



Isotopic variability of cave bears ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$) across Europe during MIS 3



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ABSTRACT

Collagen, the organic fraction of bone, records the isotopic parameters of consumed food for carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$). This relationship of isotopic signature between diet and tissue is an important tool for the study of dietary preferences of modern and fossil animal species. Since the first information on the isotopic signature of cave bear was reported, numerous data from Europe have become available. The goal of this work is to track the geographical variation of cave bear collagen isotopic values in Europe during Marine Isotopic Stage 3 (about 60,000–25,000 yr BP). In this study the results of new $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic analyses of cave bear collagen from four Central-Eastern European sites are presented, as well as a review of all published isotopic data for cave bears of the same period. The main conclusion is a lack of geographical East-West pattern in the variations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of cave bear collagen. Moreover, no relationship was found between cave bear taxonomy and isotopic composition. The cave bears from Central-Eastern Europe exhibit $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values near the average of the range of Central, Western and Southern European cave bears. Despite the fact that most cave bear sites follow an altitudinal gradient, separate groups of sites exhibit shift in absolute values of $\delta^{13}\text{C}$, what disturbs an altitude-related isotopic pattern. The most distinct groups are: high Alpine sites situated over 1500 m a.s.l. – in terms of $\delta^{13}\text{C}$; and two Romanian sites Peștera cu Oase and Urșilor – in case of $\delta^{15}\text{N}$. Although the cave bear isotopic signature is driven by altitude, the altitudinal adjustment of isotopic data is not enough to explain the isotopic dissimilarity of these cave bears. The unusually high $\delta^{15}\text{N}$ signature of mentioned Romanian sites is an isolated case in Europe. Cave bears from relatively closely situated Central-Eastern European sites and other Romanian sites are more similar to Western European than to Romanian populations in terms of isotopic composition, and probably ecology.

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1. Introduction

Bears from the spelaeus-group (*Ursus ex gr. spelaeus* Rosemüller, 1794) represent large extinct ursids with the most abundant fossil remains in Late Pleistocene caves in Europe. Cave bears exhibit a large amount of variation in size and morphology (e.g., Kurtén, 1976; Rabeder et al., 2000; Baryshnikov and Puzachenko, 2011). The large geographical range across Europe, combined

with morphological and genetic diversity of cave bears, opens the possibility of some ecological flexibility for this extinct taxon (Bocherens, 2015). Based on morphological and genetic differences, several types of cave bears have been recognized (e.g., Hofreiter et al., 2002; Rabeder et al., 2008). In Europe, two genetic types were common and coexisted between around 60,000 and 24,000 years ago, corresponding to *Ursus spelaeus*, present in the western part of Europe, and *Ursus ingressus*, present in the eastern part of continent and expanding westward (Stiller et al., 2014). The occurrence of both types is documented in the western part of Central Europe, sometimes in contemporaneous close sites, as in

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the Totes Gebirge in Austria (Hofreiter et al., 2004a), while in other cases both types occurred in chronological succession, as in the Ach valley in southwestern Germany, where *U. ingressus* is present after the extirpation of *U. spelaeus* (Hofreiter et al., 2007; Münzel et al., 2011). The third genetic type recognized in Europe is *Ursus ladinicus*, known from several cave sites in Prealpine and Alpine region (Hofreiter et al., 2002). The cave bear remains from Caucasus represent another genetic form *Ursus kudarensis* (*Ursus "deningeri" kudarensis*), the sister group of the European cave bears, which split from the rest of the cave bears between 800 and 270 ka ago (Baryshnikov, 1998; Knapp et al., 2009). All these taxonomic types are regarded as generally ecologically similar, what was deduced from their isotopic signature (Bocherens, 2015), although some minor differences between local populations are observed (Bocherens et al., 2011b), and *U. kudarensis* and *U. ladinicus* forms seem to be ecologically the most distinct (Bocherens, 2015).

Cave bear was the first extinct species for which carbon and nitrogen stable isotopes were used to document diet (Bocherens et al., 1990, 1991). Early studies found nitrogen isotopic ratios as low as those of herbivorous species, suggesting an essentially vegetarian diet, and this view was confirmed by most of later studies (e.g., Bocherens et al., 1994, 1997, 2011a; Nelson et al., 1998; Münzel et al., 2014; Bocherens, 2015). Other palaeodietary proxies such as tooth microwear, ecomorphology and taphonomy have also suggested a herbivorous diet for this species (e.g., Ehrenberg, 1927; Kurtén, 1976; Stiner et al., 1998; Van Heteren et al., 2009; Münzel et al., 2014). In contrast, some morphometric analyses based on the craniodental traits of cave bears suggested a similar level of omnivory than modern omnivorous bears (Figueirido et al., 2009), and some studies based on tooth microwear and taphonomy suggested a more omnivorous diet (e.g., Quilès et al., 2006; Peigné et al., 2009). The method of using the stable isotopes of carbon and nitrogen to evaluate palaeodiets has been applied on cave bears from dozens of cave sites, but so far mostly in Western Europe (e.g., Bocherens et al., 1994, 2006, 2011a,b; Blant et al., 2010; Pacher et al., 2012; Bocherens, 2015), and fewer sites in Southern and South-Eastern Europe have been studied (e.g., Fernández-Mosquera et al., 2001; Richards et al., 2008; Pérez-Rama et al., 2011; Horacek et al., 2012; Robu et al., 2013; Trinkaus and Richards, 2013). Interestingly, some cave bears from two South-Eastern European sites (Urşilor and Peştera cu Oase, Romania) exhibited higher concentrations of heavier nitrogen isotope than other cave bear populations studied so far and therefore did not seem to follow the general pattern of the cave bear isotopic signal (Richards et al., 2008; Robu et al., 2013; Trinkaus and Richards, 2013). This phenomenon led to the suggestion that these Romanian cave bears may have occupied a higher trophic level than Western European cave bears (Richards et al., 2008; Robu et al., 2013).

This situation raises a question about the geographical variation of isotopic patterns in cave bear. Is the Romanian isotopic signature a local phenomenon, or is it typical for East European cave bear populations? Moreover, was this phenomenon caused by specific local conditions, or did it follow a geographical trend connected with the climatic divergence between oceanic conditions of Western Europe and more continental climates of Eastern Europe? However, since two other Romanian sites (Cioclovina and Muierii) showed carbon and nitrogen isotopic signatures similar to most other cave bears (Robu et al., 2013), a continental-scale climatic hypothesis is less likely. This issue of cave bear palaeoecology is important to better address the possible interactions between this large mammal species and prehistoric human populations in Europe (e.g., Münzel and Conard, 2004; Wojtal et al., 2015), as well as to understand the causes of its final demise prior to the onset of the Late Glacial Maximum (Pacher and Stuart, 2009).

An in-depth discussion on the isotopic differences (and

ecological differences) between cave bears from Romanian sites and other Eastern and Western European sites is problematic, as isotopic data from cave bear collagen are still rare for Eastern Europe. The lack of data from parts of Eastern Europe other than Romania makes it difficult to evaluate a geographical extent of the phenomenon of high $\delta^{15}\text{N}$ values of two cave bear assemblages.

The goal of this work is to complete the picture of cave bear isotopic variability by adding new data from Central-Eastern Europe (Austria, Poland and Slovakia), and then to evaluate the distribution of C and N stable isotopes among European cave bears.

2. Principles of isotopic tracking of cave bear diet

2.1. Isotopes of C and N in terrestrial foodwebs

The organic fraction of bone, essentially made of collagen, records the isotopic parameters of consumed food for carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) (e.g., DeNiro and Epstein, 1978; Bryant and Froelich, 1995; Cerling and Harris, 1999; Bocherens, 2000; Lee-Thorp and Sponheimer, 2003; Passey et al., 2005; Koch, 2007). The carbon isotopic composition in ecosystems depends on plant communities and differs between dense and light forests, grasslands, deserts and lichen-dominated environments (DeNiro and Epstein, 1978; Bocherens, 2003). It is primarily related to the photosynthetic pathways and secondarily to environmental conditions that affect plant physiology, such as aridity, temperature, CO_2 partial pressure, salinity, light conditions, and altitude (e.g., Körner et al., 1991; Fricke, 2007; Diefendorf et al., 2010; Zhu et al., 2010). In addition, a canopy effect has an impact on the carbon isotopic signatures in ecosystems. Indeed, under dense vegetation cover, the isotopic signature of CO_2 in air becomes ^{13}C -depleted, because the lighter carbon, released by decaying organic material and soil respiration, is recycled during photosynthesis, and because of increased carbon fractionation during low-light photosynthesis (Van der Merve and Medina, 1991; Fricke, 2007; Drucker et al., 2008; Bonafini et al., 2013). The primary isotopic signal of nitrogen in ecosystems is essentially linked to microbial soil activity (Mariotti et al., 1980; Amundson et al., 2003; Sah and Brumme, 2003). The lowest $\delta^{15}\text{N}$ values are found in acidic soils (Mariotti et al., 1980; Rodière et al., 1996) and in pioneer vegetation (Hobbie et al., 1998). Factors such as altitude (Mariotti et al., 1980), cultivation (Riga et al., 1971), high grazing pressure (Schulze et al., 1998), salinity (Page, 1995) and aridity (Ambrose and DeNiro, 1986; Heaton et al., 1986; Bocherens et al., 2014a; Craine et al., 2015) also modify the nitrogen isotopic signal in plants.

The isotopic signal of primary sources is changed along with trophic level in ecosystems, due to animal metabolism (e.g., DeNiro and Epstein, 1981; Roth and Hobson, 2000; Bocherens, 2000, 2004; Bocherens and Drucker, 2003; Seminoff et al., 2009). The $\delta^{15}\text{N}$ values increase on average 3–5‰ at each trophic step (Minagawa and Wada, 1984; Schoeninger, 1985; Bocherens and Drucker, 2003), while $\delta^{13}\text{C}$ values increase 0.8–1.3‰. The phenomenon of carbon and nitrogen isotopic fractionation is a principle of isotopic ecology and palaeoecology that is used to reconstruct a position of a fossil animal in a trophic web, especially in the case of opportunistic feeders such as bears (e.g., DeNiro and Epstein, 1978; Ambrose and DeNiro, 1986; Bocherens et al., 1994, 2011b, 2014a; Fizet et al., 1995; Hilderbrand et al., 1996; Hobson et al., 2000; Vila Taboada et al., 2001; Richards et al., 2008; García et al., 2009; Drucker et al., 2011; Robu et al., 2013).

Nursing causes an additional effect on C and N isotopic composition similar to a higher trophic level, since milk consumed by young mammals during suckling will place them one trophic level higher than adults of the same species (Fogel et al., 1989; Bocherens, 2000; Jenkins et al., 2001; Dalerum et al., 2007).

2.2. Isotopes of C and N in bear collagen

Bears from middle and high latitudes, including cave bears, are unique among large mammals as they hibernate (e.g., Nelson et al., 1975; Stiner et al., 1998), which has consequences on their isotopic fractionation (e.g., Bocherens et al., 1994; Nelson et al., 1998; Lidén and Angerbjörn, 1999; Fernández-Mosquera et al., 2001; Bocherens, 2004; Pérez-Rama et al., 2011). The winter sleep has a significant impact on their physiology, as it causes changes in the metabolism of amino acids. During winter sleep the animals do not defecate, and the nitrogen-containing waste is reabsorbed (Nelson et al., 1975). The reuse of the urea component increases the trophic level of amino acids and leads to an increase in the $\delta^{15}\text{N}$ signature. During hibernation bears do not eat, but use fat stores. The typical relationship between $\delta^{13}\text{C}$ and different tissues established for modern animal follows the pattern of highest $\delta^{13}\text{C}$ in hair, then decreasing in brain, muscle and liver, with most depleted $\delta^{13}\text{C}$ in fat (Tieszen et al., 1983; De Smet et al., 2004). Therefore the bear tissues formed during hibernation may record more negative values of $\delta^{13}\text{C}$ (Hilderbrand et al., 1996; Bocherens et al., 1997). However, it is claimed that the effect of hibernation affects mostly bones of young individuals, while bones of adults seem to record a diet-related isotopic signature (Bocherens, 2004; Pérez-Rama et al., 2011). Therefore palaeodietary studies using C and N isotopes in ancient bears should use bones of adult individuals (Bocherens, 2004).

3. Material and methods

In the present study, new isotopic data from cave bears from Central-Eastern Europe were obtained, and compared to previously published data for cave bears from the rest of Europe.

3.1. Sites from Central-Eastern Europe

The studied faunal material comes from four Central-Eastern European caves located in Austria, Poland and Slovakia (Fig. 1).

3.1.1. Nietoperzowa Cave

Nietoperzowa Cave is located in the Kraków-Częstochowa

Upland, in Będkowska Valley, Poland (N 50°11'38.0" E 19°46'29.0"). The entrance elevation is located at an altitude of 438 m a.s.l. The archaeological exploration started at the beginning of 20th century and was terminated in 1969, with the most extensive excavation during 1953–1969. It is one of the most important cave sites in Poland with cultural layers of the Jerzmanowician, and sediments treated as the stratotype profile of late Middle and Late Pleistocene cave sediments (Różycki, 1967; Madeyska, 1982; Mojski, 1985; Lindner, 1992). The stratigraphy was based on geological, palaeontological and archaeological evidence (Chmielewski, 1961, 1975; Kowalski, 1961; Madeyska-Niklowska, 1969; Wysoczański-Minkowicz, 1969; Madeyska, 1981; Krajcarz and Madeyska, 2010). Palaeontological studies have been published by Wojtal (2007). Bone assemblage comprises over 11,000 of remains, representing mostly carnivorans (*U. ex gr. spelaeus*, *Canis lupus*, *Meles meles*, *Vulpes lagopus*, *V. vulpes*, *Gulo gulo*, *Felis silvestris*, *Panthera spelaea*) and in small number ungulates (*Mammuthus primigenius*, *Equus* sp., *Coelodonta antiquitatis*, *Sus scrofa*, *Capreolus capreolus*, *Cervus elaphus*, *Megaloceros giganteus*, *Rangifer tarandus*, *Bos/Bison* sp., *Ovibos moschatus*). The material is clearly dominated by cave bear bones (more than 90% of the large mammal assemblage), some bones bear traces of cut marks made by Palaeolithic hunters. The studied material comes from the following layers: 1 (mixed sediments), 3–8 (MIS 3), 9 (MIS 4), 10–16 (MIS 5–6) (Table 1).

3.1.2. Perspektywiczna Cave

Perspektywiczna Cave is situated in the Kraków-Częstochowa Upland, in Udorka Valley, Poland (N 50°26'34.0" E 19°46'01.0"), about 28 km north of Nietoperzowa Cave. The site, with the entrance located at 345 m a.s.l., was discovered in 2012. During the excavation in 2013 the sediments with abundant fossil faunal remains were discovered. All of the studied fossil remains come from one layer; the AMS ^{14}C dating of the bones yielded ages of around 40,000 years BP, i.e. representing MIS 3 (Table 1). From this layer about 750 mammalian bones were excavated, consisting of several carnivorans species: *U. ex gr. spelaeus*, *V. vulpes*, *M. meles*, *F. silvestris*, *P. spelaea*, *Crocota crocuta spelaea*; and ungulate species: *C. antiquitatis*, *C. capreolus*, *M. giganteus*, *R. tarandus*, *Bos/Bison* sp.

