ed.), Turnland, J.F. American Chemical Society, Stable Isotopes in Nutrition ACS Symposium Series, pp. 205–220.
Lee-Thorp, J.A., Sponheimer, M., 2005. Opportunities and constraints for reconstructing palaeoenvironments from stable light isotope ratios in fossils. Geological Quarterly 49 (2), 195–204.
Lee-Thorp, J.A., Van Der Merwe, N.J., 1987. Carbon isotope analysis of fossil bone apatite. S. Afr. J. Sci. 83, 71–74.
Lee-Thorp, J.A., Sealy, J.C., Van Der Merwe, N.J., 1989. Stable carbon isotope ratio differences between bone collagen and bone apatite, and their relationship to diet. J. Archaeol. Sci. 16, 585–599.
Longinelli, A., 1984. Oxygen isotopes in mammal bone phosphate: a new tool for paleohydrological and paleoclimatological research? Geochim. Cosmochim. Acta 48 (2), 385–390.
Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K., 2019. Cluster Analysis Basics and Extensions. R package version 2.0.9.
Martin, J.E., Tacail, T., Balter, V., 2017. Non-traditional isotope perspectives in vertebrate palaeobiology. Palaeontology 60 (4), 485–502.
Matthews, C.J.D., Longstaffe, F.J., Ferguson, S.H., 2016. Dentine oxygen isotopes ($\delta^{18}O$) as a proxy for odontocete ditributions and movements. Ecology and Evolution 6 (14), 4643–4653.
McLellan, B., 1994. Density dependent population regulation in brown bears. In: Ninth International Conference on Bear Research and Management. Monograph Series 3, pp. 15–25.
Meleg, N.I., Westbury, M.V., Alberti, F., Gonzalez, J., Paijmans, J.L.A., Robu, M., Vlaicu, M., Bocherens, H., Hofreiter, M., Barlow, A., 2018. Population dynamics of Late Pleistocene cave bears in the Romanian Carpathians. Proceedings of BTAK Symposium. Băile Herculane, Romania, pp. 99–100.
Mundy, K.R.D., Fuller, W.A., 1964. Age determination in the grizzly bear. J. Wildl. Manag. 28, 863–866.
Nelson, D.E., Angerbjorn, A., Liden, K., Turk, I., 1998. Stable isotopes and the metabolism of the European cave bear. Oecologia 116, 177–181.
Onac, B.P., Effenberger, H.S., Collins, N.C., Kearns, J.B., Breban, R.C., 2011. Revisiting three minerals from Cioclovina Cave (Romania). Int. J. Speleol. 40 (2), 99–108.
Pacher, M., Stuart, A.J., 2009. Extinction chronology and palaeobiology of the cave bear (*Ursus spelaeus*). Boreas 38, 189–206.
Pietrowska, N., Goslar, T., 2002. Preparation of bone samples in the Gliwice radiocarbon laboratory for AMS radiocarbon dating. Isot. Environ. Health Stud. 38 (4), 267–275.
R Core Team, 2018. A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna Retrieved from. http://www.R-project.org/.
Rausch, R.L., 1961. Notes on the black bear, *Ursus americanus* Pallas, in Alaska, with particular reference to dentition and growth. Z. Sugetierk. 26, 77–107.
Rausch, R.L., 1967. Comparative development of the canine teeth in wild and captive black bears, *Ursus americanus* Pallas. Can. J. Zool. 45, 465–471.
Rausch, R.L., 1969. Morphogenesis and age-related structure of permanent canine teeth in the brown bear, *Ursus arctos* L., in Arctic Alaska. Z. Morph. Tiere 66, 167–188.
Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Bronk Ramsey, C., Buck, C.E., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Haflidason, H., Hajdas, I., Hatté, C., Heaton, T.J., Hoffmann, D.L., Hogg, A.G., Hughen, K.A., Kaiser, K.F., Kromer, B., Manning, S.W., Niu, M., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Staff, R.A, Turney, C.S.M., Van Der Plicht, J., 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. Radiocarbon 55 (4), 1869–1887.
Reinhard, E., De Torres, T., O'Neil, J., 1996. $^{18}O/^{16}O$ ratios of cave bear tooth enamel: a record of climate variability during the Pleistocene. Palaeogeogr. Palaeoclimatol. Palaeoecol. 126, 45–59.
