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Palaeodiet during the pre-dormancy period of MIS 3 Romanian cave bears as inferred from dental microwear analysis

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ABSTRACT

Cave bears (*Ursus spelaeus*) have been recognized as being predominantly herbivorous. However, Romanian Carpathian cave bears have displayed a flexible diet based on a wide range of δ^{15}N values. In this work, we analyse 97 lower first molars of *Ursus spelaeus* and contemporaneous *Ursus arctos* from different sites in this region, using dental microwear analysis to reconstruct their pre-dormancy diets during MIS 3. Newly obtained radiocarbon dates of the individuals are also reported. The short-term diet of all populations studied is identified as omnivorous, with a preference for the consumption of hard objects. For the first time, the widespread presence of puncture pits on *U. spelaeus* populations has been observed, which could be linked to the intake of seeded and hard-shelled fruits from temperate broadleaf trees. Hence, the dietary patterns of Carpathian cave bears exhibit similarities to those of present-day brown bears inhabiting the same region and suggests that the Carpathians served as an ecological refuge for cave bear specimens. This is reinforced by an early 27.1 cal kyr B.P. date from an individual from Urşilor Cave, which sheds light on the potential dietary continuity of Romanian Carpathian cave bear populations even during the final phases leading up to their extinction.

1. Introduction

The Late Pleistocene was marked by significant climatic changes, particularly during the Last Glacial Period, the Weichselian glaciation, in Europe (Bond et al., 1999; Dansgaard et al., 1993; Rasmussen et al., 2014). The Dansgaard-Oeschger (D—O) climatic fluctuations, especially during MIS 3 (60–27 kyr B.P.), resulted in persistent ecological instability, causing rapid and frequent shifts between drastically different vegetation, within brief time intervals (Wohlfarth et al., 2008; Huntley et al., 2013; Sánchez Goñi, 2022). The environmental instability at the end of the Pleistocene was a primary factor in the extinction or displacement of a significant portion of the European megafauna that dominated European landscapes since the Middle Pleistocene, including the iconic large herbivores, as well as members of the carnivore clade (Stuart and Lister, 2012). Carnivores, despite their further adaptability to various biomes, do not depend directly on a specific habitat like herbivores (Hunter and Turner, 1997). They also experienced a significant population decline and displacement (Varela et al., 2010; Stuart and Lister, 2011), and in some cases extinction (Pacher and Stuart, 2009). This phenomenon has been proposed as being greatly influenced by the displacement and extinction of populations of large herbivores, which formerly constituted their primary food source (Croitor and

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Brugal, 2010; Stuart and Lister, 2011; Varela et al., 2010). The carnivores that prevailed and occupied the ecological niche of those extinct species were smaller-sized carnivores and omnivores with broad dietary habits (Sommer and Benecke, 2005; Croitor and Brugal, 2010) such as brown bears (*Ursus arctos*), which during the end of the Pleistocene decreased in size as a response to the climatic and environmental instability (Marciszak et al., 2015). An ecologically singular member of the carnivore order that was among the first to go extinct was the cave bear (*Ursus spelaeus*), at about 28 kyr B.P. in western Europe (Pacher and Stuart, 2009; Bocherens et al., 2014; Baca et al., 2016). There are various hypotheses regarding the causes of extinction. One identified factor contributing to the extinction is a long genetic decline leading to populations shrinking (Stiller et al., 2010). Furthermore, particular hibernation behaviours linked to a dependency on caves, unlike the closely related linage of brown bears (*U. arctos*), led them to indirectly compete for these spaces with humans and to be especially susceptible to hunting (Fortes et al., 2016). This last theory, which attributes part of the reasons for the extinction to humans, is supported by evidence of cut marks found on cave bear remains throughout Europe during the MIS 3 period (Armand et al., 2004; Münzel and Conard, 2004; Terlato et al., 2019; Blasco et al., 2020). Finally, a well-established theory suggests that their extinction can be attributed to the declining availability of plant-based resources (Pacher and Stuart, 2009; Bocherens, 2019). The cave bear is an exceptional example of an evolutionary adaptation, transitioning from a carnivore-scavenger dominated niche to establishing an ecological similarity with the niche occupied by the large-sized herbivores of the Middle Pleistocene (Croitor and Brugal, 2010).

Studying the diet of this species is crucial to understand its ecological and geographical distribution during the Pleistocene, as it currently does not seem to resemble any of the extant bear species alive today. The diet of the cave bear has been inferred as having predominantly relied on plants, as indicated by wear gradients and dental morphology (Terzea, 1966; Kurten, 1976; Jurcsák et al., 1981) and further supported by multiple isotope analyses of both carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) on bone collagen (Bocherens et al., 1994, 1997, 2006, 2011, 2014; Nelson et al., 1998; Vila-Taboada et al., 1999; Fernández-Mosquera et al., 2001; Münzel et al., 2011; Krajcarz et al., 2016; Naito et al., 2016; Bocherens, 2019; Ramírez-Pedraza et al., 2019) and three-dimensional analysis of tooth-root morphology (Pérez-Ramos et al., 2019).

Nevertheless, some other studies of Romanian Carpathian cave bears have pointed towards a flexible omnivore diet suggested by a wide range of $\delta^{15}N$ values (Richards et al., 2008; Robu et al., 2013, 2018), which is supported by morphological and dental wear analysis (Figueirido et al., 2009; Peigné et al., 2009). However, a recent study conducted on Romanian cave bears analysing nitrogen isotopic amino acids has presented evidence for a predominantly herbivorous diet for these populations (Naito et al., 2020). The study revealed that the elevated nitrogen values previously recorded in some Romanian cave bears could be attributed to the consumption of specific plant species characterized by high bulk $\delta^{15}N$ values (Naito et al., 2020). In addition, Grandal-d'Anglade et al. (2019) suggested that the high nitrogen values observed in Romanian cave bears could potentially be attributed to urea reuse processes during hibernation. Nevertheless, the wide range of results obtained using long-term inferences of dietary proxies (isotopes and amino acids) might suggest lifelong dietary flexibility of this species depending on multiple factors such as the geographical and ecological context, as well as the degree of competition for available resources, but under a plant dominated diet (Robu et al., 2013; Krajcarz et al., 2016; Naito et al., 2020).

A well-established method to infer short-term dietary patterns is microwear analysis. Low magnification microwear analyses identify microscopic features left by abrasive particles on the enamel of the occlusal surface during chewing with the goal of inferring the dietary ecology of the animal (Solounias and Semprebon, 2002; Semprebon et al., 2004). The constant formation of new features erases the previous ones, which means there is a record of the diet on a much shorter time scale than morphological, macroscopic dental wear and isotopic or amino acids analyses (Solounias and Semprebon, 2002). Thus, one can detect seasonal or occasional dietary regimes that would not be seen through other methods (Grine, 1986). Dental microwear studies had been carried out on cave bears in the past years (Ramírez-Pedraza et al., 2019, 2020, 2022). These have revealed a high variability in dietary habits among cave bear populations from different locations in Europe during the Late Pleistocene. The short-term microwear signal exhibited a varied and less specialized diet, before death, for individuals with low nitrogen values (i.e. long-term herbivorous diet) (Ramírez-Pedraza et al., 2019). Furthermore, when comparing different populations of cave bears from distinct yet closely located geographical areas in northeastern Iberia, they exhibit significant dietary variability. This variation ranges from carnivorous to more omnivorous signals, as documented by Ramírez-Pedraza et al. (2020) and could be attributed to different ecological adaptations to distinct paleoenvironmental contexts from different periods of the highly climatically variable MIS 3. Furthermore, cave bears from northeastern Europe displayed a general herbivorous diet but also exhibited occasional consumption of other things, demonstrating a remarkable capacity for dietary flexibility linked to a locally specific adaptability due to niche partitioning (Ramírez-Pedraza et al., 2022).