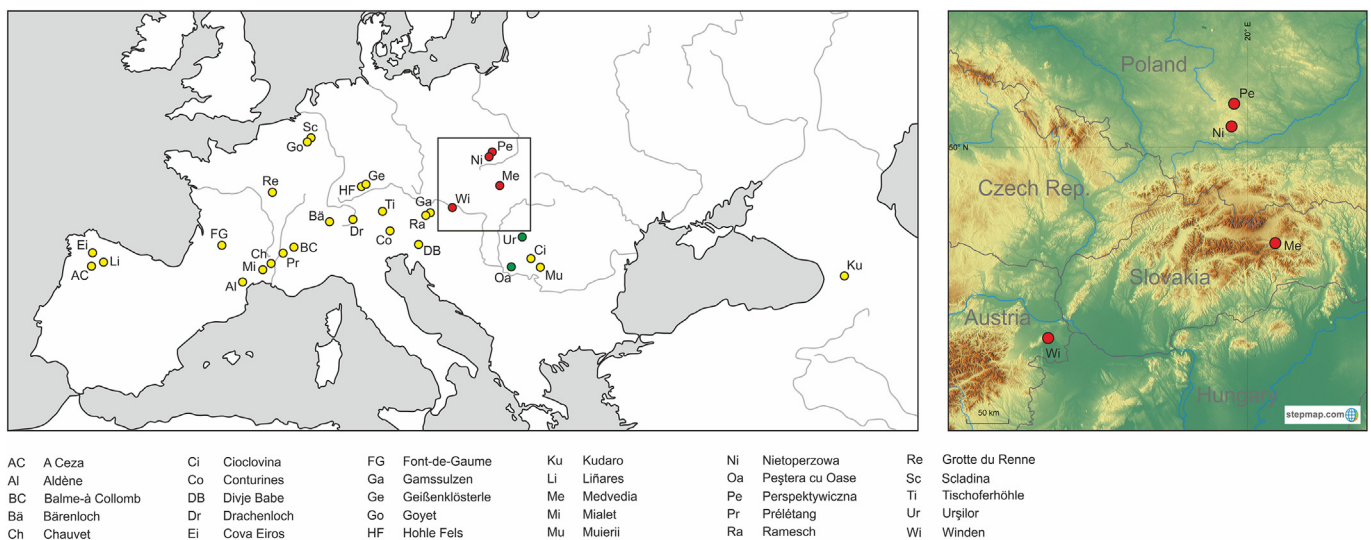


Fig. 1. Location of the newly studied sites (red spots, the more detail map to the right) and other European sites analysed in this paper (green spots – sites with unusually high $\delta^{15}\text{N}$ values according to Richards et al., 2008 and Robu et al., 2013; yellow spots – other sites). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
List of cave bear fossil samples from Austrian, Polish and Slovakian sites and of isotopic results and direct radiocarbon dating of cave bear bones (* – bone equivalent, bone – data for whole bone or tooth, coll – data for extracted collagen).

Lab. no.	Collection	Site	MIS	Bone/tooth	%N _{bone}	%C _{bone}	%C _{coll}	%N _{coll}	C/N _{coll}	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	^{14}C age determination (calibrated age acc. To IntCal2013, 95.4%)
IN-29	ISEA	Nietoperzowa Cave	3 ?	Metapodium	1.7	6.4	41.0	14.7	3.2	−21.2	2.7	
IN-55	ISEA	Nietoperzowa Cave	3	Phalanx 1	0.5	6.9	32.8	11.4	3.4	−21.8	4.2	
IN-56	ISEA	Nietoperzowa Cave	3	Phalanx 1	1.1	6.2	38.1	13.3	3.3	−21.2	2.1	26,800 ± 300 BP Poz-62582 (31,330–30,493 calBP)
IN-25	ISEA	Nietoperzowa Cave	3	Metatarsus V	0.7	4.6	35.4	12.6	3.3	−21.2	1.4	
IN-24	ISEA	Nietoperzowa Cave	3	Metacarpus III	0.6	4.9	36.6	13.0	3.3	−21.2	2.7	28,840 ± 190 BP Poz-56744 (33,587–32,418 calBP) 29,800 ± 300 BP Poz-62581 (34,515–33,441 calBP)
IN-26	ISEA	Nietoperzowa Cave	3	Phalanx 1	2.6	9.5	43.8	15.6	3.3	−21.1	3.8	26,190 ± 250 BP Poz-63860 (30,942–29,782 calBP)
IN-31	ISEA	Nietoperzowa Cave	3	Phalanx 1	1.7	7.1	39.5	14.1	3.3	−21.1	2.1	29,970 ± 350 BP Poz-63861 (34,703–33,533 calBP)
IN-54	ISEA	Nietoperzowa Cave	3	Metatarsus III	3.3	10.8	40.6	14.4	3.3	−21.3	3.0	32,550 ± 600 BP Poz-56639 (36,482–34,486 calBP) 31,500 ± 500 BP Poz-63862 (38,370–35,355 calBP)
IN-15	ISEA	Nietoperzowa Cave	3	Metatarsus III	0.5	4.9	31.1	11.0	3.3	−21.3	2.5	
IN-01	ISEA	Nietoperzowa Cave	3	Canine	3.2	10.6	43.4	15.5	3.3	−22.5 * −22.1	7.0 * 5.1	
IN-02	ISEA	Nietoperzowa Cave	3	Mandibula	0.4	3.9	10.6	3.7	3.4	−22.2	3.3	
IN-09	ISEA	Nietoperzowa Cave	3	Tibia	0.5	4.2	20.7	7.2	3.3	−21.8	2.4	
IN-32	ISEA	Nietoperzowa Cave	3	Metatarsus III	0.4	3.9	6.5	1.6	4.6	−24.4	2.5	
IN-33	ISEA	Nietoperzowa Cave	3	Metatarsus V	0.3	3.4	–	–	–	–	–	
IN-21	ISEA	Nietoperzowa Cave	4	Metapodium	1.0	5.4	31.2	11.0	3.3	−21.2	3.6	
IN-49	ISEA	Nietoperzowa Cave	5	Metatarsus I	0.7	4.4	28.8	9.8	3.4	−21.5	3.9	
IN-04	ISEA	Nietoperzowa Cave	5	Mandibula	0.2	3.1	–	–	–	–	–	
IN-28	ISEA	Nietoperzowa Cave	5	Phalanx I	0.3	3.2	–	–	–	–	–	
IN-03	ISEA	Nietoperzowa Cave	5	Metatarsus IV	2.1	7.6	41.9	14.8	3.3	−20.5	2.5	
IN-46	ISEA	Nietoperzowa Cave	5 (5e?)	Metatarsus IV	3.5	11.3	42.0	15.0	3.3	−21.3	1.7	
IN-60	ISEA	Nietoperzowa Cave	5 (5e?)	Metatarsus I	2.4	8.1	37.6	13.2	3.3	−21.2	2.8	
IN-22	ISEA	Nietoperzowa Cave	5 (5e?)	Metatarsus III	3.0	9.7	41.1	14.6	3.3	−21.0	2.1	
IN-30	ISEA	Nietoperzowa Cave	6	Phalanx 1	2.7	9.1	41.0	14.7	3.3	−23.2	2.8	
IN-23	ISEA	Nietoperzowa Cave	6?	Metacarpus V	0.4	3.2	7.4	2.6	3.3	−22.1	1.7	
IN-19	ISEA	Nietoperzowa Cave	6?	Metacarpus IV	0.2	2.9	–	–	–	–	–	
IN-20	ISEA	Nietoperzowa Cave	6?	Cranium	0.1	1.8	–	–	–	–	–	
IP-05	IGS	Perspektywiczna Cave	3	Mandibula	2.5	9.4	41.1	14.8	3.2	−21.2	1.9	
IP-06	IGS	Perspektywiczna Cave	3	Mandibula	3.4	11.1	43.8	15.9	3.2	−21.5	5.1	40,200 ± 1200 BP Poz-61114 calBP)

IP-09	IGS	Perspektywiczna Cave	3	Metacarpus IV	4.0	12.5	39.5	14.2	3.2	–21.4	3.3	39,500 ± 1000 BP Poz-63863 (45,235–42,025 calBP) 41,600 ± 1400 BP Poz-61115 (48,500–42,932 calBP)
IP-13	IGS	Perspektywiczna Cave	3	Mandible	1.9	7.6	30.7	10.4	3.4	–21.3	4.1	
IP-14	IGS	Perspektywiczna Cave	3	Phalanx 3	3.5	11.7	41.6	14.5	3.3	–21.2	3.0	
IP-15	IGS	Perspektywiczna Cave	3	Vertebra	3.5	11.4	43.3	15.2	3.3	–21.1	2.3	
IP-16	IGS	Perspektywiczna Cave	3	Fibula	2.6	9.4	39.7	13.7	3.4	–21.9	2.7	
IP-17	IGS	Perspektywiczna Cave	3	Fibula	3.8	12.2	42.8	15.0	3.3	–21.7	4.1	
IP-18	IGS	Perspektywiczna Cave	3	Metacarpus I	3.2	10.9	40.7	14.3	3.3	–21.2	2.4	
IP-19	IGS	Perspektywiczna Cave	3	Metatarsus IV	–	–	29.0	9.8	3.5	–21.0	1.6	
MJ-01	SM	Medvedia Cave	3	Metatarsus V	4.2	13.2	42.9	15.7	3.2	–20.7	1.4	
MJ-02	SM	Medvedia Cave	3	Metatarsus III	3.5	12.9	43.2	15.7	3.2	–21.0	1.9	
MJ-03	SM	Medvedia Cave	3	Metacarpus V	3.0	11.7	41.7	14.9	3.3	–21.0	3.1	
MJ-04	SM	Medvedia Cave	3	Metacarpus III	4.0	12.8	43.3	15.5	3.3	–20.9	1.9	
MJ-05	SM	Medvedia Cave	3	Metacarpus V	2.2	10.9	38.6	13.9	3.2	–21.0	2.3	
MJ-06	SM	Medvedia Cave	3	Metacarpus III	3.7	12.0	43.3	15.7	3.2	–21.0	2.2	
MJ-07	SM	Medvedia Cave	3	Metacarpus II	3.0	9.9	42.9	15.4	3.3	–21.3	1.5	
MJ-08	SM	Medvedia Cave	3	Metatarsus IV	3.7	12.1	44.7	15.8	3.3	–21.1	1.5	
MJ-09	SM	Medvedia Cave	3	Metacarpus II	3.8	12.9	39.6	14.2	3.2	–21.0	1.9	
MJ-10	SM	Medvedia Cave	3	Metacarpus IV	3.1	10.9	43.1	15.3	3.3	–20.7	3.7	
MJ-11	SM	Medvedia Cave	3	Metatarsus V	3.2	10.7	42.6	15.0	3.3	–20.9	2.8	
MJ-12	SM	Medvedia Cave	3	Metatarsus IV	3.6	11.4	43.9	15.1	3.4	–20.8	0.8	
MJ-13	SM	Medvedia Cave	3	Metatarsus II	3.5	12.3	43.4	15.5	3.3	–21.4	1.8	
MJ-14	SM	Medvedia Cave	3	Metatarsus I	3.7	12.8	43.6	15.6	3.3	–21.0	2.3	
MJ-15	SM	Medvedia Cave	3	Metatarsus I	2.9	10.5	44.0	15.2	3.4	–20.8	1.1	
MJ-16	SM	Medvedia Cave	3	Phalanx 1	3.9	12.3	41.8	14.9	3.3	–20.7	0.8	
MJ-17	SM	Medvedia Cave	3	Phalanx 1	2.7	10.4	43.8	15.3	3.3	–21.2	1.8	
MJ-18	SM	Medvedia Cave	3	Phalanx 2	2.5	9.5	44.3	15.5	3.3	–21.0	1.7	
MJ-19	SM	Medvedia Cave	3	Phalanx 2	3.4	12.4	45.2	15.5	3.4	–20.8	1.3	
MJ-20	SM	Medvedia Cave	3	Metatarsus III	0.8	4.4	42.9	14.7	3.4	–20.9	1.6	
LPZ-17	SMB, IP	Winden	3	Metapodial	–	–	33.1	11.9	3.3	–21.8	3.9	
LPZ-18	SMB, IP	Winden	3	Metapodial	–	–	26.6	9.7	3.2	–22.0	3.3	
LPZ-19	SMB, IP	Winden	3	Metapodial	–	–	32.5	11.5	3.3	–21.5	1.9	
LPZ-20	SMB, IP	Winden	3	Metapodial	–	–	38.8	13.7	3.3	–22.0	4.3	
LPZ-21	SMB, IP	Winden	3	Metapodial	–	–	39.3	13.9	3.3	–21.5	3.5	
LPZ-22	SMB, IP	Winden	3	Metapodial	–	–	33.1	11.8	3.3	–22.0	3.3	
LPZ-23	SMB, IP	Winden	3	Metapodial	–	–	36.8	13.2	3.3	–21.7	2.8	
LPZ-24	SMB, IP	Winden	3	Metapodial	–	–	29.6	10.5	3.3	–21.7	1.7	
LPZ-25	SMB, IP	Winden	3	Metapodial	–	–	35.7	12.7	3.3	–21.9	3.8	
LPZ-26	SMB, IP	Winden	3	Metapodial	–	–	28.4	10.1	3.3	–21.9	3.4	
LPZ-27	SMB, IP	Winden	3	Metapodial	–	–	24.5	8.8	3.3	–21.8	3.8	
LPZ-28	SMB, IP	Winden	3	Metapodial	–	–	27.6	10.9	2.9	–21.5	2.1	

ISEA = Institute of Systematics and Evolution of Animals of the Polish Academy of Sciences, Kraków (Poland).

IGS = Institute of Geological Sciences of the Polish Academy of Sciences, Warszawa (Poland).

SM = Spiš Museum in Spišská Nová Ves (Slovakia).

SMB = State Museum of Burgenland in Eisenstadt; IP = Institute of Palaeontology, University of Vienna (Austria).

3.1.3. Medvedia Cave

Medvedia Cave is located on the south-eastern extremity of the Glac Plateau within the territory of the Slovenský Raj Mountains, eastern Slovakia (N 48°54'56.5" E 20°23'54.1"), with the entrance at an altitude of 905 m a.s.l. The cave was discovered in 1952 and the first palaeontological investigations were started by Fejfar (1953) and Janáček and Schmidt (1965). The analysed cave bear remains (*U. ingressus*) come from one fossiliferous layer of the cave part "Cintorín jaskynných medvedov" ("Cave Bears Cemetery"). This layer has been dated to the MIS 3 period, between 40,000 and 50,000 years BP, as confirmed by AMS radiocarbon dating (Sabol et al., 2008). Preliminary palaeontological studies have been presented by Sabol et al. (2008). Apart from remains of cave bears (forming the majority of all found mammalian fossils), the fossil record contains also findings of *C. lupus*, *P. spelaea*, *G. gulo*, and *Lepus* sp. Osteological remains of *U. arctos*, *V. vulpes*, *Caprinae* gen. et spec. indet. as well as birds (Galliformes? gen. et spec. indet.) from Holocene layers complements the whole faunal assemblage from the site.

3.1.4. Winden

Winden cave (Widener Bärenhöhle) is located in the mountains of Leithagebirge, North Burgenland, about 3 km north of the village Winden am See, Austria. The cave is situated at 190 m a.s.l. This site has two entrances and is about 45 m long, 20 m broad and only 1.60 m high. The first collection of fossils took place in the cave in 1923. Under the direction of Ehrenberg the palaeontological excavations were carried out from the year 1929 till 1931. The recovered fossil material is archived at the Institute of Palaeontology and in the State Museum of Burgenland in Eisenstadt (Döppes and Rabeder, 1997). The sediments were strongly disturbed by fox dens (from *V. vulpes*) and therefore the differences between the layers could not be distinguished. The fossil remains of the large mammals, consisting of *U. ingressus*, *U. arctos priscus*, *C. crocuta spelaea* and *C. lupus*, date back to the Middle Würmian warm period (MIS 3). However, in the cave they are compounded with the micro-vertebrate fossils of the Late Glacial period and the Early Holocene. One cave bear bone from this site was AMS radiocarbon dated to 38,500 ±450/–430 years BP (Pacher, 2003). For cave bears from this site genetic studies are available (Hofreiter et al., 2004b; Rabeder et al., 2008).