Richards, M.P., Pacher, M., Stiller, M., Quilès, J., Hofreiter, M., Constantin, S., Zilhão, J., Trinkaus, E., 2008. Isotopic evidence for omnivory among European cave bears: Late Pleistocene Ursus spelaeus from the Peştera cu Oase, Romania. Proceedings of the National Academy of Sciences USA 105 (2), 600–604.
Robu, M., 2016. Age re-assessment of the cave bear assemblage from Urşilor Cave, northwestern Romania. Int. J. Speleol. 45 (2), 123–133.
Robu, M., Fortin, J., Richards, M., Schwartz, C., Wynn, J., Robbins, C.T., Trinkaus, E., 2013. Isotopic evidence for dietary flexibility among European Late Pleistocene cave bears (*Ursus spelaeus*). Can. J. Zool. 91, 227–234.
Robu, M., Wynn, G.J., Mirea, I.C., Petculescu, A., Kenesz, M., Puşcaş, C.M., Vlaicu, M., Trinkaus, E., Constantin, S., 2018. The diverse dietary profiles of MIS 3 cave bears from the Romanian Carpathians: insights from stable isotope ($\delta^{13}C$ and $\delta^{15}N$) analysis. Palaeontology 61 (2), 209–219.
Rountrey, A.N., Fisher, D.C., Vartanyan, S., Fox, D.L., 2007. Carbon and nitrogen isotope analyses of a juvenile woolly mammoth tusk: evidence of weaning. Quat. Int. 169, 166–173.
Sandberg, P.A., Sponheimer, M., Lee-Thorp, J., Van Gerven, D., 2014. Intra-tooth stable isotope analysis of dentine: a step toward addressing selective mortality in the reconstruction of life history in the archaeological record. Am. J. Phys. Anthropol. 155, 281–293.
Sauer, P.R., 1966. Determining sex of black bears from the size of the lower canine tooth. New York Fish and Game Journal 18, 140–145.
Sauer, P.R., Free, S., Browne, S., 1966. Age determination in black bears from canine tooth sections. New York Fish and Game Journal 18, 125–139.
Shackleton, N.J., Hall, M.A., 2001. Phase relationships between millennial-scale events 64,000–24,000 years ago. Paleoceanography 15, 565–569.
Skrzypek, G., Wiśniewski, A., Grierson, P.F., 2011. How cold was it for Neanderthals moving to Central Europe during warm phases of the last glaciation? Quat. Sci. Rev. 30, 481–487.
Soficaru, A., Petrea, C., Doboş, A., Trinkaus, E., 2007. The human cranium from the Peştera Cioclovina Uscată, Romania: context, age, taphonomy, morphology and paleopathology. Curr. Anthropol. 48, 611–619.
Stoneberg, R.P., Jonkel, C.J., 1966. Age determination of black bears by cementum layers. J. Wildl. Manag. 80, 411–414.
Sullivan, C.H., Krueger, H.W., 1981. Carbon isotope analysis of separate chemical phases in modern and fossil bone. Nature 292, 333–335.
Torres, De T.J., Quintero, I.A., Gomez, E.N., Mansilla, H.I., Martinez, C.D., 1978. Estudio comparativo de las mandíbulas de *Ursus spelaeus*, Rosemmuller – Heinrooth – *Ursus deningeri*, Von Reichenau y *Ursus arctos*, Linneo. Bol. Geol. Min. 89 (3), 203–222.
Tsoukala, E., Grandal-D'Anglande, A., 2002. Systeme de mesures sur le squelette d'Ursidae. Actes du Colloque d'Auberives-en-Royans. Etudes et recherche archéologiques de l'Université de Liège, pp. 265–287.
Vălenas, L., 1979. Studiu complex al zonei Valea Crăiasa-Valea Vârtoape, cu referire specială la Peştera Urşilor (Munţii Bihor). Nymphaea 7, 139–176.
Van Meerbeeck, C.J., Renssen, H., Roche, D.M., 2009. How did marine isotope stage 3 and last glacial maximum climates differ? – perspectives from equilibrium simulations. Climates of the Past 3, 33–51.
Wickham, H., 2009. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York, pp. 213. https://doi.org/10.1007/978-0-387-98141-3.