In this work our purpose is to analyse several populations from the Romanian Carpathians using dental microwear analysis (DMA) to infer the diet of the last weeks before the death of the individuals. It is interesting to study this region during a period close to the extinction of the cave bear, in a context where the Carpathians experienced significant climatic instability (Constantin et al., 2007), although they also served as a refuge for fauna and flora, hosting diverse ecosystems beyond the steppe (Sommer and Nadachowski, 2006; Magyari et al., 2014). Therefore, the Carpathian Mountains recorded a wider range of dietary patterns than other more environmentally homogeneous regions. Furthermore, we present the largest sample of cave bear individuals from southeastern Europe analysed using this method, in relation to already published stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) (Richards et al., 2008; Robu et al., 2013, 2018) and new chronological dates. This allows us to correlate them with the climatic conditions they experienced and to examine their lifelong diet as well as their diet during specific periods, particularly before hibernation. Additionally, our work includes samples from different regions of the Carpathian Mountains: Urşilor Cave (northwest), Oase (southwest), Bisericuța (central-northwest), Muierilor Cave (central-southwest), Onceasa (northwest), Avenul Măţului (northwest), La Adam (southeast) and the Cloșani area (southwest) which can indicate different paleoenvironmental contexts and specific adaptations. To these we added contemporary *U. arctos* individuals with which we compare patterns and observe different dietary responses and adaptations to varying geographic and paleoclimatic contexts.

2. Materials and methods

2.1. Sample selection

The materials analysed in this study are housed at the "Emil Racoviță" Institute of Speleology (ERIS), Romanian Academy. A total of 97 lower first molars ($n = 97$) were carefully selected, belonging to a diverse range of individuals, including juveniles, adults in their prime, and older adults of both sexes. The inventory of specimens – sampled and analysed along with its microwear raw data and their corresponding previously recorded stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) (Robu et al., 2013, 2018) – is available in the Supplementary Materials (ST1).

2.2. Sampled sites and context

We sampled MIS 3 cave bears and modern brown bears from some of the most relevant sites from the Romanian Carpathians (Fig. 1), where

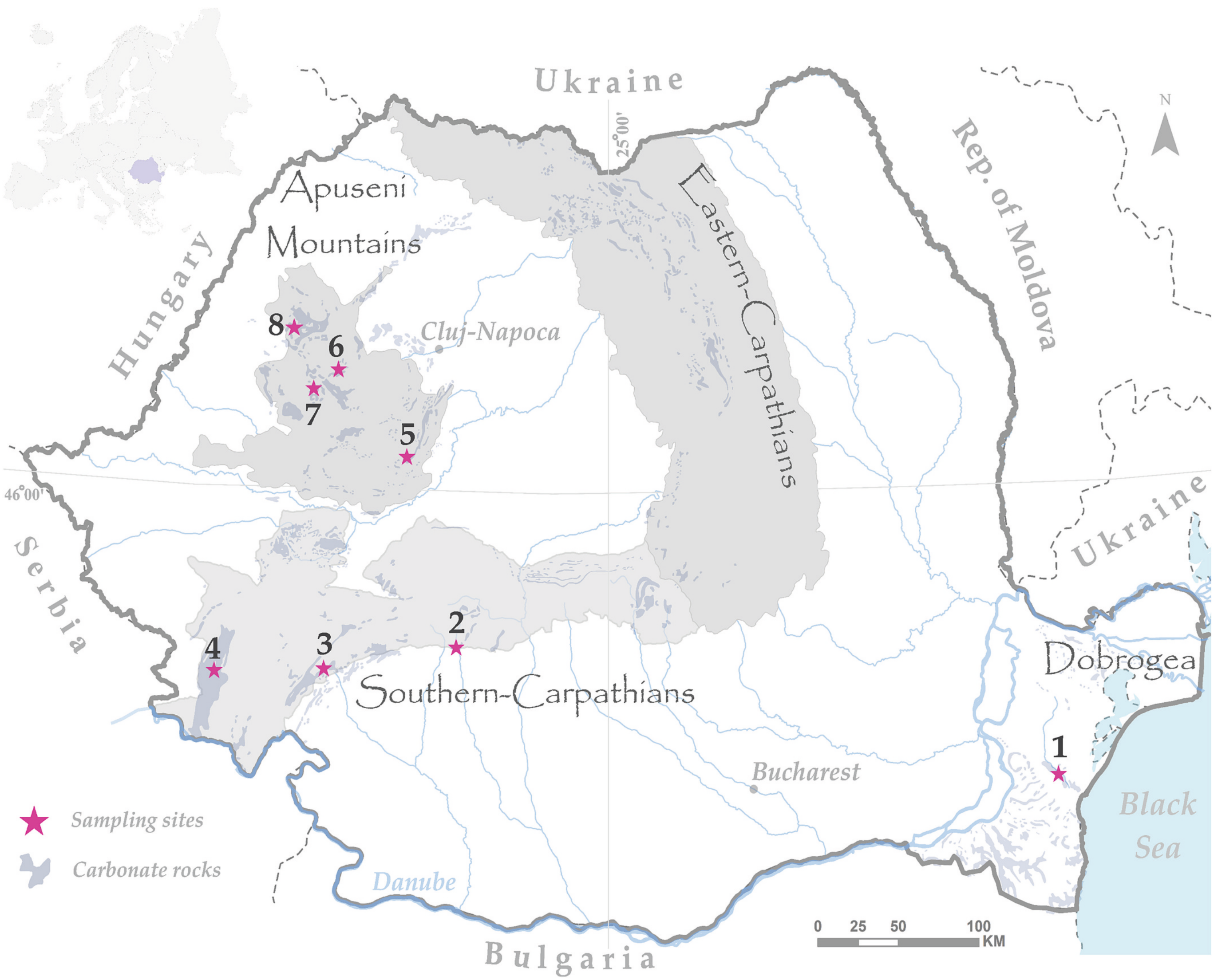

Fig. 1. Location of the sampled MIS 3 cave bear sites in the Romanian Carpathians. 1 – La Adam; 2 – Muierilor; 3 – P.-Aven nr. 2 din Cracul de la Cioaca Goală (ACCG; Cloșani); 4 – Oase; 5 – Cioclovina; 6 – Onceasa; 7 – Urșilor; 8 – Avenul Mâțului.

systematic palaeontological excavations have been carried out during the last two decades, primarily by our team (e.g. Constantin et al., 2014; Mirea et al., 2021).

Urșilor Cave (henceforth: Urșilor) is situated in the Apuseni Mountains, northwestern Romania (46° 55′ 37″ N, 22° 56′ 92″ E; Fig. 1). Urșilor is one of the most emblematic show caves in the region, given the impressive MIS 3 cave bear bone assemblage (Robu, 2016a). The cave has a total length of ca. 1500 m, roughly divided into two levels (a hydrologically inactive upper one and a hydrologically active lower one; Constantin et al., 2014). The sampled area was the Excavation Chamber, from the lower level of the cave (the scientific reserve), where a ca. 10 m^2 paleontological excavation has been in progress since 2010. The thanatocoenosis is cave bear dominated and spans the time from ca. 47 to 39.5 cal kyr B.P. (Constantin et al., 2014; Robu, 2016b).

Peştera cu Oase (henceforth: Oase) is located in the Banatului Mountains, southwestern Romania (45° 05′ N, 21° 51′ E – coordinates imprecise for conservation concerns; Fig. 1). Oase is a typical through-cave, with a total length of ca. 2000 m (Constantin et al., 2013; Fig. 1), famous for harbouring one of the earliest anatomically modern humans in Europe (Trinkaus et al., 2013). The cave has roughly two karstic levels, a hydrologically inactive upper karstic level and an active lower one. The analysed cave bear samples were excavated from the upper level of the cave (Sala Mandibulei and Panta Strămoşilor) and were dated to ca. 50–41.5 cal kyr B.P. (Higham and Wild, 2013).