3.2. Fossil material

The material includes 35 remains of cave bear from the Polish sites, 23 remains from the Slovakian site (Table 1), and 12 remains from the Austrian site. In addition, several bones and tooth of carnivores and ungulates from the same sites were sampled (Table 2) to achieve a wider context of ecosystems where the bears lived.

The sampled remains were bones with exception of two cases of teeth: the cave bear canine from Nietoperzowa Cave no. IN-01 and the wolf canine no. MJ-23 from Medvedia Cave. The sample no. IN-01 was taken from a tooth still attached to its mandible that was sampled as IN-02. All studied remains represent only adult specimens. The samples of cave bear bones chosen from Nietoperzowa and Perspektywiczna Caves were AMS radiocarbon dated (Poznań Radiocarbon Laboratory, Poland) to confirm the geological age of the bone assemblages (Table 1).

The palaeogenetic analysis confirmed that bears from Medvedia Cave and Winden belong to *U. ingressus* genetic type (Hofreiter et al., 2004b; Rabeder et al., 2008; Sabol et al., 2008). The detailed taxonomy of the cave bears from Nietoperzowa and Perspektywiczna Caves has not yet been investigated. Until now, the palaeogenetic analysis of cave bears from other sites in Poland

yielded the *U. ingressus* type (Baca et al., 2012, 2014; Popovic et al., 2015) for each analysed site. Also only *U. ingressus* type has been identified in the neighbouring territories (Stiller et al., 2014). Therefore it is very likely that the cave bears from Nietoperzowa and Perspektywiczna Caves also represent the same taxonomic unit.

3.3. Isotopic values from Western, Central and Southern Europe

To correlate the results for Central-Eastern European cave bears with other parts of Europe, we used the previously published results for Western, Central and Southern Europe. Only sites within the chronological framework of MIS 3 (about 60,000–25,000 yr BP) that yielded isotopic results for at least three specimens were chosen. This comprises 26 sites from different regions of Europe (Fig. 1) within altitudinal range from 125 to 2800 m a.s.l. A complete list of locations, together with average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of cave bear collagen and standard deviation is given in Table 3 along with references. The complete list of isotopic values in specimens from presented sites is shown in the Appendix. Additional sites with single isotopic analysis of cave bear remains are also presented in Appendix.

3.4. Methods of isotopic analysis

For each specimen, a small fragment was carefully sawn with a dremmel rotating tool equipped with a circular diamond-coated blade, ultrasonicated in acetone and water, rinsed with distilled water, dried and crushed to a powder of <0.7 mm grain size (Bocherens et al., 1997). Then an aliquot of around 5 mg was used to measure the nitrogen content (%N) of the whole bone, in order to screen out samples with excessive collagen loss (Bocherens et al., 2005). For instance, fresh bones contain 4% nitrogen while ancient bones with less than 0.4% nitrogen usually fail to yield good collagen (Bocherens et al., 2005). The measurements were performed using a Vario EL III elemental analyser using Sulfanilic acid from Merck as internal standard. The mean standard errors were better than 0.05% for %N.

The collagen was purified according to a well-established protocol (Bocherens et al., 1997). The elemental and isotopic measurements were performed at the Geochemical unit of the Department of Geosciences at the University of Tübingen (Germany), using an elemental analyser NC 2500 connected to a Thermo Quest Delta + XL mass spectrometer. The elemental ratios C/N were calculated as atomic ratios. The isotopic ratios are expressed using the "δ" (delta) value as follows: $\delta^{13}\text{C} = [(^{13}\text{C}/^{12}\text{C})_{\text{sample}} / (^{13}\text{C}/^{12}\text{C})_{\text{standard}} - 1] \times 1000\text{‰}$, and $\delta^{15}\text{N} = [(^{15}\text{N}/^{14}\text{N})_{\text{sample}} / (^{15}\text{N}/^{14}\text{N})_{\text{standard}} - 1] \times 1000\text{‰}$. The international standards are V-PDB for $\delta^{13}\text{C}$ values, and atmospheric nitrogen (AIR) for $\delta^{15}\text{N}$ values. Measurements were normalized to $\delta^{13}\text{C}$ values of USGS 24 ($\delta^{13}\text{C} = -16.0\text{‰}$) and to $\delta^{15}\text{N}$ values of IAEA 305 A ($\delta^{15}\text{N} = 39.8\text{‰}$). Analytical error, based on within-run replicate measurement of laboratory standards (albumen, modern collagen, USGS 24, IAEA 305 A), was $\pm 0.1\text{‰}$ for $\delta^{13}\text{C}$ values and $\pm 0.2\text{‰}$ for $\delta^{15}\text{N}$ values.

The reliability of the isotopic signatures of the extracted collagen was addressed using their chemical composition (%C, %N, and C/N ratios). These values must be similar to those of collagen extracted from fresh bone to be considered reliable for isotopic measurements and radiocarbon dating. Several studies have shown that collagen with atomic C/N ratios lower than 2.9 or higher than 3.6 is altered or contaminated and should be discarded, as well as extracts with %N <5% (e.g., DeNiro, 1985; Ambrose, 1990).

3.5. Statistical processing

For statistical analyses only samples dated to MIS 3 were chosen, to be sure that we compare data derived from the cave bears that lived during one period. Therefore the results obtained for layers 1 and 9–14 from Nietoperzowa Cave were excluded from the calculations. For each site the average (arithmetic mean) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were calculated and all further processing was applied to average values.

The PAST software (version 2.17b, Hammer et al., 2001) was used for statistical analysis. To document possible similarities between the isotopic composition of cave bear populations from European sites we applied the multivar cluster analysis of average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data from each site (separately altitudinal adjusted data and raw data) using the Euclidean distance and paired group algorithm, recommended for environmental data processing (Hammer, 1999–2014). The number of bootstrap replicates *Boot. N* = 1000 was given. To track the possible relationships between the isotopic compositions of cave bear remains from different sites and their geographic distribution, the parametric correlation was used with Pearson's *r* coefficient. The significance of correlation showing that the columns are uncorrelated was computed using a two-tailed *t* test with *n*-2 degrees of freedom.

3.6. Adjustment of isotopic data – bone equivalent

Comparing the isotopic values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ extracted from different tissues raises some methodological problems (Bocherens, 2015). The collagen in mammalian bones is constantly remodelled during the life span and shows average diet isotopic composition of several years before death (e.g., Hindelang et al., 2002; Huja and Beck, 2007). The dentine collagen is formed during the tooth growth, including the moment of milk diet, and that is why the tooth dentine reveals higher $\delta^{15}\text{N}$ values than bone (Bocherens et al., 1994). Before comparing isotopic values of teeth and bones, an adjustment should be performed to compensate the differences. In this study, the following adjustment of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between dentine and bone collagen was applied: $\delta^{13}\text{C}_{\text{bone}} = \delta^{13}\text{C}_{\text{teeth}} + 0.4\text{‰}$ and $\delta^{15}\text{N}_{\text{bone}} = \delta^{15}\text{N}_{\text{teeth}} - 1.9\text{‰}$ for cave bear (Bocherens, 2015), and $\delta^{13}\text{C}_{\text{bone}} = \delta^{13}\text{C}_{\text{teeth}} - 0.2\text{‰}$ and $\delta^{15}\text{N}_{\text{bone}} = \delta^{15}\text{N}_{\text{teeth}} - 1.9\text{‰}$ for wolf (Bocherens et al., 2011a).

3.7. Adjustment of isotopic data – altitudinal and latitudinal gradient of isotopes

The isotopic values from different European cave bear sites come from a wide range of altitudes, and altitude may be a strong driving factor of variations of isotopic composition. To compare the isotopic values from sites located at different altitudes and to avoid considering the differences linked to elevation as if they were differences in palaeoecology, an adjustment of isotopic values needs to be applied.

Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in soils and plants are known to follow altitudinal gradient, which is a function of among others: air pressure, air temperature and precipitation changing along topography (Schoor and Matson, 2001; Amundson et al., 2003; Zhu et al., 2010). Since the $\delta^{15}\text{N}$ gradient depends primary on physical parameters, we assume that the recent value can be used for MIS 3 period, as to our knowledge there is no reason for different altitudinal gradient of air pressure or temperature to be different during different periods of the Quaternary. The $\delta^{13}\text{C}$ gradient derives from multiple physical, biological and ecological factors, therefore recent values may differ from those for MIS 3. We therefore used recent gradient for $\delta^{13}\text{C}$ values with caution, as we are aware that the real value may be different for MIS 3, as discussed in more detail in the

discussion section.

In this study we tested the usefulness of the altitudinal correction using the altitudinal gradient reported for both plants and herbivorous animals by Männel et al. (2007): $\delta^{15}\text{N}\text{-adj-alt} = \delta^{15}\text{N} + (0.0011 \cdot \text{altitude})$, and $\delta^{13}\text{C}\text{-adj-alt} = \delta^{13}\text{C} - (0.0011 \cdot \text{altitude})$, where altitude is given in meters. The correction removes the effect of altitude and allows to equalizing all data to the same level (i.e., 0 m a.s.l.) to make them comparable. In the following text the $\delta^{13}\text{C}\text{-adj-alt}$ and $\delta^{15}\text{N}\text{-adj-alt}$ mean the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values adjusted according to altitude. We also attempted to search for internal altitudinal gradient exhibited by our dataset.

In contrast with the altitudinal gradient, a latitudinal gradient is less unequivocal. On the basis of data presented by Körner et al. (1991) for plant communities from tropical, temperate and sub-arctic zones, a latitudinal gradient $0.0255\text{‰}/^\circ$ from Equator to North pole for $\delta^{13}\text{C}$ may be calculated. Du et al. (2015) found a $0.21\text{‰}/^\circ$ gradient for $\delta^{13}\text{C}$ in modern tree leaves in China, but also showed strong correlation between $\delta^{13}\text{C}$ values and air temperature and precipitation in the same samples, which means that the observed gradient may be more related to non-latitudinal factors, such as regional precipitation pattern. Bakwin et al. (1998) reported decreasing latitudinal gradient of air $\delta^{13}\text{C}$ values in a 35°N – 55°N latitude range, and Suits et al. (2005) simulated a similar gradient in terrestrial biosphere, at least for the 40°N – 50°N latitude range, on the basis of meteorological data. Miller et al. (2003) found no latitudinal gradient of $\delta^{13}\text{C}$ values. Craine et al. (2015) showed that latitudinal gradient of $\delta^{15}\text{N}$ does not occur in soils. Therefore we decided against using a latitudinal adjustment of data a priori, but we explored in this study the possible occurrence of latitudinal gradient in MIS 3 cave bears.

4. Results

4.1. Preservation and quality of collagen

For the new sites, the N content in whole bones varied among the analysed samples. The lowest values were obtained from the samples from Nietoperzowa Cave, with 5 samples (IN-04, IN-19, IN-20, IN-28, IN-33) excluded from further analysis at this stage because of their extremely low N content (<0.3%), making the collagen extraction difficult. All remains from Winden, Perspektywiczna and Medvedia Caves exhibited sufficient N content in whole bone.

The extracted collagen of samples from Nietoperzowa Cave exhibited atomic C/N ratio between 3.2 and 3.4, which is the standard for collagen (DeNiro, 1985), except for one sample no. IN-32. The $\%C_{\text{coll}}$ in samples ranged from 6.5 to 43.8%, and the $\%N_{\text{coll}}$ ranged from 1.6 to 15.6%. Values lower than 15.3% for %C and lower than 5.5% for %N are beyond the expected range for well-preserved collagen (acc. to Ambrose, 1990) and such samples (nos. IN-2, IN-23) were also excluded from further analysis.

In the cases of Winden, Perspektywiczna and Medvedia Caves, the C/N ratios, %N and %C confirmed good preservation of collagen.

4.2. Isotopic results from new Central-Eastern European sites

The $\delta^{13}\text{C}$ values ranged from -23.1‰ to -20.5‰ (Nietoperzowa Cave), from -21.9‰ to 21.0‰ (Perspektywiczna Cave), from -21.4‰ to -20.7‰ (Medvedia Cave) and from -22.0 to -21.5‰ (Winden) (Table 1). Samples from Perspektywiczna and Medvedia Caves and Winden showed a narrow range of $\delta^{13}\text{C}$ values, while the difference between samples from Nietoperzowa Cave reaches 2.7‰ . However, this difference is visible only in samples from older sediments, dated to MIS 5–6 (*sd* = 0.92). Samples from

the MIS 3 period exhibited the maximum difference in $\delta^{13}\text{C}$ of 0.7‰ (sd = 0.27), similar to the differences observed in Perspektywiczna Cave (0.9‰, sd = 0.28), Medvedia Cave (0.7‰, sd = 0.18), and Winden (0.5‰, sd = 0.18) for the same geological age.

The $\delta^{15}\text{N}$ values ranged from 1.4‰ to 5.1‰ (Nietoperzowa Cave), from 1.6‰ to 5.1‰ (Perspektywiczna Cave), 0.8‰–3.7‰ (Medvedia Cave) and from 1.7 to 4.3‰ (Winden) (Table 1). The $\delta^{15}\text{N}$ values were more variable than the $\delta^{13}\text{C}$ values, even among samples from one site. In Nietoperzowa Cave the difference in range of $\delta^{15}\text{N}$ between the older and younger periods were not as distinct as in case of $\delta^{13}\text{C}$, however there were differences in the average values.

The additional isotopic results obtained for other species are presented in Table 2. The $\delta^{13}\text{C}$ values measured for carnivores ranged from –20.4‰ to –17.7‰ and the $\delta^{15}\text{N}$ values ranged from 7.4‰ to 10.3‰. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values measured for reindeer ranged respectively from –19.2‰ to –18.5‰ and from 2.7‰ to 4.5‰. For other herbivores the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ranged from –20.5‰ to 19.9‰, and from 3.3‰ to 7.7‰.

The pattern of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in cave bears from Poland, Slovakia and eastern Austria is similar to that previously found in sites in Western and Central-Western Europe (Bocherens et al., 2006, 2011a, 2011b; Blant et al., 2010; Pérez-Rama et al., 2011; Horacek et al., 2012; Pacher et al., 2012). Low values of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ place Central-Eastern European bears in a position within the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ isospace characteristic for herbivores (Fig. 2). The position of cave bears in the Central-Eastern European palaeoecosystem during MIS 3 is clearly the same as it was in Western Europe, for example in Ardennes and Swabian Jura (Bocherens et al., 1997, 2011a), Pyrenees and southern France (Bocherens et al., 1991, 1994) as well as the Swiss Alps (Blant et al., 2010; Pacher et al., 2012). The range of isotopic fractionation between the collagen of prey and predator (+0.8‰–+1.3‰ for $\delta^{13}\text{C}$ and from +3‰ to +5‰ for $\delta^{15}\text{N}$, according to Bocherens and Drucker, 2003; Bocherens et al., 2011a), allows the reconstruction of the average prey isotopic signatures for predators. In case of studied remains there is no evidence for predation of large carnivores on cave bear in Central-Eastern Europe, as the predators feeding on cave bear would show lower $\delta^{13}\text{C}$ than those measured. Individual specialization in the hunting of cave bear is known for some cave lions from Belgium and the Swabian Jura based on isotopic studies (Bocherens et al., 2011a), and for cave hyenas based on taphonomic investigation of German caves (Diedrich, 2009). In the present study, none of the analysed predators exhibit low $\delta^{13}\text{C}$ values that could indicate an individual prey preference on cave bears in southern Poland or Slovakia.