Muierilor Cave (henceforth: Muierilor) is situated in the Căpățânii Mountains, in the southern part of the Southern Carpathians (45°11′29″ N, 23°45′14″ E; Fig. 1). It is a ca. 8000 m long complex cave system along five levels, the lowest one being hydrologically active. The cave is also known for the discovery of early modern human remains (Doboş et al., 2010). The MIS 3 cave bear material was extracted from Galeria Urşilor (Bears' Passage), from a 9 m^2 palaeontological excavation and was dated between ca. 51–29 cal kyr B.P. (Doboş et al., 2010; Robu, 2015; Mirea et al., 2021).

Onceasa Cave (henceforth: Onceasa) is located in the Apuseni Mountains, northwestern Romania (46° 39′ 41″ N, 22° 45′ 46″ E). It is one of the richest MIS 3 cave bear bone deposits in the Romanian Carpathians and it consist of ca. 350 m of large passages. The analysed MIS 3 cave bear bone material was sampled from the ERIS's palaeontological collection and was extracted from the cave during the 1960s (Terzea, 1966).

Bisericuța Cave (henceforth: Bisericuța) is located in the Trascăului Mountains, western Romania (46° 12′ N, 23° 20′ E – coordinates imprecise for conservation concerns). It consists of ca. 100 m of hydrologically inactive passages. The sampling area is situated at the bottom of a small shaft in the excavation chamber (3 m^2). The deposit comprises an important MIS 3 cave bear bone assemblage at the lower level of the cave, dated to ca. 50–31 cal kyr B.P. (unpubl. data).

La Adam Cave (henceforth: Adam) is situated in the Dorobanțului Plateau, in the southeastern part of Romania, close to the Black Sea (44° 27′ 44″ N, 28° 28′ 15″ E). It is one of the richest Late Pleistocene sites from this region, in terms of species' diversity and has a total length of ca. 100 m. The MIS 3 cave bears, stored in the ERIS's collection and analysed here, were excavated during the 1960s (Dumitrescu et al., 1966).

Peștera-Aven din Cracul de la Cioaca Goală (henceforth: ACCG; 45° 03′ 50″ N, 22° 41′ 49″ E) is a ca. 50 m-long vertical-horizontal cave, with a ca. 20 m drop from its entrance, situated in the Cloșani area of the Mehedinți Mountains, in the southwestern Carpathians. In 2011, our team collected, from the undisturbed surface of the cave, the bones of three medieval brown bear individuals (one sub-adult female, a juvenile and a sub-adult male; Ersmark et al., 2019) were found close to the shaft's bottom, identified and partially collected.

Avenul Mâțului (46° 50′ 07″ N, 22° 23′ 46″ E) is a ca. 100 m-long vertical and horizontal cave from the Cuților Gorges, in the western part of the Apuseni Mountain group (Pădurea Craiului Mountains). In 2018, our team collected samples from a female brown bear skeleton, found at the base of a ca. 20 m drop, inside the cave.

2.3. Tooth microwear

The samples were prepared following the protocol developed by Solounias and Semprebon (2002) and Semprebon et al. (2004). The occlusal surface of the teeth was cleaned using acetone, then 96% ethanol. A high-precision mould of the surface was made using polyvinylsiloxane silicone (Heraeus Provil novo, Light CD2, regular set) and a second layer using silicone putty (Heraeus Provil novo, Putty). Finally, transparent high-resolution casts were produced using epoxy resin (CTS EPO150 resin+K151 hardener). The casts were observed using a standard light stereomicroscope (Zeiss Stemi 2000C) at ×35 magnification to identify and quantify the microfeatures using an optical reticule of 0.16 mm^2 (Solounias and Semprebon, 2002; Semprebon et al., 2004). We examined the non-faceted and grinding enamel surfaces of the molars because they provide the most reliable reflection of the dietary patterns of ursid specimens, in comparison to other areas of the tooth surface (Ungar and Teaford, 1996; Münzel et al., 2014; Pappa, 2016; Pappa et al., 2019; Ramírez-Pedraza et al., 2019, 2020, 2022).

The features analysed in this work include (1) the number of fine and coarse scratches – elongated and narrow features, that can be classified as either fine (characterized by narrow and shallow marks) or coarse (distinguished by wider and deeper marks); and (2) the number of small and large pits: circular or semi-circular shapes with similar length and width. They can be classified as either small, which are characterized by being shallow and appearing as shiny, bright, white dots, or large, which are wider and deeper, reflecting less light. The scratch width score (SWS) was assessed by giving a score of 0 to enamel surfaces with predominantly fine scratches, a score of 1 to surfaces with a mixture of coarse and fine scratches, and a score of 2 to surfaces with predominantly coarse scratches. We also quantified the number of puncture pits (very deep and symmetrical crater-like morphology with regular margins) and number of gouges (crater-shaped but with irregular margins).

To reconstruct the paleodiet of the fossil populations, the obtained results were compared to the reference dataset of extant bear species established by Pappa et al. (2019). The reference collection allowed us to compare extinct ursids with their closely related living counterparts, *U. arctos*, from various regions (Kamchatka, Greece, Central Europe, Northern Europe, and North America) and *U. americanus* from North America. Both species exhibit a variety of food preferences, including consumption of vertebrates, invertebrates, hard mast, and soft mast. To prevent any inter-observer error, a sole observer (PDI) conducted the analysis on all specimens.

The graphs were generated using the software Past 4.02 (Hammer et al., 2001) and RStudio (version 4.1.2) (RStudio Team, 2021). Photomicrographs were captured using an Invenio 5SII digital camera in extended focus mode and the Helicon Focus software to combine the images acquired at different focal planes to create a single image with an increased depth of field. The scale bars were incorporated using ImageJ software.

2.4. Radiocarbon dating

For radiocarbon dating, we sampled cave bear ($n = 18$) and brown bear ($n = 1$) mandible bones from: Urşilor ($n = 10$), Oase ($n = 3$), Muierilor ($n = 4$) and Bisericuța ($n = 2$). The AMS ^{14}C dating was performed at the Poznan Radiocarbon Laboratory (Poland). Analytical procedures were described by Longin (1971) and modified by Piotrowska and Goslar (2002). The bone treatment followed the method described by Brock et al. (2010), including the collagen extraction, purification (using Elkay 8 μm filters) and ultrafiltration (Vivaspin 15 MWCO 30 kd filters). All radiocarbon data used here was calibrated using the OxCal v4.4.2 software (Bronk Ramsey, 2009; Bronk Ramsey, 2020) against the INTCAL13 radiocarbon calibration curve (Reimer et al., 2020). Moreover, available results from radiometric dating of the studied MIS 1 brown bears, previously published (Ersmark et al., 2019; $n = 1$), were added to our new data.

3. Results

3.1. Tooth microwear

A number of the 71 lower first molars (out of 97) were suitable for microwear analyses: 28 from Urşilor, 26 from Oase, 6 from Bisericuța, 3 from Muierilor, 3 from Onceasa, 2 from Adam, 2 from the Cloșani area and 1 from Avenul Mâțului. A total of 26 individuals were excluded from the analysis, comprising the youngest individuals without wear facets (sensu Rivals et al., 2007), as well as those with occlusal surface damage resulting from taphonomic processes (sensu King et al., 1999; El-Zaatari, 2010; Uzunidis et al., 2021; Micó et al., n.d.); from Cioclovina ($n = 2$) from the Cloșani area ($n = 3$), from Colțu Surpat ($n = 2$), from Magura ($n = 2$), Onceasa ($n = 3$), Oase ($n = 8$), and Urşilor ($n = 6$).