4.3. Isotopic signature of European cave bear in geographical layout

The average values of newly analysed sites together with other European sites (Tables 3 and 4) plotted against the geographical measurements of the sites, i.e. altitude, latitude and longitude, are presented on Fig. 3. A clear trend may be observed only in the case of $\delta^{15}\text{N}$ plotted against altitude ($R^2 = 0.3603$) and indicates a decrease of $\delta^{15}\text{N}$ with altitude. This observation stays in accordance with data known for modern soils, plants and animals (Garten, 1993; Garten and Migroet, 1994; Amundson et al., 2003; Craine and Lee, 2003; Sah and Brumme, 2003; Männel et al., 2007). The linear correlation between $\delta^{15}\text{N}$ and altitude is strong (correlation coefficient –0.60026) and is statistically significant ($p = 0.00045376$) (Table 5). There is no other correlation between raw average isotopic values and geographical measurements (Table 5). Moreover, there is no mutual correlation between geographical measurements of the sites, meaning that there are no random relationships between the geographical parameters of the

sites and therefore that the geographical locations of the analysed set of sites has no impact on the statistical processing.

When plotted against altitude, the average $\delta^{13}\text{C}$ values do not follow any trend known from the literature and observed in modern plants and herbivores (Arroyo et al., 1990; Körner et al., 1988, 1991; Männel et al., 2007; Zhu et al., 2010). Contrary to the expected increasing trend, the cave bear data shows a weak ($R^2 = 0.0801$) decrease with altitude (Fig. 3). The known relation between $\delta^{13}\text{C}$ and latitude, described for plant communities by Körner et al. (1991), is also not visible in the case of cave bears.

4.4. Altitudinal gradient

The strong correlation between $\delta^{15}\text{N}$ values and altitude (Section 4.3) suggests that an altitudinal adjustment is necessary if one wants to compare isotopic cave bear data from European sites. When applied, the adjustment leads to a unification of $\delta^{15}\text{N}$ values (Fig. 4), with the slope of $\delta^{15}\text{N}$ /altitude trend changing from –0.0015 in raw data to –0.0004 in adjusted data (more horizontal trend on Fig. 4 in comparison with that on Fig. 3). The altitudinal adjusted $\delta^{15}\text{N}$ data do not correlate with altitude (Table 5), what may indicate that the used adjustment is properly working. However, two Romanian sites (Peștera cu Oase and Urșilor) that were outstanding from raw data, still remain outliers even when the altitudinal adjustment is applied.

As one may expect from the lack of correlation between $\delta^{13}\text{C}$ and altitude (Table 5), the altitudinal adjustment will not work properly in the case of $\delta^{13}\text{C}$. The slope of $\delta^{13}\text{C}$ /altitude trend is changing from –0.0002 in raw data (Fig. 3) to –0.0012 in adjusted data (Fig. 4), which leads to a widening of variability and stands in contradiction with the concept of data adjusting. The expected situation after applying altitudinal adjustment is that the arrangement of points on $\delta^{13}\text{C}$ -alt-adj/altitude graph follows more or less a horizontal line, which is not the case with our data. Here, we observed stronger correlation between altitude and $\delta^{13}\text{C}$ after altitudinal adjustment (Table 5), what means the used adjustment is not leading to expected effect.

4.5. Latitudinal and longitudinal gradient

A weak correlation between raw $\delta^{13}\text{C}$ values and latitude (Section 4.3) suggests that the latitudinal gradient observed in modern plant communities and air (Körner et al., 1991; Bakwin et al., 1998; Du et al., 2015) might be absent in MIS 3 cave bear populations. Only a weak decreasing trend in $\delta^{13}\text{C}$ /latitude plot is observed (Fig. 3) and is the reverse of the ones reported by Körner et al. (1991) or Du et al. (2015), but has similar monotonicity as presented by Bakwin et al. (1998). A latitudinal gradient for $\delta^{15}\text{N}$ is also not visible in our data (Fig. 5). Altitudinal adjusted $\delta^{15}\text{N}$ data exhibit a weak decreasing trend with latitude.

The lack of correlation between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and longitude (Section 4.3) also suggests that longitudinal gradient in cave bears did not exist. Applying the altitudinal adjustment causes even lowering of $\delta^{13}\text{C}$ /longitude relation, and in case of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ the R^2 values are very low, regardless if altitudinal adjusting is applied or not (Fig. 5).

5. Discussion

5.1. Cave bear isotopes and altitude

5.1.1. Altitudinal gradient of $\delta^{15}\text{N}$

The values of $\delta^{15}\text{N}$ in soils and plants depend mainly on aridity and temperature (Schuur and Matson, 2001; Amundson et al., 2003; Pardo and Nadelhoffer, 2010; Craine et al., 2015), but also

on mineralization of nitrogen in soil (Garten and Miegroet, 1994), which may be dependent on mineralization rate but also on age and maturity of soil. Usually $\delta^{15}\text{N}$ decrease along altitude in different environments worldwide (Garten, 1993; Amundson et al., 2003; Craine and Lee, 2003; Sah and Brumme, 2003; Männel et al., 2007), however it may be disturbed by local precipitation distribution and interspecific response to N supply (Garten, 1993). Altitudinal gradient in modern ecosystems is known to be variable, ranging from $-0.0007\text{‰}/\text{m}$ for domestic cattle (Männel et al., 2007), to $-0.0012\text{‰}/\text{m}$ for African high mountain plants (Amundson et al., 2003) and $-0.0017\text{‰}/\text{m}$ for domestic sheep (Männel et al., 2007), and to below $-0.002\text{‰}/\text{m}$ in soils and plants (Amundson et al., 2003; Craine and Lee, 2003; Sah and Brumme, 2003). For some environments the relatively low altitudinal gradient was reported, for example $-0.0025\text{‰}/\text{m}$ for Kyle Canyon, USA (Amundson et al., 2003), and even -0.0046 to $-0.0078\text{‰}/\text{m}$ for grasslands of New Zealand (Craine and Lee, 2003). This probably reflects some interspecies differences (Garten, 1993; Miller and Bowman, 2002). We should be aware that an absolute value for the $\delta^{15}\text{N}$ altitudinal gradient cannot be given with the current state of knowledge.

We found the decreasing trend of $\delta^{15}\text{N}$ signature of cave bear collagen along altitude, which reflects the altitudinal gradient known for modern plants and animals (Männel et al., 2007). The strong correlation between $\delta^{15}\text{N}$ and altitude (Section 4.3) indicates that altitudinal adjustment of $\delta^{15}\text{N}$ data is valid and necessary if we want to find ecological differences between sites located at different elevations. All sites except two of them, namely the Romanian sites Peștera cu Oase and Urșilor, follow the decreasing trend (Fig. 3). The value of gradient for all sites ($-0.0015\text{‰}/\text{m}$) and for the sites excluding the two outstanding ones ($-0.0013\text{‰}/\text{m}$) is similar to the altitudinal gradient observed in modern grassland plants and grazers in the Alps ($-0.0011\text{‰}/\text{m}$, Männel et al., 2007). It is also similar to the gradient detected for a smaller set of cave bear sites by Bocherens (2015), being $-0.0017\text{‰}/\text{m}$. This similarity supports the use of an altitudinal adjustment based on the gradient observed by Männel et al. (2007). However, using of internal gradients deriving from our results seems to be more accurate for cave bears.

Factors responsible for the altitudinal gradient of $\delta^{15}\text{N}$ are physical parameters, i.e. altitudinal gradients of precipitation and air temperature (Schoor and Matson, 2001; Amundson et al., 2003). As absolute values of both precipitation and temperature were for sure differentiated between regions and periods of Pleistocene, there are no premises that altitudinal gradients of precipitation and temperature changed significantly through time.

5.1.2. Altitudinal gradient of $\delta^{13}\text{C}$

The discussion on altitudinal gradient of $\delta^{13}\text{C}$ is more complicated than in the case of $\delta^{15}\text{N}$. The altitudinal gradient for $\delta^{13}\text{C}$ has been measured for different modern ecosystems and geographical location, and it is known that the $\delta^{13}\text{C}$ values tend to increase with altitude. The rate oscillates between $0.0006\text{‰}/\text{m}$ measured for temperate grassland (Körner et al., 1991) and high-alpine vegetation of Andes (Arroyo et al., 1990), and $0.0018\text{‰}/\text{m}$ measured for open habitats of Swiss Alps (Zhu et al., 2010) and $0.0019\text{‰}/\text{m}$ reported for subarctic grassland (Körner et al., 1991). The average values for European grassland is $0.0011\text{‰}/\text{m}$ according to Männel et al. (2007); $0.0012\text{‰}/\text{m}$ for high mountain ecosystems according to Körner et al. (1988); and $0.0014\text{‰}/\text{m}$ for European mountains according to Zhu et al. (2010). Data given by Kohn (2010) allow calculating a gradient of $0.0003\text{‰}/\text{m}$ as a global average for the great database of different plant taxa from different environments. The altitudinal gradient observed in plants is followed by gradient in herbivore tissues (Männel et al., 2007), which oscillates between

0.0009 , 0.001 and $0.0015\text{‰}/\text{m}$ in different species. However, a reverse altitudinal trend may occur in some types of environments, for instance in semi-arid areas of southern United States (Van de Water et al., 2002).

The main driver of the $\delta^{13}\text{C}$ altitudinal gradient is air pressure and partial pressure of CO_2 in atmosphere (Körner et al., 1991; Zhu et al., 2010), but additional factors such as air temperature, precipitation and hydrological regime also play a role and may disturb the gradient (Van de Water et al., 2002). However, Schoor and Matson (2001) did not find a relationship between precipitation and $\delta^{13}\text{C}$ in plants in mountain forest. In addition to the physical drivers, biological and ecological factors also regulate the $\delta^{13}\text{C}$ signature in plants, such as the density of leaf cover, known as canopy effect (Van der Merve and Medina, 1991; Fricke, 2007; Drucker et al., 2008; Bonafini et al., 2013) as well as leaf thickness, leaf N content, stomatal conductance and stomatal density (Körner et al., 1989; Vitousek et al., 1990; Meinzer et al., 1992; Morecroft and Woodward, 1990; Cordell et al., 1999). These factors are difficult to recognize in the case of palaeoecosystems, since the layout of vegetation zones with different taxa and canopy effect, such as more forested and more open environments, is dependent on altitude, soil type, regional distribution of biomes, and is climate-sensitive.

In case of ancient ecosystems, including Pleistocene ones, the factors responsible for the $\delta^{13}\text{C}$ altitudinal gradient might occur in different configurations and changed through times. It should be noticed that MIS 3 period, which is the chronological range for our research material, was not a time of constant climate, but of numerous climatic fluctuations (Houmark-Nielsen, 2009; Fletcher et al., 2010; Helmens, 2014). It means that vegetation cover changed multiple times, what is also confirmed by pollen data (e.g., Komar et al., 2009) and climate modelling (Alfano et al., 2003; Huntley et al., 2003; Willis and van Andel, 2004; Van Meerbeek et al., 2011). The partial pressure of CO_2 also changed many times through MIS 3 period (Sigman and Boyle, 2000).

Taken together, the European cave bear $\delta^{13}\text{C}$ data do not follow the expected altitudinal gradient (see also Section 4.3 and Bocherens, 2015) as a whole set. However, if we try to search for altitudinal trends close to the expected one on a $\delta^{13}\text{C}$ /altitude graph, we can point out several groups of points, each of them following the increasing trend known for modern plants and animals (Fig. 6). The subdivision of dataset into groups is arbitrary, and it is based on the tracing of sets of points that are arranged along increasing trend lines similar to those described in recent ecological contexts. Assignment of some points to groups may be problematic, for example in case of Kudaro and A Ceza caves. The most abundant group (black diamonds on Fig. 6) shows an increasing trend (gradient $0.0006\text{‰}/\text{m}$), close to the altitudinal gradients $0.0006\text{‰}/\text{m}$ and $0.0009\text{‰}/\text{m}$ observed in modern plants and animals (Arroyo et al., 1990; Körner et al., 1991, 1998; Hultine and Marshall, 2000; Männel et al., 2007) and corresponds to sites from different altitudes (from 125 to 1600 m a.s.l.) and from different parts of Europe (Iberian Peninsula, Western, Central and South-Eastern Europe, Caucasus and all new sites from Central-Eastern Europe). Five sites clearly stand out from this group: Conturines, Balme à Collomb, Bärenloch, Drachenloch and Ramesch. All of them are sites situated in the Alps at high altitudes. The last four show a trend parallel to the main group (blue circles on Fig. 6). The slope of the altitudinal gradient of this group ($0.0003\text{‰}/\text{m}$) is lower than that of main group, however the dataset is not numerous. Despite this, the trend is similar to the altitudinal trend in plants (calculated from the huge worldwide dataset shown by Kohn, 2010). Conturines alone forms its own set. Five other sites (red squares on Fig. 6: Aldène, Chauvet, Divje Babe, Mialet and Font-de-Gaume with Olaskoa) are less distinctly separated from the main group, but may also be treated

Table 2
List of additional species fossil samples from Polish and Slovakian sites and of isotopic results (* – bone equivalent, coll – data for extracted collagen, collection symbols are the same as those used at Table 1).

Lab. no.	Collection	Site	Species	Bone/tooth	%C _{coll}	%N _{coll}	C/N _{coll}	δ ¹³ C	δ ¹⁵ N
IP-07	IGS	Perspektywiczna cave	<i>Crocota crocuta spelaea</i>	Cranium	43.2	15.6	3.2	−19.2	9.4
IP-21	IGS	Perspektywiczna cave	<i>Crocota crocuta spelaea</i>	Femur	39.9	14.1	3.3	−19.3	10.3
IP-22	IGS	Perspektywiczna cave	<i>Crocota crocuta spelaea</i>	Ulna	34.1	11.9	3.3	−19.5	9.1
IP-23	IGS	Perspektywiczna cave	<i>Panthera spelaea</i>	Metacarpus IV	42.7	15.1	3.3	−17.7	7.4
IP-08	IGS	Perspektywiczna cave	<i>Rangifer tarandus</i>	Metacarpus	44.0	15.9	3.2	−18.7	3.6
IP-10	IGS	Perspektywiczna cave	<i>Rangifer tarandus</i>	Phalanx 2	37.0	13.4	3.2	−19.2	2.8
IP-24	IGS	Perspektywiczna cave	<i>Rangifer tarandus</i>	Phalanx II	42.2	14.9	3.3	−19.0	2.7
IP-25	IGS	Perspektywiczna cave	<i>Rangifer tarandus</i>	Phalanx I	39.6	13.9	3.3	−18.7	2.9
IP-26	IGS	Perspektywiczna cave	<i>Rangifer tarandus</i>	Metacarpus	42.6	14.9	3.3	−18.5	4.5
IP-11	IGS	Perspektywiczna cave	<i>Megaloceros giganteus</i>	Metacarpus	32.4	11.1	3.4	−19.9	4.2
IP-12	IGS	Perspektywiczna cave	<i>Bos/Bison</i>	Mandibula	41.3	14.8	3.3	−20.1	4.6
IP-27	IGS	Perspektywiczna Cave	<i>Bos/Bison</i>	Scapula	44.4	15.6	3.3	−20.4	7.7
IP-20	IGS	Perspektywiczna Cave	<i>Coelodonta antiquitatis</i>	Metapodial	38.1	13.3	3.3	−20.5	3.3
MJ-21	SM	Medvedia cave	<i>Panthera spelaea</i>	Phalanx	39.9	13.8	3.4	−19.2	8.4
MJ-22	SM	Medvedia cave	<i>Canis lupus</i>	Vertebra	40.5	14.2	3.3	−19.3	8.5
MJ-23	SM	Medvedia cave	<i>Canis lupus</i>	Canine	38.1	13.5	3.3	−20.2 * −20.4	10.6 * 8.7

as a separate set. They also show an increasing trend (altitudinal gradient 0.0008‰/m). These sites are situated in Mediterranean/Atlantic region, although not all sites from this region tend to follow the trend of this group (for example Iberian sites or Prélétang are closer to the main group). The difference in δ¹³C values might be due to differences in water stress effect on the plants, linked to aridity.

Such situation may suggest that altitudinal gradient in MIS 3 cave bears existed. However, the whole population was divided into subpopulations, each of them followed a similar gradient but with different absolute δ¹³C values. The differences in δ¹³C values in cave bears suggest different δ¹³C values at the basis of the ecosystems, i.e. in plants. We can propose two hypotheses explaining this observation:

- 1) The bears were feeding on the plants that followed altitudinal gradient, but were foraging and hibernating at different altitudes. This hypothesis explains the lower values in some specimens or populations, with assumption that bear hibernate at higher elevation, for example to avoid predators (Bocherens, 2015), but were moving to lower elevation to find more abundant plant food. However, in the case of our data this explanation is insufficient, since differences should be recorded both in δ¹³C and δ¹⁵N values. The cave bear exhibiting relatively low δ¹³C values (for example blue circle group or Conturines on Fig. 6) in comparison with the main group, show the same δ¹⁵N pattern as the main group. In other words, several trend lines in δ¹³C along altitude suggest that particular populations might have been feeding at different altitude than hibernating, while one trend line in δ¹⁵N along altitude indicates that each population had been feeding and hibernating at the same altitude. This contradiction falsifies this first hypothesis in case of MIS 3 cave bears treated globally. However, this explanation may be correct in the case of some sites, for example Conturines (see also Bocherens, 2015). This site exhibits both δ¹³C values below the main trend and δ¹⁵N values above the main trend. This suggests that feeding and hibernating at different altitudes may be at least partially responsible for the relatively low δ¹³C values. This hypothesis seems reasonable if we take into consideration the unusually highly elevated hibernating place, as Conturines cave is situated at 2800 m a.s.l.
- 2) The different bear populations were feeding on plants with different δ¹³C signatures, related to factors other than altitudinal gradient. This situation is possible when:

- a. Animals are feeding on different types of plants. It is widely known that different photosynthetic groups of plants, such as C3, C4, CAM or lichens, exhibit different δ¹³C signature (e.g., DeNiro and Epstein, 1978; Bocherens, 2003), and also different genera growing at the same altitude may exhibit different δ¹³C values and different altitudinal gradient (Zhu et al., 2010);
- b. Animals inhabited environments with different canopy effects, i.e. with different density of vegetation. It is known that specimens of one plant taxon may exhibit different δ¹³C signature if living in different environments (van der Merwe and Medina, 1991; Bonafini et al., 2013);
- c. Observed populations are chronologically distant, i.e. they might have been living during periods with different layout of physical parameters, such as air temperature, precipitation, CO₂ partial pressure. During the long time span represented by the analysed sites, covering most of the MIS 3, numerous environmental shifts occurred (e.g., Sigman and Boyle, 2000; Fletcher et al., 2010; Helmens, 2014). Therefore cave bears populations with different altitudinal trends may represent different ecosystems or periods with different physical parameters, which were changing in time.

All these situations a, b and c are connected to the occurrence of different environmental conditions (Fig. 7). This may be related to either altitudinal vegetation zones, different biomes or different pattern of physical parameters not related to ecological differences, such as CO₂ partial pressure. These differences followed environmental variations either in geographical regions or chronological periods. All these situations are expected to give similar isotopic pattern and may not be differentiated with isotopic methods.

Looking more regionally at our data we could try to find isotopic differences between elevation zones inside one region (what might indicate the impact of altitude related vegetation zones). The best region for comparing bears from different altitudes among our research area are the Alps, thanks to the great altitudinal differences occurring there. To the Alpine region we can include the following sites: Balme à Collomb, Bärenloch, Conturines, Drachenloch, Gamssulzen, Prélétang, Ramesch and Tischoferhöhle. Sites located at elevations below and above ca. 1500 m a.s.l. follow different trend lines and may be easily separated into separate groups (Fig. 8). The sites from lower elevation exhibit higher δ¹³C values, which may be related to more open habitats. Higher elevated sites represent relatively more C3 plants in diet or stronger canopy effect. Such situation seems to be unusual in modern Alps,

Table 3List of Western and Southern European cave bear sites dated to MIS 3 and average isotopic values. Adjusted $\delta^{13}\text{C}$ -adj-alt and $\delta^{15}\text{N}$ -adj-alt with use of altitudinal gradients given by Männel et al. (2007).

Site	Site symbol	Region	Altitude m a.s.l.	Latitude °N	Longitude °E	Palaeogenetics	n	$\delta^{13}\text{C}$ (av \pm sd)	$\delta^{15}\text{N}$ (av \pm sd)	$\delta^{13}\text{C}$ -adj-alt (av)	$\delta^{15}\text{N}$ adj-alt (av)	Reference for isotopic data
A Ceza	AC	Spain	1004	42,691108	-7,100708	–	10	-21.7 \pm 0.2	3.2 \pm 1.2	-22.8	4.3	Pérez-Rama et al. (2011)
Aldène (Grotte d'Aldène)	Al	France	270	44,117908	2,674142	–	5	-20.9 \pm 0.4	3.8 \pm 1.4	-21.1	4.1	Bocherens et al. (1994); Bocherens (2015)
Balme à Collomb	BC	French Alps	1700	45,689632	5,816232	<i>spelaeus</i> (Orlando et al., 2002)	6	-21.4 \pm 0.7	1.5 \pm 0.5	-23.3	3.4	Bocherens et al. (2011b)
Bärenloch	Bä	Switzerland	1645	47,068951	7,925607	–	7	-21.7 \pm 0.9	0.2 \pm 1.3	-23.6	2.0	Blant et al. (2010)
Chauvet	Ch	France	240	44,839072	3,81672	<i>spelaeus</i> (Baca et al., 2012)	26	-20.6 \pm 0.3	4.0 \pm 0.9	-20.9	4.2	Bocherens et al. (2006); Bon et al. (2011)
Cioclovina	Ci	Romania	770	45,949955	23,042794	–	30	-21.2 \pm 0.6	3.0 \pm 1.2	-22.0	3.9	Robu et al. (2013)
Conturines	Co	Italy	2800	46,994069	11,92463	<i>ladinicus</i> (Hofreiter et al., 2002)	13	-22.3 \pm 0.6	1.6 \pm 1.3	-25.4	4.7	Horacek et al. (2012)
Cova Eirós	Ei	Spain	780	42,763562	-7,20534	<i>spelaeus</i> (Stiller et al., 2010)	36	-21.2 \pm 0.5	4.5 \pm 0.8	-22.0	5.4	Pérez-Rama et al. (2011)
Cova Liñares	Li	Spain	1115	42,695681	-7,074094	<i>spelaeus</i> (Loreille et al., 2001)	23	-21.0 \pm 0.3	1.9 \pm 0.5	-22.2	3.1	Vila Taboada (1998); Vila Taboada et al. (1999); Pérez-Rama et al. (2011)
Divje Babe	DB	Slovenia	450	46,497209	13,902169	<i>ingressus</i> (Baca et al., 2012)	14	-20.5 \pm 0.4	1.9 \pm 0.7	-21.0	2.4	Nelson and Ku (1997); Nelson et al. (1998)
Drachenloch	Dr	Switzerland	2475	47,233323	9,44172	–	3	-21.3 \pm 0.4	0.3 \pm 0.6	-24.0	3.1	Pacher et al. (2012)
Font-de-Gaume III + Olaskoa	FG	France	140	45,735566	0,828439	<i>spelaeus</i> (Stiller et al., 2014)	4 + 1	-20.7 \pm 0.4	2.8 \pm 0.6	-20.8	3.0	Bocherens et al. (2011b)
Gamszulzen	Ga	Austria	1300	47,717845	14,305917	<i>ingressus</i> (Hofreiter et al., 2004b)	9	-20.8 \pm 0.2	1.1 \pm 0.4	-22.3	2.6	Bocherens et al. (2011b); Hofreiter et al. (2004b)
Geißenklösterle	Ge	Germany	580	48,409605	9,770841	<i>spelaeus</i> + <i>ingressus</i> (Baca et al., 2012)	20	-20.9 \pm 0.3	2.8 \pm 0.9	-21.5	3.5	Münzel et al. (2011)
Goyet	Go	Belgium	130	51,095544	4,959298	<i>spelaeus</i> (Stiller et al., 2014)	23	-21.5 \pm 0.4	4.1 \pm 1.0	-21.7	4.3	Bocherens et al. (2011a)
Grotte du Renne (Arcy-sur-Cure)	Re	France	125	47,591539	3,766046	<i>ladinicus</i> Frischauf et al., 2010)	14	-21.3 \pm 0.4	3.4 \pm 0.6	-21.4	3.5	Bocherens (2015)
Hohle Fels	HF	Germany	534	48,389546	9,755048	<i>spelaeus</i> + <i>ingressus</i> (Baca et al., 2012)	22	-20.9 \pm 0.3	3.4 \pm 1.0	-21.5	4.0	Münzel et al. (2011)
Kudaro	Ku	Caucasus	1600	43,451671	43,6092	<i>kudarensis</i> (Baca et al., 2012)	7	-20.2 \pm 0.4	2.4 \pm 0.8	-22.0	4.2	Bocherens et al. (2014)
Mialet	Mi	France	300	44,49528	3,904611	–	5	-20.2 \pm 0.5	2.8 \pm 1.6	-20.5	3.2	Bocherens et al. (1994)
Muierii (Peștera Muierilor)	Mu	Romania	585	45,535933	23,745919	–	4	-21.0 \pm 0.1	4.0 \pm 0.3	-21.6	4.6	Robu et al. (2013)
Peștera cu Oase	Oa	Romania	600	45,474335	21,812326	<i>ingressus</i> (Richards et al., 2008)	74	-21.4 \pm 0.4	7.9 \pm 1.4	-22.1	8.5	Robu et al. (2013); Trinkaus and Richards (2013)
Prélétang	Pr	France	1225	45,086853	5,428964	<i>ladinicus</i> (Orlando et al., 2002; Frischauf et al., 2010)	7	-21.0 \pm 0.8	1.9 \pm 0.9	-22.3	3.3	Bocherens (2015)
Ramesch	Ra	Austria	1960	47,699363	14,242746	<i>spelaeus</i> (Hofreiter et al., 2004b)	11	-21.7 \pm 0.4	0.6 \pm 0.7	-23.9	2.8	Bocherens et al. (2011b); Hofreiter et al. (2004b)
Scladina	Sc	Belgium	138	50,50906	5,023374	<i>spelaeus</i> (Orlando et al., 2002)	7	-22.1 \pm 0.2	4.9 \pm 1.2	-22.2	5.1	Bocherens et al. (1997)
Tischoferhöhle	Ti	Austria	594	47,5925	12,196278	–	9	-21.0 \pm 0.3	2.9 \pm 0.8	-21.6	3.5	Spötl et al. (2014)
Urșilor	Ur	Romania	482	46,889057	22,515451	–	28	-21.7 \pm 0.5	7.4 \pm 1.9	-22.2	7.9	Robu et al. (2013)

where forested area is situated at lower elevations, and grasslands at higher position. However, in more arid regions such as the southern United States where lower parts of mountains are occupied by open environment of shrublands and higher elevations are forested, the $\delta^{13}\text{C}$ values in higher elevated plants are lower (Van de Water et al., 2002).

However, we may try to look at the same situation visible on Fig. 8 in relationship with chronology. Cave bear assemblages from high Alpine sites mostly yielded open radiocarbon dates (Appendix), a fact that suggests a chronology corresponding to an older part of MIS 3. The lower Alpine sites provided younger radiocarbon ages, about 31–40 thousand years BP for Tischoferhöhle and 37–47 thousand years BP for Gamssulzen (Appendix), i.e. indicating a younger part of MIS 3. The chronological distance may reflect occurrence of different ecosystems or periods with different conditions, such as CO_2 pressure, which may be a reason for isotopic dissimilarity in case of these sites. Despite this, each group follows an altitudinal gradient, but with different $\delta^{13}\text{C}$ baselines.

5.1.3. To use or not use $\delta^{13}\text{C}$ altitudinal adjustment for cave bears?

The $\delta^{13}\text{C}$ altitudinal trends exhibited by several groups of cave bear sites (Fig. 6) are in our opinion a strong hint in favour of using some altitudinal adjustment. If an altitudinal adjustment was not applied, then the differences in $\delta^{13}\text{C}$ values related to altitude that occur inside groups would be included in the variation patterns. As a consequence, identifying sites where cave bears were ecologically different might become difficult. For example, the site-to-site differences exceed in numerous cases the intra-site variability for the main group of cave bears defined here (black diamonds on Fig. 6). In such a situation the comparison of isotopic signatures between sites for palaeoecological or physiological studies would show differences, which in fact are an effect of elevation differences, rather than being related to ecological or physiological differences. Therefore using an adjustment for altitude is recommended to sort out difference patterns linked to ecological differences among cave bears.

The remaining question is which value of altitudinal gradient is appropriate to be used in altitudinal adjustment in the case of cave bears. The internal trends exhibited by groups on Fig. 6 are characterised by less steep slopes than observed by Männel et al. (2007) (0.0003, 0.0006 and 0.0008‰/m against 0.0011‰/m). On the basis of our data we can accept internal altitudinal gradient and use it for

altitudinal adjustment. On the Fig. 9 we compared the effects of altitudinal adjustment made with use of Männel et al. (2007) gradient and cave bear internal gradient. Here we used a 0.0006‰/m gradient, which is the gradient exhibited by the most numerous group (black diamonds on Fig. 6). The adjustment is used with equation: $\delta^{13}\text{C}\text{-adj-alt} = \delta^{13}\text{C} - (0.0006 \cdot \text{altitude})$, where altitude is given in meters.

We also tried to use separate gradients for particular groups (0.0003 for blue circles, 0.0006 for black diamonds and 0.0008‰/m for red squares), as shown in Appendix. However, in our opinion gradients derived from less numerous groups are less reliable since these groups are not statistically representative. In addition, using different adjustments for different groups may eliminate the non-altitude-related diversity, which is an unwanted effect. For example, the main group would incorporate the 'high Alpine' group because of stronger lowering of the main group due to its steeper gradient. Such a homogenisation of two groups would eliminate the differences not related to altitude, as sites from 'high Alpine' group (such as Bärenloch and Balme à Collomb) have significantly lower $\delta^{13}\text{C}$ signature than sites from the main group that are located at similar altitude (such as Gamssulzen and Kudaro).

5.2. Cave bear isotopes and latitude

We did not find evidence for significant impact of latitude on the cave bear isotopic signature. This may be because the cave bear sites in Europe are distributed in a relatively narrow latitudinal range. We can expect that in the case of European cave bear sites altitude may play a more important role than latitude in the impact on isotopic values. The maximum altitudinal distance among analysed sites is 2675 m (Grotte du Renne as the lowest site – 125 m a.s.l., Conturines as the highest – 2800 m a.s.l.), which corresponds to a 2.94‰ difference in $\delta^{13}\text{C}$ if using 0.0011‰/m altitudinal gradient according to Männel et al. (2007); while the maximum latitudinal distance is only 8.4° (A Ceza as most southern site – 42.691°N, Goyet as the most northern one – 51.096°N), which represents only the 0.21‰ difference in $\delta^{13}\text{C}$ if using 0.0255‰/° latitudinal gradient according to data by Körner et al. (1991), which is less than the intra-site variability for almost each analysed site, or 1.76‰ if using 0.21‰/° latitudinal gradient according to data by Du et al. (2015). After altitudinal adjustment of $\delta^{13}\text{C}$ data the latitudinal gradient is even less visible (–0.0209‰/°, $R^2 = 0.0022$, Fig. 5).