The tooth microwear results obtained for *U. spelaeus* from Urşilor ($n = 28$), Oase ($n = 26$) and Bisericuța ($n = 5$) present a very similar average for both the number total of scratches and pits (NTS and NTP) (Table 1). There is an analogue distribution of the numbers of fine (NFS) and coarse (NCS) scratches which slightly favours fine scratches, therefore reflected in a SWS close to 1 for all three populations. They also present similar average values of number of total pits (NTP), with a clear predominance of small pits. The number of small pits (NSP) ranges from 17.65 to 19.35 per counting area, while the number of large pits (NLP) ranges from 2.60 to 3.60 on average. All three populations exhibited puncture pits (NPP) (Fig. 2) which appeared equally distributed without significant variations within populations and between populations ($F = 0.9889$, $p = 0.3784$, mean square value $= 2.04$) and with a similar mean value ranging from 2.23 to 2.87 per counting area. Finally, regarding gouges, these are also present, with an average of around 1, varying from 0.60 to 1.12 per counting area.

The individuals from Muierilor ($n = 3$), despite constituting a small sample, exhibit a total score of scratches and pits that aligns with the trend observed in the more representative sites, albeit slightly lower (which can be attributed to the smaller number of individuals). As a result of the insufficient number of reliable samples, Muierilor was excluded from the further statistical multivariate analysis. The average number of total scratches (NTS) is 17 and the average number of total pits (NTP) is 21.72 per counting area. In addition, the three individuals from Muierilor display a higher average number of coarse scratches (NCS) compared to the sites of Urşilor, Oase, and Bisericuța. This is reflected by a higher SWS with an average of 1.67. When it comes to the distribution of pits, there is a clear predominance of small pits (NSP =

Table 1
Comparison of the dental microwear results of the fossil populations of *U. spelaeus* and *U. arctos* from the Romanian Carpathians with the reference dataset of extant bear species of *U. arctos* from different locations and *U. americanus* established by Pappa et al. (2019). Abbreviations: *n* = number of specimens, NFS = number of fine scratches, NCS = number of coarse scratches, NTS = number of total scratches, SWS = scratch width score, NLP = number of large pits, NSP = number of small pits, NPP = number of puncture pits, NTP = number of total pits, NG = number of gouges.

Species - Location	*n*	NFS	NCS	NTS	SWS	NLP	NSP	NPP	NTP	NG
Extinct										
U. spelaeus (Urşilor)	28	12.66	10.27	22.93	1.04	3.39	17.65	2.23	23.28	0.86
U. spelaeus (Oase)	26	13.00	10.05	23.05	1.04	3.60	19.35	2.87	25.81	1.12
U. spelaeus (Bisericuța)	5	14.27	9.10	23.37	0.80	2.80	19.03	2.50	24.33	0.60
U. spelaeus (Muierilor)	3	7.00	10.00	17.00	1.67	0.67	19.39	1.67	21.72	1.67
U. spelaeus (Onceasa)	3	15.17	10.00	25.17	1.00	5.00	17.33	1.00	23.17	0.00
U. spelaeus (Adam)	2	16.00	4.00	20.00	0.50	2.00	25.00	2.00	29.00	0.00
U. arctos (ACCG)	2	10.50	14.75	25.25	1.50	5.50	14.25	1.50	21.25	1.00
U. arctos (Bisericuța)	1	6.00	21.00	27.00	2.00	27.00	9.00	2.00	38.00	1.00
U. arctos (Avenul Mâțului)	1	4.00	20.00	24.00	2.00	10.00	20.00	3.00	33.00	0.00
Extant										
U. americanus (North America)	9	13.56	2.56	16.12	0.00	5.44	19.00	3.00	22.00	0.00
U. arctos (Greece)	4	13.00	7.00	20.00	0.5	9.25	8.50	2.25	20.00	2.00
U. arctos (Central Europe)	10	17.50	3.4	20.90	0.00	5.4	22.50	8.30	36.20	2.10
U. arctos (North America)	8	18.25	3.00	21.25	0.00	6.75	18.38	3.25	28.38	0.25
U. arctos (Kamchatka)	23	16.22	3.83	20.05	0.1	6.96	19.78	4.78	31.52	0.35
U. arctos (North Europe)	9	15.78	3.78	19.56	0.00	6.44	23.33	2.67	32.44	0.22

19.39) over large pits (NLP = 0.67). Additionally, the number of PP is 1.67, slightly exceeding the count in other sites. Finally, the number of gouges (NG) is higher in comparison to all other sites, scoring at 1.67.

The Onceasa site has a limited sample size, consisting of only 3 individuals. Consequently, the obtained values lack statistical significance and hold limited statistical value. As a result, it was excluded from the further statistical multivariate analysis. The average number of total pits (NTP = 23.17) is nearly identical to Urşilor's average (NTP = 23.28). The pits exhibit a similar distribution pattern as observed in the other sites, with a clear preponderance for small pits. On the other hand, the average number of total scratches (NTS = 25.17) is slightly higher in comparison to the other fossil populations. However, the scratch distribution follows the same pattern observed for Urşilor, Oase, and Bisericuța, with an SWS of 1. The individuals from Onceasa exhibited a presence of puncture pits (NPP = 1), but no gouges (NG = 0). It is important to note that the sample size for the Onceasa site is relatively small, which should be taken into consideration when interpreting these results.

The Adam site also exhibits a limited sample size, comprising only 2 individuals. Consequently, the obtained values lack statistical significance and have limited statistical value. As a result, they were excluded from the further statistical multivariate analysis. The average number of total pits (NTP = 29) for the two speciemens from Adam is higher than that exhibited by the other fossil populations. However, the average number of total scratches (NTS = 20) falls within the range observed in the other cave bears. Furthermore, the distribution of pits and scratches follows the same trend observed in Urşilor, Oase, Bisericuța, and Onceasa, with a predominance of small pits and fine scratches, respectively. Notably, the average number of puncture pits (NPP) for Adam is 2. However, the two individuals from this site did not exhibit gouges (NG = 0).

3.2. AMS ^{14}C dating

11 samples (*n* = 11) out of 19 which had ^{14}C AMS dating, with a yield higher or equal to 1%, were considered suitable for our analyses (according to Van Klinken, 1999; Brock et al., 2010; Table 2). Eight (*n* = 8) bear samples provided reliable data for both radiocarbon and microwear data. The majority of the radiocarbon ages belong to the MIS 3 cave bears (ca. 46–27 cal kyr B.P.; median ages), whereas one sample is a MIS 3 brown bear (ca. 41.6 cal kyr B.P.; median age) (Fig. 3). To these, a medieval brown bear (Cl/009 from ACCG site; 1 cal kyr B.P.; median age; Ersmark et al., 2019) was added to our analyses as a reference. The highest number of cave bears with reliable data from both sets are derived from Urşilor (*n* = 5) and belong to the ca. 46–27 cal kyr B.P. time interval. Except for the ages of ca. 35 cal kyr B.P. and ca. 27 cal kyr B.P., the rest of the MIS 3 bear samples range from ca. 45.5 to 41.7 cal kyr B.P.

3.3. MIS 3 cave bears from the Romanian Carpathians

When compared with the extant ursid populations, the *U. spelaeus* specimens from the most numerous sites (Urşilor, Oase, Bisericuța) display a slightly higher number of scratches. Regarding pits, the fossil specimens from the most significant populations aforementioned display a similar number of small pits (NSP) when compared to extant ursids (*U. americanus* and *U. arctos*) from North America. Moreover, they also display a smaller number of large pits (NLP) compared to extant populations. Regarding gouges, the populations of Urşilor, Oase, and Bisericuța exhibit higher values compared to other extant bear populations, excepting the brown bears from Central Europe and Greece, which display even higher counts. Finally, the most numerous fossil populations (Urşilor, Oase, and Bisericuța) display a number of puncture pits similar to that found in *U. americanus* and *U. arctos* from North America and Northern Europe, respectively.