If we tried to analyse the impact of latitudinal adjustment on $\delta^{13}\text{C}$ average values, we can observe mainly a shift of absolute values, but the relations between sites remain almost unchanged. It may be observed for example in the impact of latitudinal adjustment according to latitudinal gradient by Körner et al. (1991), on $\delta^{13}\text{C}/\text{altitude}$ relation (Fig. 10). This indicates that irregularities observed in altitudinal pattern of $\delta^{13}\text{C}$ values are not an effect of latitudinal impact. This also indicates that the impact of latitude may be ignored in comparison of $\delta^{13}\text{C}$ signature of cave bear collagen across Europe.

5.3. Cave bear isotopes and longitude

Climatic differences between Western and Eastern Europe are visible today, and were also marked during MIS 3 (Kjellström et al., 2010), the most important differences being in the mean temperature of winter and precipitation, as derived from pollen data and climate modelling (Van Meerbeek et al., 2011). The climatic shift from West to East was also followed by differences in vegetation (Alfano et al., 2003; Huntley et al., 2003; Willis and van Andel, 2004; Komar et al., 2009). Despite this, the isotopic values of cave bears from the West to the East of Europe do not seem to follow

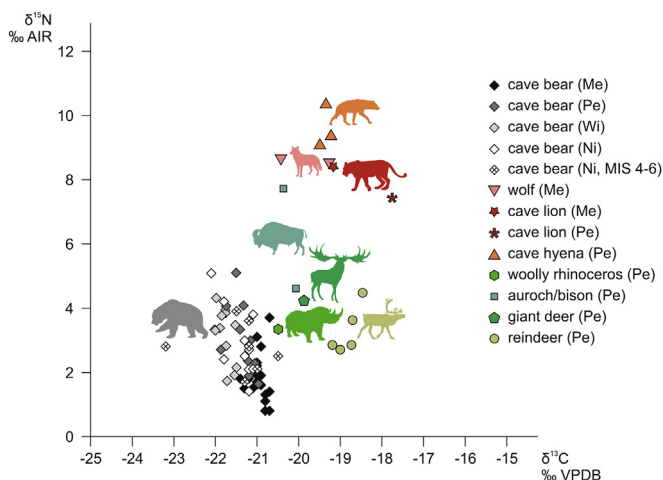


Fig. 2. Bone collagen $\delta^{13}\text{C}/\delta^{15}\text{N}$ diagram of cave bear and other fossil animals from MIS 3 deposits of Central-Eastern European sites.

Table 4

Average values and standard deviation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in analysed sites from Central-Eastern Europe (new data), with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ adjusted to altitude with use of altitudinal gradient given by Männel et al. (2007).

Site	Site symbol	Region	Altitude m a.s.l.	Latitude °N	Longitude °E	Palaeogenetics	n	$\delta^{13}\text{C}$ (av \pm sd)	$\delta^{15}\text{N}$ (av \pm sd)	$\delta^{13}\text{C}$ -adj-alt (av)	$\delta^{15}\text{N}$ -adj-alt (av)
Winden MIS 3	Wi	Austria	190	47,975515	16,748062	<i>ingressus</i> (Hofreiter et al., 2004b; Rabeder et al., 2008)	12	-21.8 ± 0.2	3.2 ± 0.8	-22.0	3.4
Nietoperzowa	Ni	Poland	438	50,194317	19,774488	–	18	-21.4 ± 0.6	2.9 ± 0.9	-21.9	3.3
Nietoperzowa (all)							10	-21.4 ± 0.4	2.9 ± 1.1	-21.9	3.4
Nietoperzowa (MIS 3)						<i>ingressus</i> ?					
Nietoperzowa (MIS 4)						?	1	-21.2	3.6	-21.7	4.1
Nietoperzowa (MIS 5–6)						?	6	-21.5 ± 0.9	2.6 ± 0.8	-21.9	3.1
Perspektywiczna (MIS 3)	Pe	Poland	345	50,442602	19,766957	<i>ingressus</i> ?	10	-21.4 ± 0.3	3.1 ± 1.1	-21.7	3.4
Medvedia MIS 3	Me	Slovakia	905	48,915863	20,398344	<i>ingressus</i> (Sabol et al., 2008)	20	-21.0 ± 0.2	1.9 ± 0.7	-22.0	2.9

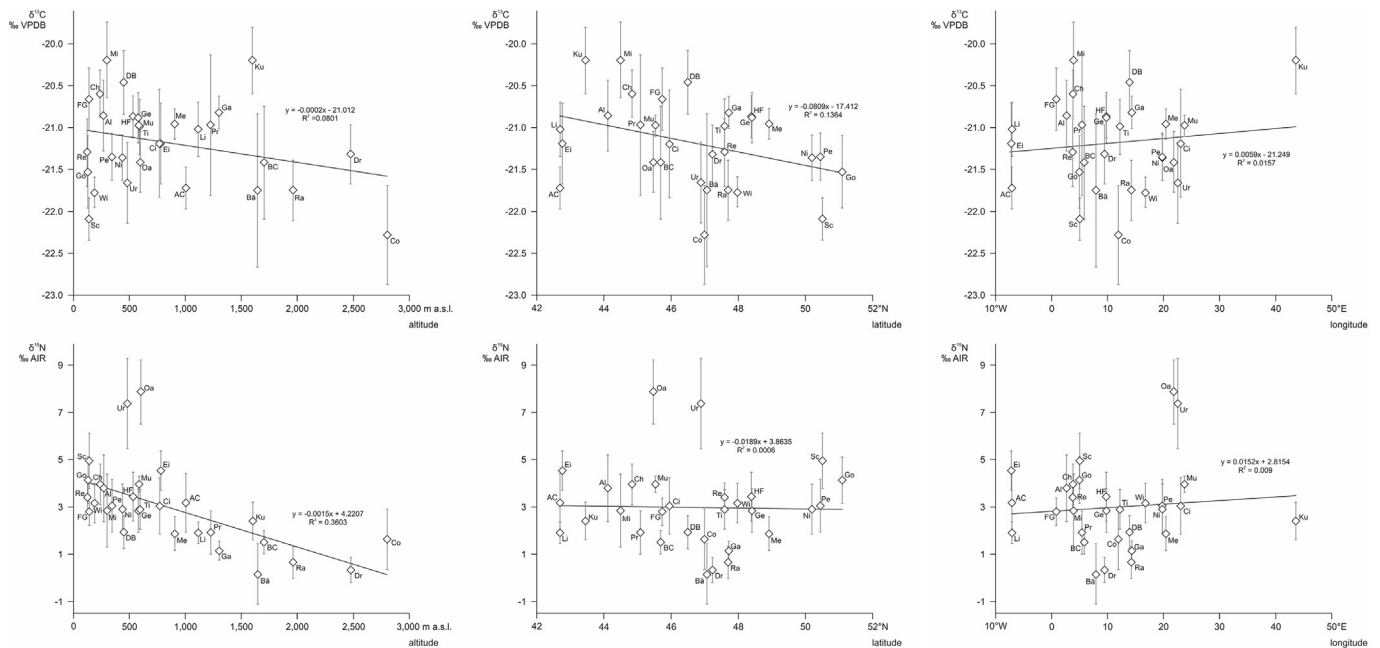


Fig. 3. Raw isotopic values (diamonds – average for sites, bars – standard deviations) plotted against geographical factors: altitude, latitude, longitude of sites.

Table 5

Linear correlation matrix of mean values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in bone collagen of cave bears from MIS 3 European sites and geographical localization of these sites. Correlation coefficients over 0.5 or below -0.5 are bolded.

	$\delta^{13}\text{C}$	$\delta^{13}\text{C}$ -adj-alt	$\delta^{15}\text{N}$	$\delta^{15}\text{N}$ -adj-alt	Altitude	Latitude	Longitude
$\delta^{13}\text{C}$	0	1.7657E-05	0.63733	0.15308	0.12971	0.044626	0.50887
$\delta^{13}\text{C}$ -adj-alt	0.69851	0	0.026768	0.97556	9.4848E-11	0.8068	0.91364
$\delta^{15}\text{N}$	-0.08971	0.40413	0	2.2414E-11	0.00045376	0.89377	0.61818
$\delta^{15}\text{N}$ -adj-alt	-0.26744	0.0058425	0.89593	0	0.33432	0.49164	0.34812
Altitude	-0.28298	-0.88401	-0.60026	-0.18253	0	0.34461	0.564
Latitude	-0.36926	-0.046607	-0.025458	-0.13057	-0.17875	0	0.17141
Longitude	0.12546	-0.020678	0.094823	0.17747	0.10967	0.2564	0

Correlation values are given in the lower triangle of the matrix, and the two-tailed probabilities that the columns are uncorrelated are given in the upper.

longitudinal gradient. This suggests that the cave bear isotopic ecology was independent from climatic W–E shift, for example because cave bear fed on the same plants that occurred in different biomes. It should be noticed, however, that MIS 3 was not a time of constant climate, but of numerous climatic fluctuations of

millennial duration (Fletcher et al., 2010; Helmens, 2014), when minor events of glacial advance occurred (Houmark-Nielsen, 2009). We cannot exclude the scenario in which cave bear populations followed the certain climatic-vegetation zones that moved across Europe during the climatic turnovers; and particular populations,

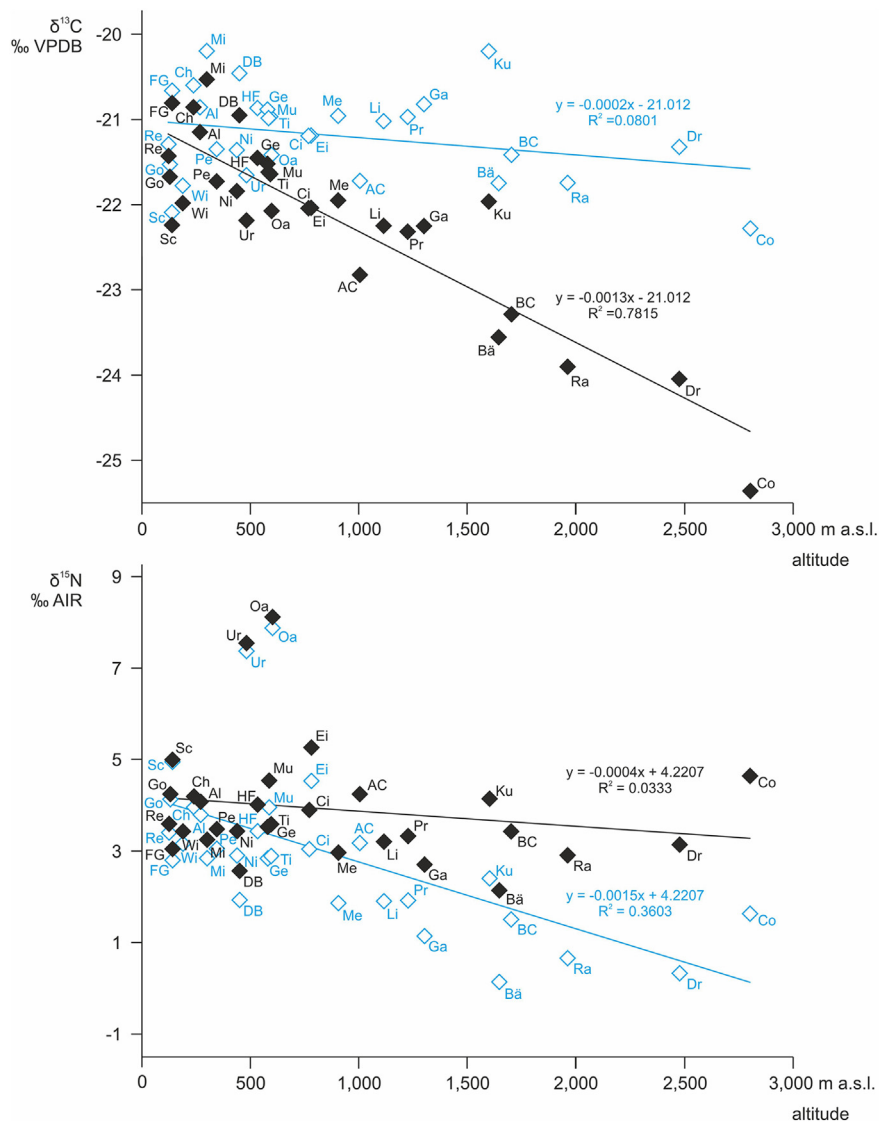


Fig. 4. Raw average isotopic values (open diamonds) and altitudinal adjusted (dark diamonds) plotted against altitude. The expected trend after adjustment should be horizontal in case of data following altitudinal gradient.

distinct in terms of both geography and time, lived in similar habitats. The isotopic record of $\delta^{13}\text{C}/\delta^{18}\text{O}$ in cave bear enamel, which does not change significantly between layers accumulated during warm and cold periods in long profiles of Bišnik Cave and Grotte d'Aldène (Bocherens et al., 1991; Krajcarz and Krajcarz, 2014), suggests that cave bear was present in particular areas only when environmental conditions were suitable. Our data may support this lack of ecological variability in cave bear. Whatever the reason, it caused the homogenization of cave bear isotopic composition in Europe.

5.4. Isotopic similarity between cave bears from European sites

We did not find any significant relation between isotopic signature of cave bears and latitude or longitude. It suggests that cave bear population during MIS 3 period was not ecologically (or strictly speaking, dietary) altered from South to North, nor from West to East. However, cave bear isotopic data gathered from numerous European sites exhibit inter-site variation.

5.4.1. Geographical variability of cave bear isotopic signature

To track the similarities/dissimilarities between cave bear sites, a cluster analysis was applied. Both carbon and nitrogen isotopic values averaged for sites were used. There are several possibilities in data selection: to compare raw $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, or $\delta^{13}\text{C}$ -adj-alt and $\delta^{15}\text{N}$ -adj-alt with altitudinal adjustment applied according to different altitudinal gradients. It is also possible to combine different types of data. However, not all of them seem to be justified. The raw $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values allow us to recognize the general variability, including altitude-dependant differences (Fig. 11a). Because the altitudinal gradient occurs, the most reasonable way for palaeoecological application is to use only altitudinally adjusted data. Being aware that choosing the absolute values of altitudinal gradient for extant species and past environments is imperfect on the basis of current state of research, we present two variants. Fig. 11b and c show clustering of data adjusted using altitudinal gradient of Männel et al. (2007), and adjusted using internal gradients of cave bears ($-0.0013\text{‰}/\text{m}$ for $\delta^{15}\text{N}$ and $0.0006\text{‰}/\text{m}$ for $\delta^{13}\text{C}$, see also discussion in Section 5.1.2).