A hierarchical clustering analysis was conducted using the paired group method with Euclidean distance (Fig. 4A). The analysis incorporated seven microwear variables, namely small pits, large pits, fine scratches, coarse scratches, SWS, gouges and puncture pits. We compared the microwear signal of the most numerous fossil populations with that from extant populations of *U. arctos* from different regions and *U. americanus*.

The cave bear populations of Urşilor, Oase, and Bisericuța show a high degree of similarity, indicating a close relationship without significant intergroup distinctions (Table 3). On the other hand, extant bear populations of *U. arctos* from Kamchatka and North America are grouped together, which both include a hard and soft mast diet but with a predominance of vertebrates (Fig. 4A). Grouped on a closely related level is *U. americanus* which has a predominant soft mast diet but is classified as omnivorous, including a variety of food types in its diet. The *U. arctos* population from Greece is notably distinct from the other groups, as it exhibits a specialized dietary preference for exclusively soft food. Furthermore, the fossil populations exhibit the greatest resemblance to the extant populations of *U. americanus* (Table 3). However, there are also nearly equal similarities with the extant populations of *U. arctos* from Kamchatka, North America, and the northern regions of Europe. All the most-related extant species share an omnivorous nature, encompassing a wide range of dietary components including soft and hard mast, as well as vertebrates and invertebrates. However, it is

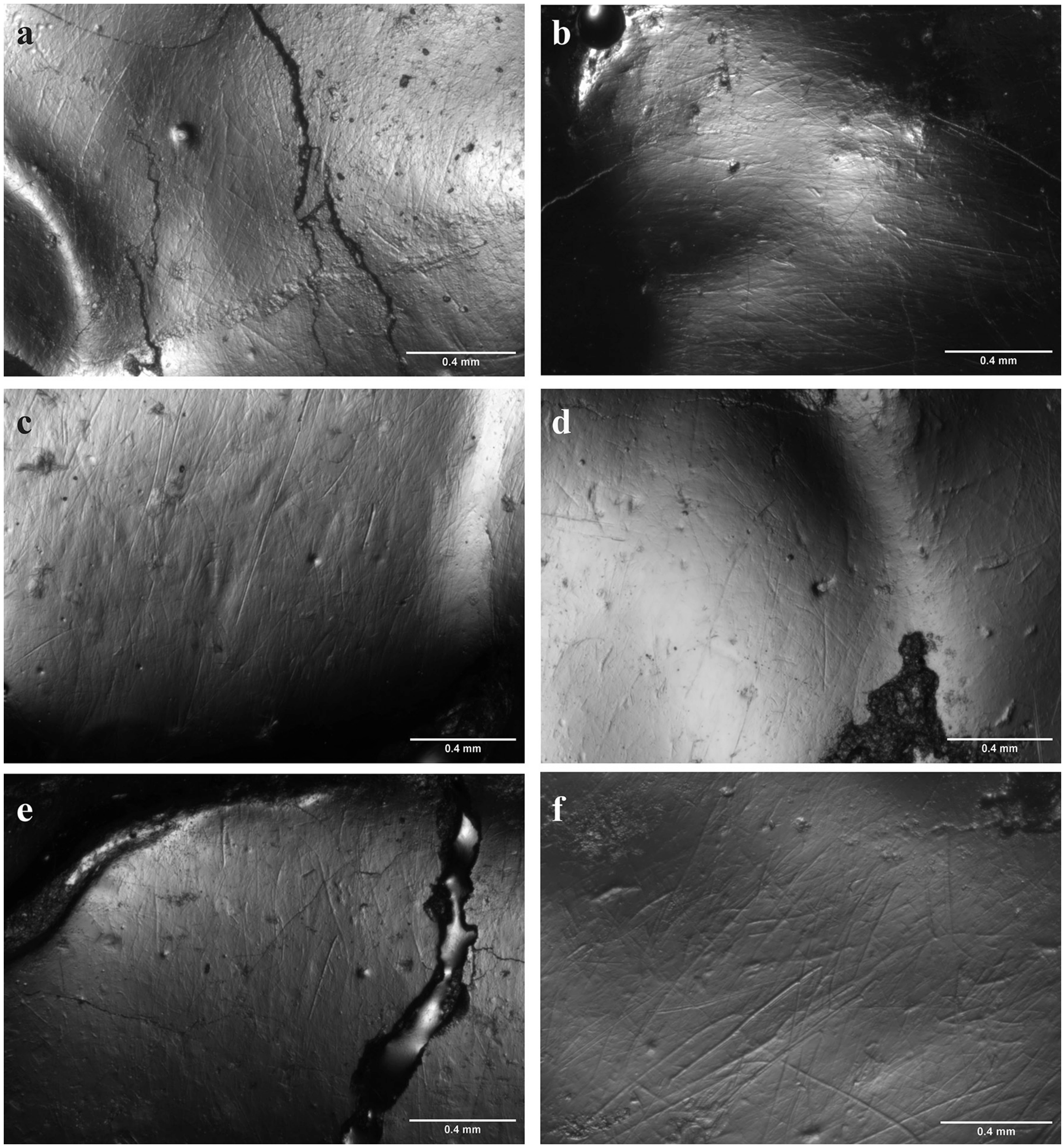

Fig. 2. Photomicrographs (at ×35 magnification) of the grinding non-faceted enamel surface of selected fossil individuals of *U. spelaeus* from the Carpathians. (a): Urşilor (#PU/F); (b): Urşilor (#PU/E2-III-1164); (c): Oase (# O35.138); (d): Bisericuța (#PB/C1-IX); (e) Bisericuța: #PB/A1-I-II-1); (f): Onceasa (#POc/016).

noteworthy that the species with an extreme dietary preference, specifically *U. arctos* from Greece, which is clearly specialized in consuming soft mast, displays the highest level of differentiation.

To display the distribution and variability of the samples, a correspondence analysis (CA) was conducted using the same variables and individuals as in the hierarchical clustering analysis (Fig. 4B). The results for the first two dimensions (i.e. Dim. 1 and Dim. 2), owing to their higher percentage of variance, were utilized, and plotted (Table 4 and Fig. 4B). The correspondence analysis plot illustrates a similar and overlapping distribution pattern among the extant bears, *U. arctos* from various regions, and *U. americanus*. Significantly, these extant species are predominantly clustered on the left side of the Dim 1 axis, showing both intra-population and inter-population variability. However, the extant *U. arctos* population from Greece stands out as a distinctive outlier, occupying a solitary position in the upper section of the CA plot. This distinct placement can be attributed to its unique characteristics, higher average number of large pits compared to small pits and the highest number of coarse scratches, setting them apart from the other extant bear species.

The extinct *U. spelaeus* populations from the Carpathians (Urşilor, Oase, Bisericuța) are predominantly clustered together and overlap on the right side of the first-dimensional axis in the CA plot. This distinct positioning, separate from the extant bear species, aligns with the grouping of the three sites observed in the hierarchical clustering results (Fig. 4A) and in the similarity and distance indices (Table 3).

In relation to the second dimension, the fossil populations show a tendency to cluster in the lower section or around the 0.0 axis of the second dimension. This clustering pattern can be attributed to their relatively higher number of small pits, ranging from 17.65 to 19.35, although it is lower compared to other populations such as *U. arctos* from Central Europe or North America. This feature distinguishes them from the *U. arctos* population in Greece, which, in contrast, displays a low number of small pits. The dissociation between the fossil populations and *U. arctos* from Greece is consistent with the highest divergence observed in the similarity and distance indices (Table 3).