Independently of data selection, two Romanian sites (Peștera cu

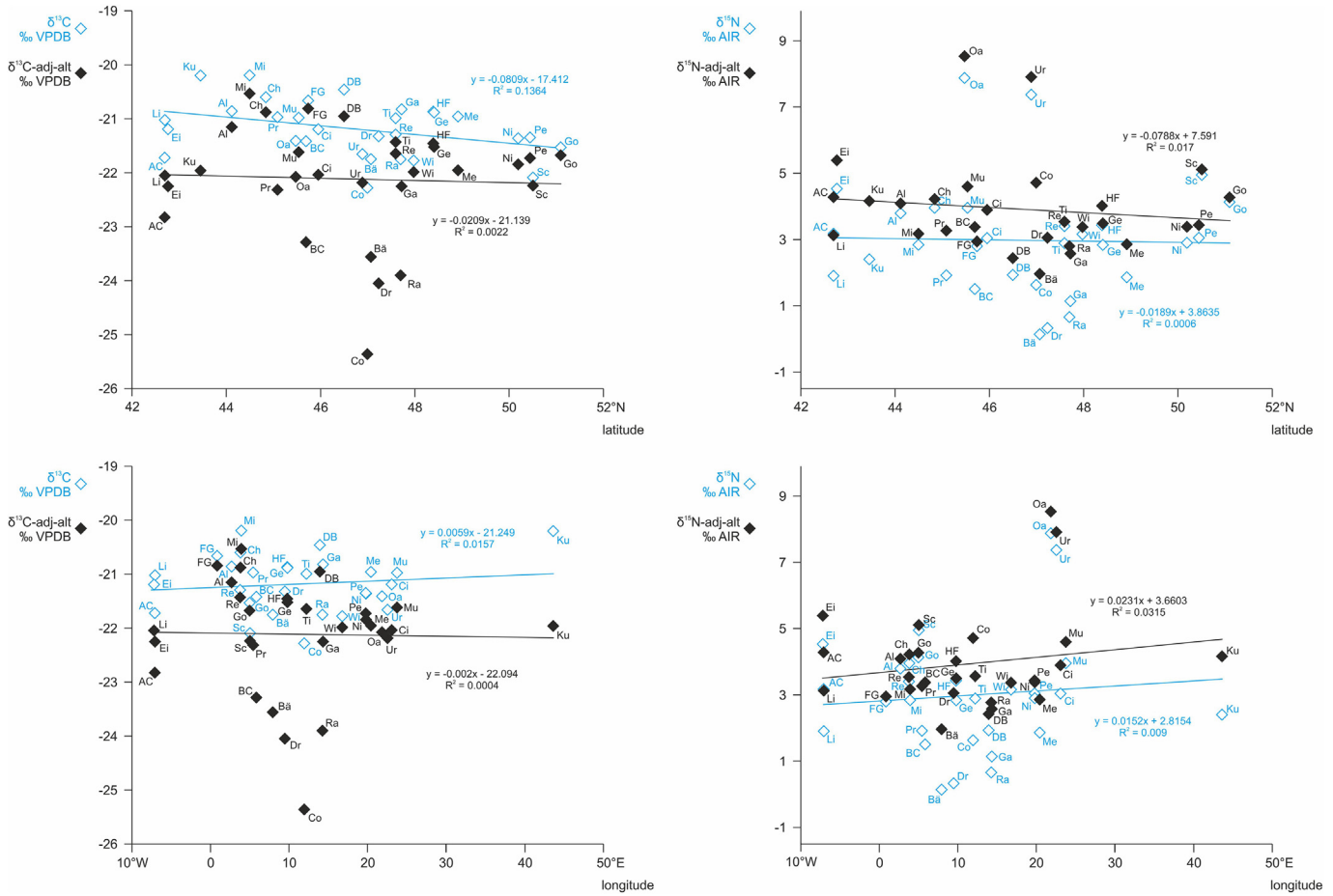
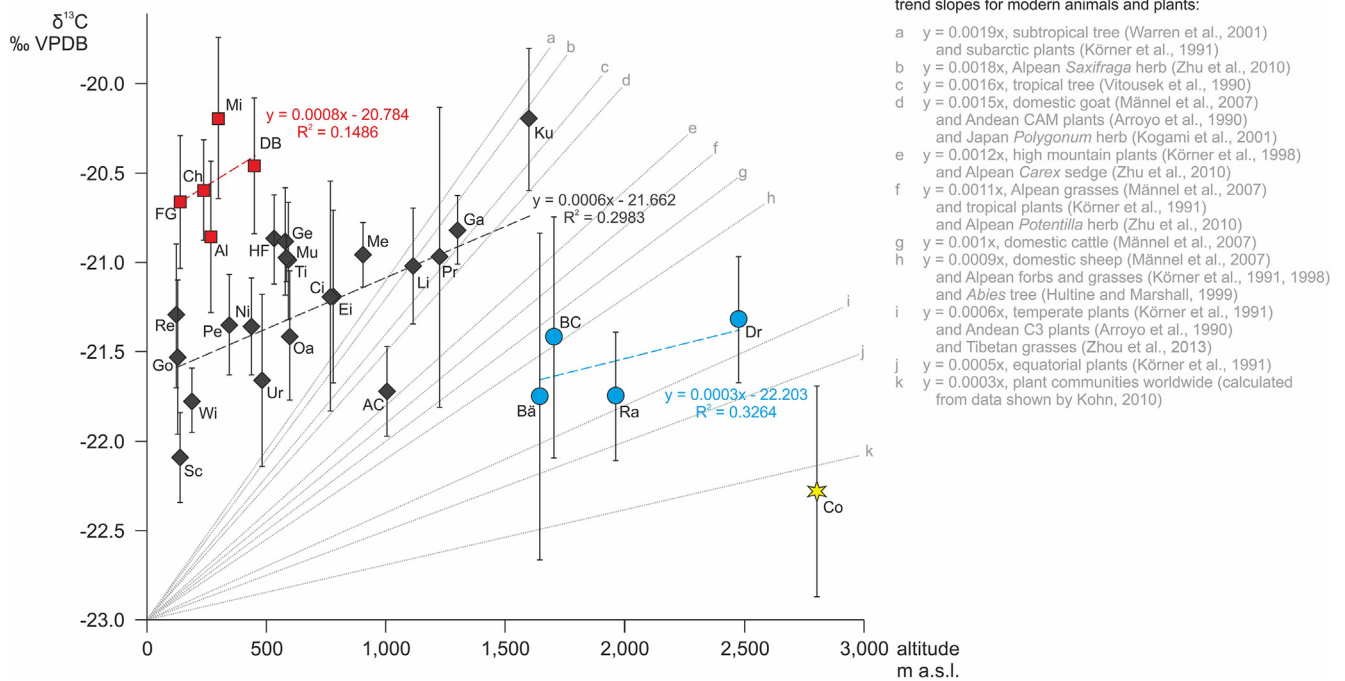


Fig. 5. Raw average isotopic values (open diamonds) and altitudinal adjusted (dark diamonds) plotted against latitude (upper diagrams) and longitude (lower diagrams) of sites.



trend slopes for modern animals and plants:

- a $y = 0.0019x$, subtropical tree (Warren et al., 2001) and subarctic plants (Körner et al., 1991)
- b $y = 0.0018x$, Alpean *Saxifraga* herb (Zhu et al., 2010)
- c $y = 0.0016x$, tropical tree (Vitousek et al., 1990)
- d $y = 0.0015x$, domestic goat (Männel et al., 2007) and Andean CAM plants (Arroyo et al., 1990) and Japan *Polygonum* herb (Kogami et al., 2001)
- e $y = 0.0012x$, high mountain plants (Körner et al., 1998) and Alpean *Carex* sedge (Zhu et al., 2010)
- f $y = 0.0011x$, Alpean grasses (Männel et al., 2007) and tropical plants (Körner et al., 1991) and Alpean *Potentilla* herb (Zhu et al., 2010)
- g $y = 0.001x$, domestic cattle (Männel et al., 2007)
- h $y = 0.0009x$, domestic sheep (Männel et al., 2007) and Alpean forbs and grasses (Körner et al., 1991, 1998) and *Abies* tree (Hultine and Marshall, 1999)
- i $y = 0.0006x$, temperate plants (Körner et al., 1991) and Andean C3 plants (Arroyo et al., 1990) and Tibetan grasses (Zhou et al., 2013)
- j $y = 0.0005x$, equatorial plants (Körner et al., 1991)
- k $y = 0.0003x$, plant communities worldwide (calculated from data shown by Kohn, 2010)

Fig. 6. $\delta^{13}\text{C}$ (raw data) plotted against altitude. Knowing the expected altitudinal gradient (grey lines – different trends according to different authors; note that only trend directions are shown here, not absolute values), we may try to divide data into several groups (marked by squares, diamonds, circles and star), each of them showing a trend similar to expected altitudinal gradient.

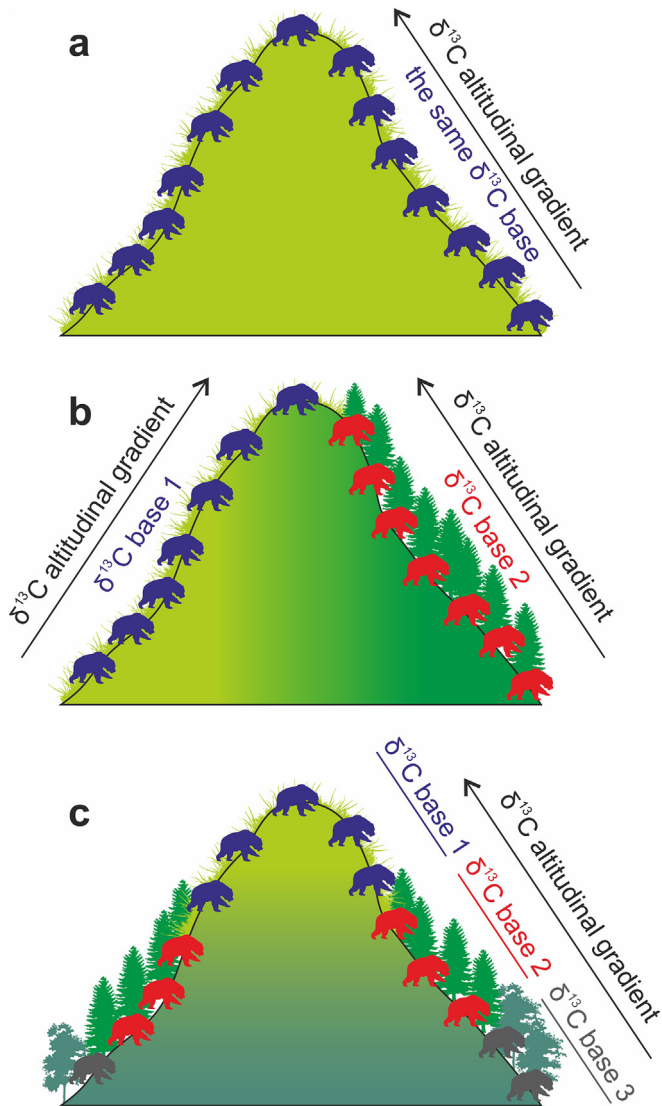


Fig. 7. Scheme showing the possible mechanisms responsible for different values of $\delta^{13}\text{C}$ in different populations: **a** – all animals inhabit one vegetation zone and follow the same altitudinal gradient; **b** – animals from regions occupied by different biomes or with different conditions exhibit different $\delta^{13}\text{C}$ base; **c** – animals from elevations occupied by different vegetation zones exhibit different $\delta^{13}\text{C}$ base; in situations b and c the altitudinal gradient is the same in each population, but the absolute values are shifted.

Oase and Urşilor) always form an outstanding cluster. These sites are famous for their unusually high $\delta^{15}\text{N}$ values (Richards et al., 2008; Robu et al., 2013; Bocherens, 2015). Reconsidering Romanian data in terms of altitudinal gradient of isotopes (Fig. 11b,c), these sites still remain the most isotopically distinct in Europe. Addition of new sites from Central-Eastern Europe, which are relatively geographically close to the Romanian ones, did not reveal similarities between them and Peştera cu Oase and Urşilor.

All other sites are grouped together, but can also be divided into subclusters. The arrangement of these subclusters changes along different adjusting treatment. Some general patterns however appear. A distinct group of bears in terms of stable isotopes are those from the high Alpine region (Fig. 11a–c). Remains of bears found in Alpine caves situated over 1500 m a.s.l. (Conturines, Ramesch, Drachenloch, Bärenloch, Balme à Collomb) are characterized by low to extremely low $\delta^{15}\text{N}$ values and average to low $\delta^{13}\text{C}$

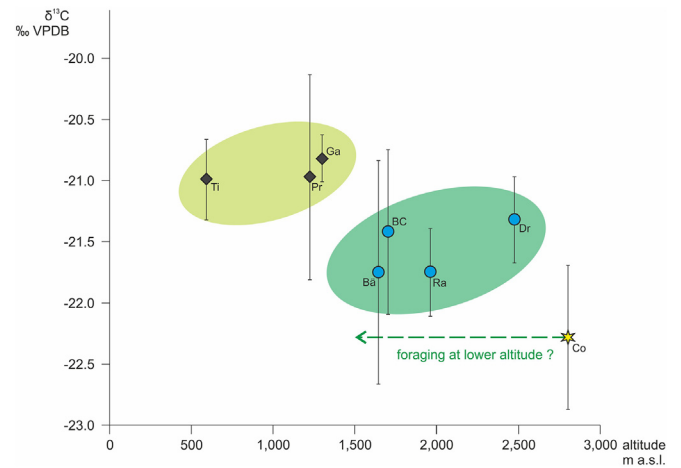


Fig. 8. $\delta^{13}\text{C}$ average values of Alpine sites plotted against altitude. Two subpopulations may be found, corresponding to lower and higher elevations. Conturines may represent the high Alpine group (explanation in text).

values. The most elevated cave bear site, Conturines (2800 m a.s.l.), represents the most extreme case of Alpine isotopic signature, with the lowest $\delta^{13}\text{C}$ values in Europe. The second distinct group is formed by Scladina, Cova Eiros and A Ceza, all situated in Western Europe. These sites are characterized by relatively high $\delta^{15}\text{N}$ values and extremely low $\delta^{13}\text{C}$ values. They tend to cluster together if altitudinal adjustment is applied (Fig. 11b and c), which means that isotopic signature in this case is strongly altitude-related, although Scladina is distinct from other sites even if raw data are analysed. All other sites form one wide cluster (Fig. 11a–c). The statistical similarity of these sites becomes slightly rearranged along different adjusting treatment, however the isotopic similarity remains. Cave bears of these sites lived in lowland and upland regions, ranging from the westernmost to easternmost fringes of Europe (Fig. 11: maps). The sites corresponding to this group are located at different altitudes, from 125 to 1600 m a.s.l.

The group of Mediterranean/Atlantic sites that differs in $\delta^{13}\text{C}$ values (red squares on Figs. 6 and 9) is less distinct if both carbon and nitrogen values are analysed together (Fig. 11). If altitudinal adjustment is applied, three of these sites (Divje Babe, Mialet and Font-de-Gaume with Olaskoa) tend to cluster together, however still remain similar to most of European sites.

5.4.2. Isotopic variability and cave bear taxonomy

The isotopic variability of cave bears does not seem to be related to taxonomic position, although such relation was observed on the local scale, between particular pairs of sites (Bocherens et al., 2011b; Bocherens, 2015). The various genetic forms, named *U. kudarensis*, *U. spelaeus*, *U. ingressus* and *U. ladinicus*, are scattered among different clusters. Cave bear from Conturines, included to *U. ladinicus* species (Hofreiter et al., 2002), seems to represent the isotopically distinct form (Fig. 11). However, other sites with cave bear identified as *U. ladinicus* (Grotte du Renne and Prélétang, according to Orlando et al., 2002; Frischauf et al., 2010) do not tend to cluster together with Conturines, which does not allow us to treat *U. ladinicus* as an ecologically distinct taxon. The most genetically distinct form, *U. kudarensis* from Caucasus (Baca et al., 2012), is characterised by relatively high $\delta^{15}\text{N}$ values (Bocherens, 2015), but altitudinal correction reveals the isotopic similarity of this bear to both *U. spelaeus* and *U. ingressus* from different parts of Europe (compare Fig. 11b and c and Table 3).