Finally, the plot reveals that some cave bear individuals fall within

Table 2
The microwear samples which were AMS ^{14}C dated (mandible bone). The radiocarbon dates were calibrated using the IntCal13 calibration dataset (Reimer et al., 2013). * = Source. 1 – This study; 2 – Ersmark et al., 2019; 3 – Mirea et al., 2021. Notes: All depths are in cm below surface. Collagen yields are given in percent of extracted collagen with respect to the initial weight of the sample. PU: Urșilor; PM: Muierilor; PB: Bisericuța; Cl: P.-Aven nr. 2 from Cracul de la Cioaca Goală (ACCG; Cloșani); N32.-N35., O36: Oase. PB/C1-IV-V is associated with PB/A1-V (both hemimandibles belong to the same specimen).

#ERIS	#PRL	#Microwear	Specimen	Depth (cm)	Coll. Yield (%)	% Cb	% Nb	^{14}C age (uncalibrated)	Cal yr B.P. age (median)	Age range cal yr B.P. (2σ)	*
Urșilor Cave											
PU/Y1	Poz-161,933	–	*U. spelaeus*	−10	1.3	3.9	0.6	36,900 ± 800	**41,653**	42,529–40,572	1
PU/B-I-14	Poz-161,894	58	*U. spelaeus*	−10	6.1	9.9	3.1	37,300 ± 800	**41,883**	42,730–40,912	1
PU/G-I-13a	Poz-161,928	83	*U. spelaeus*	−10	1.4	3.1	0.5	43,000 ± 2000	**46,363**	52,322–42,845	1
PU/B-II-a1	Poz-161,895	–	*U. spelaeus*	−20	1.5	3.1	0.6	38,200 ± 900	**42,385**	43,478–41,312	1
PU/E1-III-125	Poz-162,373	42	*U. spelaeus*	−30	1.7	3.3	0.6	41,000 ± 2000	**44,696**	50,623–42,016	1
PU/E1-III-808	Poz-162,375	43	*U. spelaeus*	−30	1.8	5.1	1	42,000 ± 2000	**45,474**	51,485–42,427	1
PU/D1-VIII-116	Poz-53,620	35	*U. spelaeus*	−80	1	1.6	0.6	22,690 ± 130	**27,056**	27,281–26,860	1
Muierilor Cave - Bears' Passage											
PM/S6-I-II-1	Poz-161,930	–	*U. spelaeus*	−15	1.4	4.4	1.1	39,500 ± 1100	**43,223**	44,852–42,071	1
PM/U6-II-III-C	Poz-161,929	–	*U. spelaeus*	−25	2.3	6.3	1.4	38,500 ± 1000	**42,575**	44,205–41,476	1
Bisericuța											
PB/C1-IV-V/01	Poz-109,333	93	*U. spelaeus*	−50	2.1	9.1	3.6	31,300 ± 500	**35,229**	36,095–34,513	1
PB/B1-X-XI	Poz-161,818	1	*U. arctos*	−100	6.7	8.3	2.8	37,000 ± 1200	**41,668**	43,269–39,717	1
Cloșani											
Cl/009		91	*U. arctos*	−10				1109 ± 26	**1007**	1065–956	2
Discarded ages											
PU/F-I-12b	Poz-0	32	*U. spelaeus*	−10		1.9	0.1	>0 BP			1
PU/D1-V-146	Poz-161,927	82	*U. spelaeus*	−50	0.3	4.8	0.8	34,700 ± 600	**39,895**	41,203–38,393	1
PU/C1-VIII-110	Poz-53,619	–	*U. spelaeus*	−80		4.6	2.1	30,780 ± 290	**35,129**	35,821–34,545	1
PM/O6–0-89	Poz-77,727	60	*U. spelaeus*	0	0.4	3.8	1.0	27,980 ± 210	**31,941**	32,886–31,455	3
PM/U6-I-14	Poz-0	–	*U. spelaeus*	−10		3.5	0.5	>0 BP			1
PM/V6-II-III-B	Poz-0		*U. spelaeus*	−25		2.5	0.2	>0 BP			1
N32.27	Poz-161,934	17	*U. spelaeus*		0.7	3.7	0.6	35,500 ± 700	**40,616**	41,846–39,428	1
N35.143	Poz-161,935	–	*U. spelaeus*		0.7	5.9	0.6	39,000 ± 1000	**42,863**	44,444–41,934	1
O36.113	Poz-161,936	–	*U. spelaeus*		0.7	3.2	0.5	37,300 ± 800	**41,883**	42,730–40,912	1

the range of *U. americanus* and *U. arctos* from Kamchatka, North America, and the northern regions of Europe, with a small overlap observed with the central European population. The compatibility towards these extant populations aligns with the associations observed in the similarity and distance indices (Table 3). Therefore, it is important to highlight the shared omnivorous nature of these extant species that exhibit some degree of overlap with the fossil samples.

3.4. Fossil U. arctos from the Romanian Carpathians

For the fossil specimens of brown bear *U. arctos*, although the number of individuals per site is small (Bisericuța: $n = 1$, ACCG: $n = 2$, Avenul Mâțului: $n = 1$), making them statistically insignificant, there is a notable consistency in the total number of scratches (NTS) observed, ranging from 24 to 27 (Table 1). However, when considering the total number of pits (NTP), there is a higher range of variability, spanning from 21 to 38. The Pleistocene individuals from Avenul Mâțului and Bisericuța exhibit a higher total number of pits compared to *U. spelaeus* from the most numerous sites (Urşilor, Oase and Bisericuța), but their counts are similar to those from Adam, which also has a small sample size. The distribution of scratches clearly exhibits a higher count of coarse scratches (NCS), as evidenced by an SWS of 2 for the individuals from Bisericuța and Avenul Mâțului, and an SWS of 1.50 for the medieval individuals from the Cloșani area (Table 1; Fig. 5). These results suggest a greater proportion of coarse scratches in these fossil *U. arctos* individuals compared to the contemporaneous *U. spelaeus* populations (Fig. 6). In terms of pit distribution, the Bisericuța population shows a higher count of large pits (NLP = 27) compared to small pits (NSP = 9), which opposes the general trend observed in *U. spelaeus* with a predominance of small pits. Conversely, the Holocene brown bears from the Cloșani area exhibit a distribution pattern similar to *U. spelaeus*, with a higher count of small pits (NSP = 14.25) compared to large pits (NLP = 5.50). Likewise, the Avenul Mâțului individual demonstrates a prevalence of small pits (NSP = 20) over large pits (NLP = 10). The number of puncture pits (NPP) displays a consistent distribution, ranging from 2.00 (Bisericuța) to 3.00 (Avenul Mâțului), and with a 1.50 for the medieval Cloșani area individuals. In terms of gouges, both the Cloșani area and Bisericuța populations exhibit an average count of 1, while the individual from Avenul Mâțului does not show any gouges. The puncture pits and gouges observed in the fossil *U. arctos* specimens are consistent with those observed in *U. spelaeus* populations.

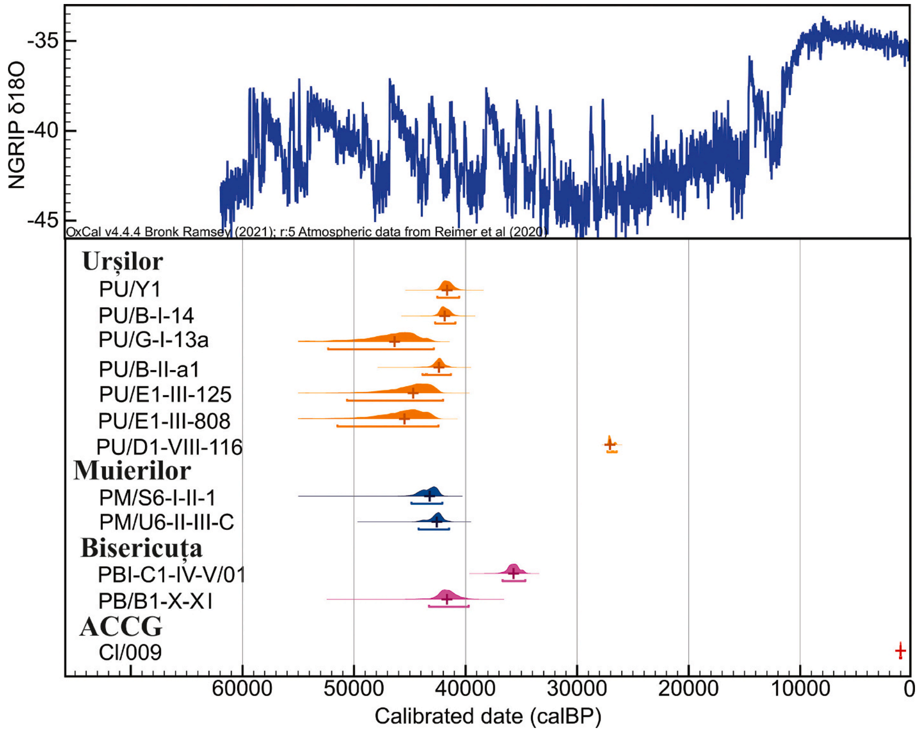

Fig. 3. Calibration of the reliable AMS ^{14}C data of the analysed bears.

4. Discussion

The microwear results obtained for *U. spelaeus* specimens from the Carpathians provide compelling evidence of dietary homogeneity during the pre-dormancy phase within and among the examined populations, regardless of age and sex. Their diet did not exhibit specialization, being neither fully herbivorous nor carnivorous, but rather omnivorous, with a preference for the consumption of hard objects. This dietary pattern persisted throughout the MIS 3 period, spanning from over 46 to 27.1 cal kyr B.P. at least, despite the climatic fluctuations (Constantin et al., 2007). We analysed individuals from both distant and recent time periods leading up to their extinction around 27.8 cal kyr B.P. (Pacher and Stuart, 2009; Terlato et al., 2019); however, no dietary changes or differences were observed among them.

4.1. *Long-term (stable isotopes) vs short-term (dental microwear) dietary patterns*

Distinctly, the isotopic results of nitrogen ($\delta^{15}N$) for the analysed individuals exhibit substantial variability ($\delta^{15}N$ values range from 3.3 to 11.5‰) (Richards et al., 2008; Robu et al., 2013, 2018). This may suggest that over the year, there was indeed a differentiated diet. However, during this pre-dormancy specific period of the year, Carpathian cave bear populations from Urşilor, Oase, and Bisericuţa had a similar dietary pattern, characterized by a highly flexible omnivorous intake. Therefore, no correlations between stable isotopes and dental microwear at the individual or population-level were identified due to the different time resolutions of each method. Bone collagen stable isotopes provide the average annual dietary signal while dental microwear indicate a short term and seasonal dietary signal. The substantial significance of this common dietary regime is underscored by the notable geographic separation between the Urşilor, Oase, and Bisericuţa populations. These populations, situated within the Carpathian region, were at a significant distance from one another. Specifically, there was 180 km between Urşilor and Oase, the same distance between Bisericuţa and Oase, and 70 km separating Bisericuţa from Urşilor.

4.2. *Omnivorism during the predormancy period*

On the contrary, the microwear patterns of the cave bear specimens differ from those of extant *U. arctos* and *U. americanus*. This differentiation may be attributed to the consumption of particular items, potentially consisting of plant matter, such as roots (Mattson, 1998; Athen, 2006; Ramírez-Pedraza et al., 2022), as opposed to living bear species (Krajcarz et al., 2016; Bocherens, 2019; Naito et al., 2020). However, the correspondence analysis (CA) reveals some intra-population variability, with some individuals falling within the range of extant species that share a highly variable (including both hard and soft mast) omnivorous diet, mainly *U. americanus* (Hatler, 1967; Raine and Kansas, 1990), *U. arctos* from Kamchatka (Bergman, 1936; Kistchinski, 1972; Vereschagin, 1976; Krechmar, 1995) and *U. arctos* from Northern Europe (Elgmork and Kaasa, 1992; Persson et al., 2001; Bojarska and Selva, 2012), as well as *U. arctos* from North America (Mattson, 1998; Hilderbrand et al., 1999; Mowat and Heard, 2011) and Central Europe (Rigg and Gorman, 2005; Bojarska and Selva, 2012), respectively. In contrast, cave bears significantly differentiate from the diet-specialized *U. arctos* from Greece (soft-mast) (Vlachos et al., 2000; Paralikidis et al., 2010).

4.3. *Cave bear seeded and hard-shelled fruit consumption*

The observed omnivorous trends, distinct from the specialized diet of the Greek *U. arctos*, may be inferred from the consumption of a diverse array of dietary food types during this pre-dormancy period, a trend observed in modern bear species. Ursids actively forage for food sources rich in lipids or carbohydrates during the pre-hibernation/dormancy hyperphagic period, which typically takes place in late summer and autumn (Coogan et al., 2014). This behaviour is driven by their physiological need to accumulate energy reserves before entering hibernation, and in the case of females, to support the energy demands associated with reproduction and the production of milk for lactation (Farley and Robbins, 1995; López-Alfaro et al., 2013). Therefore, in extant bears, it translates into diet diversification, particularly through