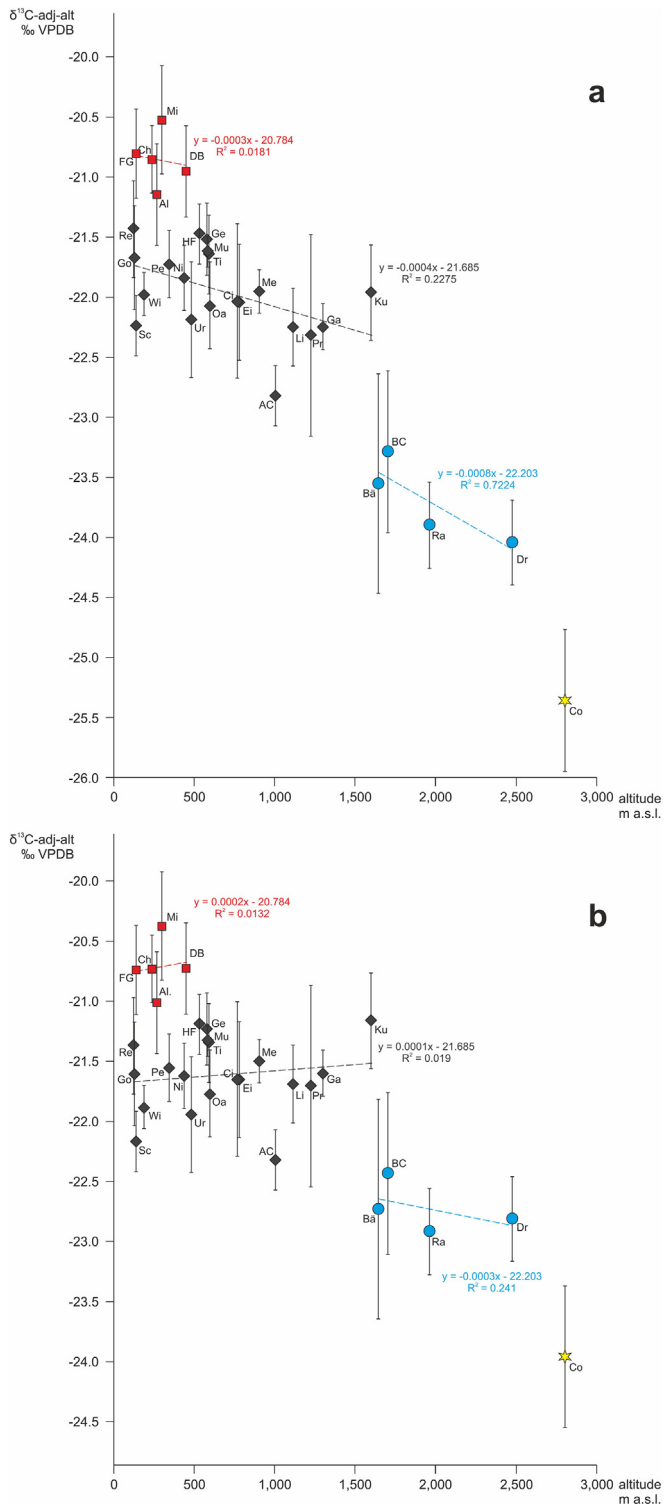


Fig. 9. Altitudinal adjusted $\delta^{13}\text{C}$ average values of sites plotted against altitude. Adjustments use altitudinal gradients: **a** – 0.0011‰/m reported for modern Alpine plants and grazers by Männel et al. (2007); **b** – internal gradient 0.0006‰/m calculated for main group of cave bear sites (black diamonds at Fig. 6). Symbols are the same as used in Fig. 6.

5.4.3. Central-Eastern European cave bears and unusual Romanian isotopic pattern

All newly studied Central-Eastern European sites (Medvedia Cave, Nietoperzowa Cave, Perspektywiczna Cave and Winden) are

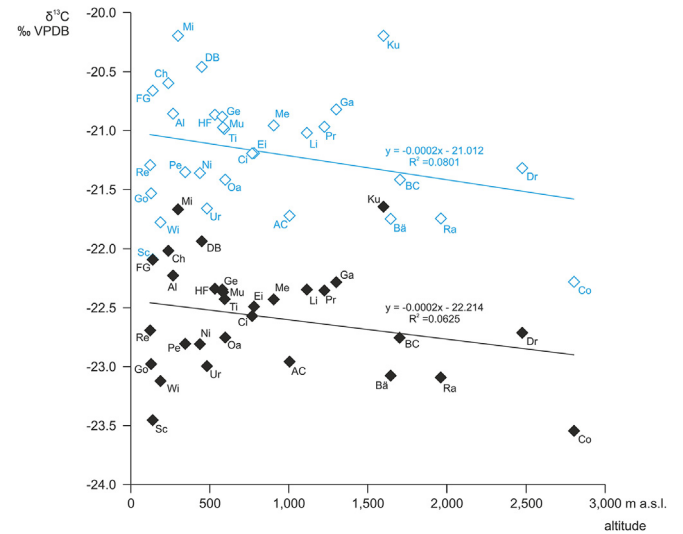


Fig. 10. Impact of latitudinal adjustment on the altitudinal gradient exhibited by $\delta^{13}\text{C}$ average values of sites. Open symbols – raw values; black symbols – values adjusted with use of 0.0255‰/° latitudinal gradient according to Körner et al. (1991).

clustering together independently of the adjusting treatment. After altitudinal adjustment these sites become even more similar (Fig. 11b and c), which indicates very similar palaeoecology of bear populations from these sites, and most of observed differences (Fig. 11a) are caused by elevation. Central-Eastern European sites exhibit isotopic similarity to most sites of Central, Western and Southern Europe and Caucasus, but are clearly distinct from both mentioned Romanian sites and group of high Alpine sites.

The newly added Central-Eastern European sites filled the gap in a map of Europe, and are situated relatively closely to two unusual Romanian sites, Peștera cu Oase and Urșilor. However, isotopic signatures of cave bears from Austria, Poland and Slovakia are clearly far from Romanian cave bears with unusually high $\delta^{15}\text{N}$ values. New data had emphasised the isotopic uniqueness of Romanian sites.

The attempt to explain the isotopic isolation of Romanian sites is beyond the scope of this paper. The hypothesis that this cave bear population had a more omnivorous diet, including meat and/or fish, was presented by Richards et al. (2008). The Romanian cave bear $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures were presented as overlapping on those of modern omnivorous brown bears (Robu et al., 2013). Bocherens et al. (2014b) also discussed this problem and showed that the most herbivorous modern brown bears overlap with the Romanian cave bears, while more carnivorous modern brown bears are clearly different from the Romanian cave bears. In addition, these Romanian cave bears overlap only with two types of Pleistocene herbivores: the woolly mammoths and the fallow deer (Bocherens, 2015). Another possibility is that these bears still had a herbivorous diet, but that they relied on a different type of plant food than the other cave bear populations, more similar to that consumed by mammoth or fallow deer (Bocherens, 2015). Instead of a carnivorous diet, these cave bears with high $\delta^{15}\text{N}$ may have recorded in their bone collagen the isotopic signature of hibernation (Grandal d'Anglade and Fernández Mosquera, 2008). The Romanian cave bears with unusual nitrogen isotopic signature seem to follow the general pattern presented by Fernández-Mosquera et al. (2001), according to which the higher $\delta^{15}\text{N}$ values may have been connected with longer time of hibernation during cool periods of Pleistocene. However, since other cave bear populations that lived during the same time interval (MIS 3) do not

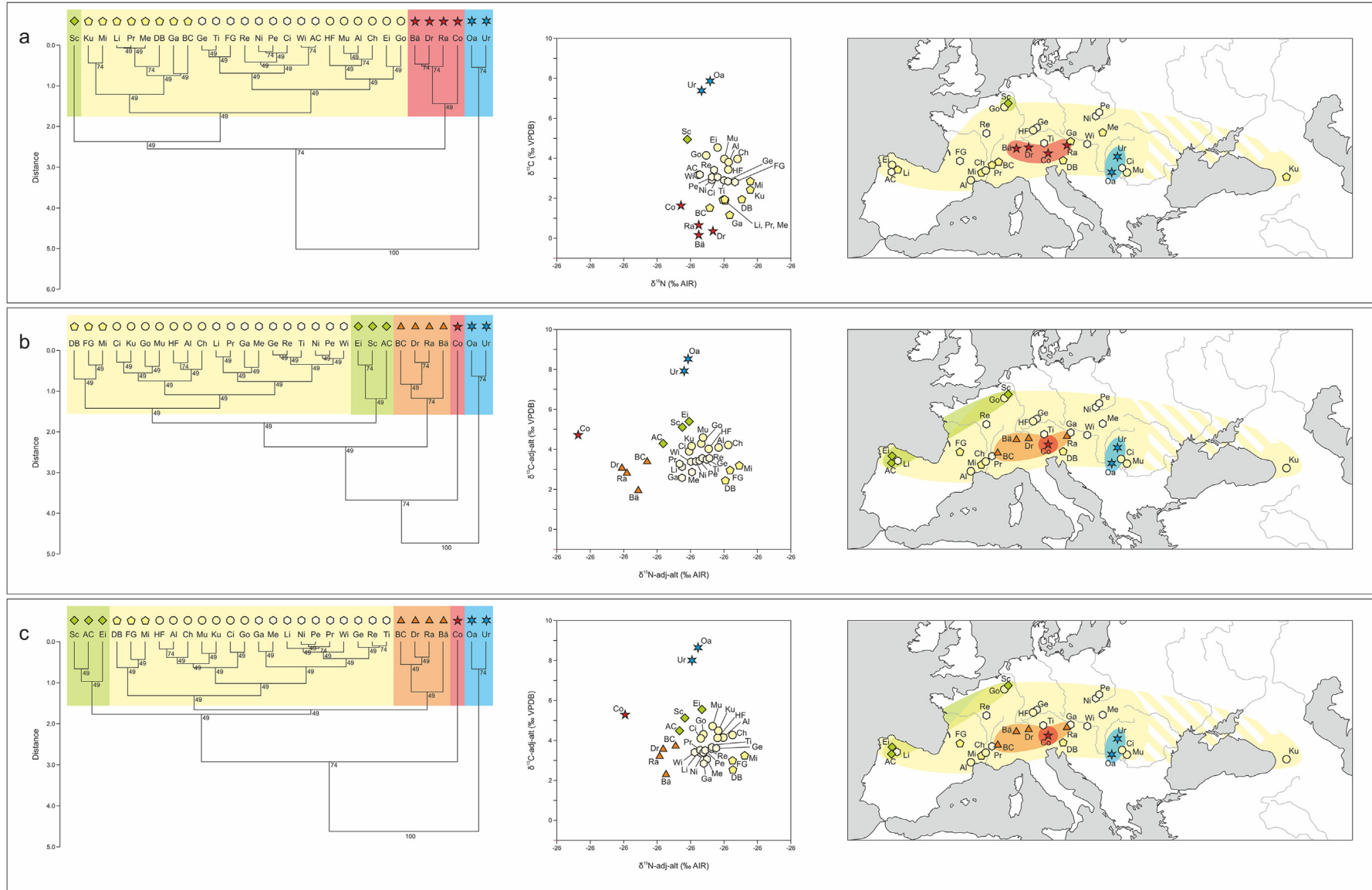


Fig. 11. Results of cluster analysis of the isotopic similarity of MIS 3 cave bears sites with regards to average values of collagen carbon and nitrogen isotopic signature, supplemented with carbon/nitrogen average ratios plots and map of the distribution of clusters in Europe: **a** – $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ raw values (coph. corr. = 0.8785); **b** – $\delta^{13}\text{C}$ -adj-alt and $\delta^{15}\text{N}$ -adj-alt adjusted with use of altitudinal gradients 0.0011‰/m for $\delta^{13}\text{C}$ and -0.0011 ‰/m for $\delta^{15}\text{N}$ according to Männel et al. (2007) (coph. corr. = 0.9211); **c** – $\delta^{13}\text{C}$ -adj-alt and $\delta^{15}\text{N}$ -adj-alt adjusted with use of internal altitudinal gradients 0.0006‰/m for $\delta^{13}\text{C}$ and -0.0013 ‰/m for $\delta^{15}\text{N}$ (coph. corr. = 0.9267).

exhibit such signature, a question arises: why would some bears have stronger impact of physiology than others? It is possible that not only climate controlled the duration of hibernation. The duration of winter sleep also depended on biological factors, as it is in case of modern bears (Seryodkin et al., 2003; Manchi and Swenson, 2005; Baldwin and Bender, 2011).

In the light of analysis of geographic variability of cave bear isotopic signature presented in this study, the locations of Romanian sites with high $\delta^{15}\text{N}$ values sites are not connected to latitude or longitude. Although the cave bear isotopic signature is driven by altitude, the altitudinal adjustment of isotopic data is not enough to explain the isotopic dissimilarity of these cave bears. Further investigations are required to understand the reason for such isotopic isolation. Especially the analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of more sites located to the south of Romanian ones are necessary, to widen the regional context of these unusual sites.

6. Conclusion

In this study the results of new isotopic analysis of cave bear collagen from four Central-Eastern European sites were presented and the spatial variation of cave bear collagen isotopic values in Europe was discussed.

This study demonstrates that there is no geographical East-West and South-North pattern of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of cave bear collagen in assemblages dated to MIS 3. The distribution of isotopic signature does not vary with relation to longitude nor latitude. This means that the shift from oceanic climates in Western Europe to more continental climates in the eastern part of the continent was not a main agent affecting the cave bear ecology during MIS 3. The cave bears from Central-Eastern Europe exhibit the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values near the middle of the range typical for most of the cave bears from Central, Western and Southern Europe. This isotopic homogeneity may either reflect the climatic and vegetational unification of ecosystem, which stays in contradiction to palaeoclimatic data, or may be a characteristic of cave bear, for example due to low ecological flexibility. This phenomenon needs further study and has to be also investigated in the case of other European mammalian species during MIS 3.

Most of the cave bear sites in Europe follow an altitude-related isotopic pattern. Altitudinal gradient $-0.0013\text{‰}/\text{m}$ of $\delta^{15}\text{N}$ values is followed by most of sites except of two Romanian sites Peștera cu Oase and Urșilor, exhibiting unusually high $\delta^{15}\text{N}$ signature. In case of $\delta^{13}\text{C}$ values the expected increasing altitudinal gradient is visible in several groups of sites, but these sets exhibit the group-to-group shift of absolute values. The most abundant group of sites reveals $0.0006\text{‰}/\text{m}$ internal gradient of $\delta^{13}\text{C}$ values. The other groups of sites also exhibit increased altitudinal gradient, however with absolute values shifted. The most distinct of such groups are high Alpine sites situated over 1500 m a.s.l.

The unusual nitrogen isotopic values of Romanian cave bears from Urșilor and Peștera cu Oase, observed by Robu et al. (2013) and Richards et al. (2008), are isolated cases in Europe. These outstanding isotopic signatures are probably local phenomenon, as the locations of these sites are not connected to any basic geographical factor such as altitude, latitude or longitude. Also the distance from the sea coast may not be a responsible factor. The new isotopic data for Central-Eastern European cave bears emphasized the unusual isotopic values of these two Romanian cave bear populations, for which further investigations are required to understand the reason for such values, since omnivory is not the sufficient explanation (Bocherens et al., 2014b; Bocherens, 2015).

Data on isotopic variability of European cave bears presented in this study may serve as a background for further research on palaeoecology and palaeogeography of this taxon.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.quascirev.2015.10.028>.

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