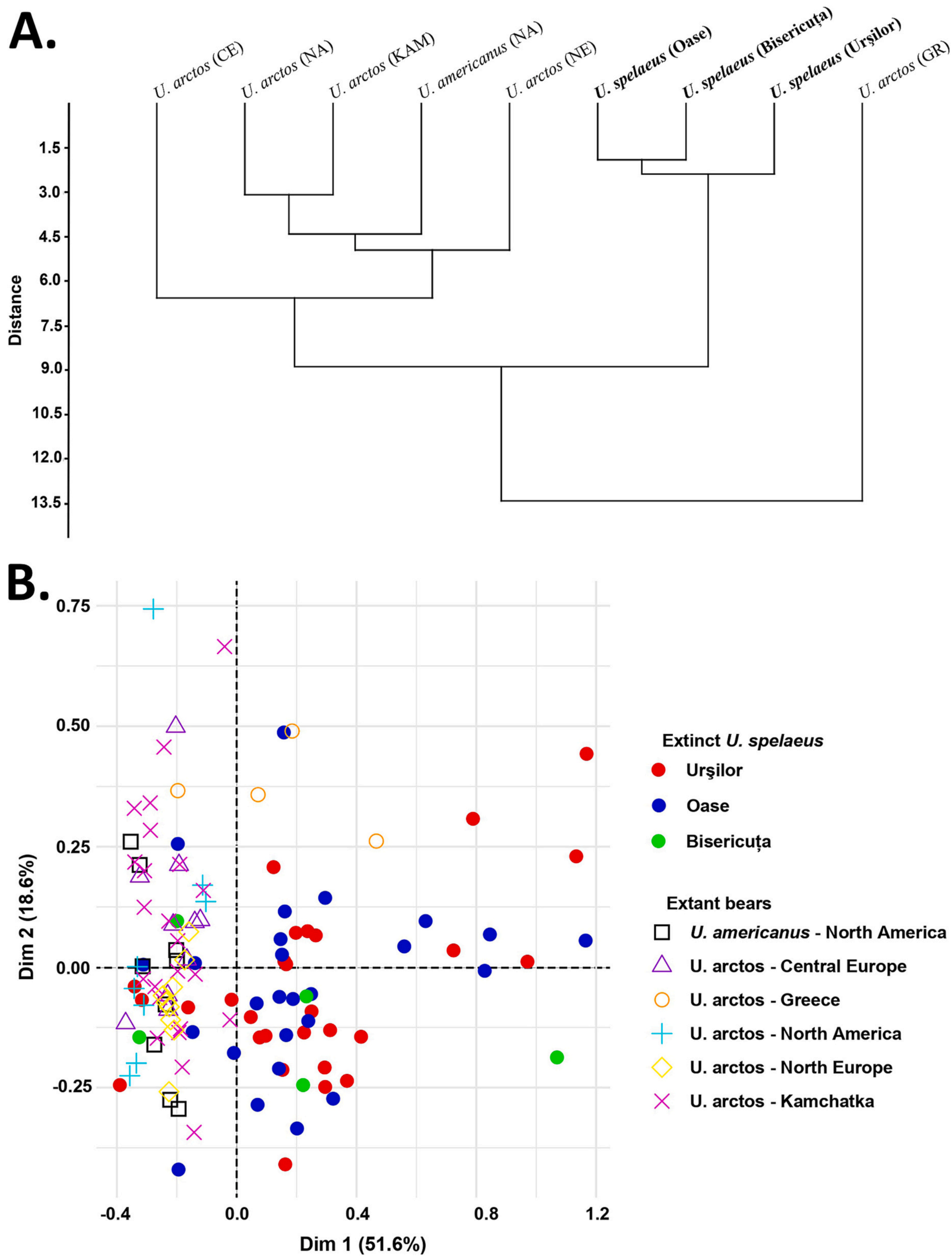

Fig. 4. A) Hierarchical clustering diagram employing seven microwear variables: number of fine and coarse scratches, small and large pits, gouges, puncture pits, and the scratch width score. Comparison of the fossil populations of *U. spelaeus* from Urşilor, Oase and Bisericuța with the extant bears. Abbreviations: CE = Central Europe; NA = North America; KAM = Kamchatka; NE = North Europe; GR = Greece. B) Correspondence analysis (CA) based on seven variables: number of fine and coarse scratches, small and large pits, gouges, puncture pits, and the scratch width score. Comparison of the fossil populations of *U. spelaeus* from Urşilor, Oase and Bisericuța with the extant bears.

Table 3
Euclidean similarity and distance indices based on seven microwear variables (Table 1): number of fine and coarse scratches, small and large pits, gouges, puncture pits, and the scratch width score. Comparison of the fossil populations of *U. spelaeus* from Urşilor, Oase and Bisericuța with the extant bears. Abbreviations: CE = Central Europe; NA = North America; KAM = Kamchatka; NE = North Europe; GR = Greece.

	U. americanus (NA)	*U. arctos* (GR)	*U. arctos* (CE)	*U. arctos* (NA)	*U. arctos* (KAM)	*U. arctos* (NE)	*U. spelaeus* (Oase)	*U. spelaeus* (Urşilor)	*U. spelaeus* (Bisericuța)
U. americanus (NA)	–	12.247143	7.7846002	4.9721726	3.8392708	5.0892043	7.7935871	8.2607506	7.1742595
U. arctos (GR)		–	16.771479	12.348684	12.767635	15.786782	12.719375	11.484446	13.184555
U. arctos (CE)			–	6.9507194	5.2153619	6.2976186	10.383641	11.719215	9.7360156
U. arctos (NA)				–	3.0761177	5.601116	9.4917069	9.958037	8.5030877
U. arctos (KAM)					–	4.1472883	8.0907354	8.9330846	7.4545288
U. arctos (NE)						–	8.436824	9.6932967	7.628237
***U. spelaeus* (Oase)**							–	**1.9078784**	**1.8947295**
***U. spelaeus* (Urşilor)**								–	**2.8548205**
***U. spelaeus* (Bisericuța)**									–

Table 4
Representation of the results for each axis in the correspondence analysis (CA): eigenvalues, percentages of variance, and cumulative percentages.

Axis	Eigenvalue	% total	Cumulative
1	0.120666521	51.564	51.564
2	0.043569598	18.618	70.182
3	0.028035030	11.980	82.162
4	0.021993366	9.398	91.560
5	0.017292613	7.289	98.950
6	0.002456043	1.049	100

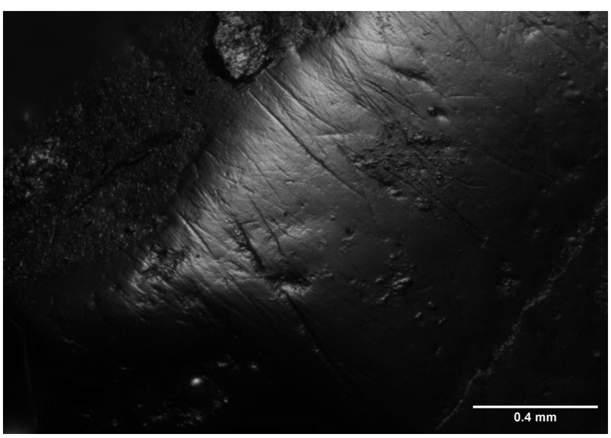

Fig. 5. MIS 3 *U. arctos* from Bisericuța displaying coarse scratches (#PB/B1-X-XI).

the substantial consumption of core carbohydrate items (Bojarska and Selva, 2012; Coogan et al., 2018). Consequently, bears ranging from northern cold regions to mild Mediterranean zones (Graber and White, 1983; Cicnjak et al., 1987; Clevenger et al., 1992; Vlachos et al., 2000; Persson et al., 2001) heavily rely on the ingestion of small, wild fruits like berries or nuts which serve as a principal means of accumulating energy reserves (Welch et al., 1997; Stenset et al., 2016; Soofi et al., 2017; Ogurtsov, 2018; García-Rodríguez et al., 2021). On the other hand, in regions with harsh winters, particularly those characterized by heavy snowfall, bears may rely more heavily on a meat-based diet (Wiegand et al., 2008; Bojarska and Selva, 2012), although one does not necessarily exclude the other (e.g. Dahle et al., 1998; Persson et al., 2001). Regarding this particular behaviour, the presence of puncture pits and gouges was consistently observed in all fossil populations, a microwear feature characteristic of hard-object consumers (Solounias and Semprebon, 2002; Godfrey et al., 2004; Semprebon et al., 2004; Williams and Geissler, 2014). Specifically, carnivore clade omnivores from temperate woodland environments (*e. g. Vulpes vulpes*, *Genetta genetta* or *Nandinia binotata*) present puncture pits, due to the consume of fruit coverings and seed coats (Xafis et al., 2017). This evidence suggests, for the first time, the consumption of seeded and hard-shelled fruits, for *U. spelaeus*. It is important to stress that the presence of puncture pits (i.e. hard-object consumption) was not observed in other cave bears analysed using low-magnification microwear techniques (Ramírez-Pedraza et al., 2019, 2020, 2022). This applies to cave bears residing in both steppe-like habitats in northern latitudes (Ramírez-Pedraza et al., 2022), and forested landscapes in southern latitudes (Ramírez-Pedraza et al., 2019, 2020).

During the Last Glacial Period, the Carpathian Mountain range has been recognized as a large forest refugium (Jankovská and Pokorný, 2008; Tzedakis et al., 2013; Juřičková et al., 2014). This region exhibited a diverse range of canopy forest landscapes, with certain valleys with more humid and enclosed environments maintaining temperate plant specimens (Jankovská et al., 2002; Juřičková et al., 2014). Dominant tree species during this time included larch (*Larix*), Swiss stone pine (*Pinus cembra*), Scots pine (*Pinus sylvestris*), and spruce (*Picea*), forming a relatively dense forest canopy (Jankovská et al., 2002). In more favourable locations within the Carpathian region, isolated patches of temperate broadleaf trees, such as hazel (*Corylus avellana*), black alder/grey alder (*Alnus glutinosa/A. incana*), linden (*Tilia)*, elm (*Ulmus*), oak (*Quercus*), beech (*Fagus*), hornbeam (*Carpinus*), fir (*Abies*), and maple (*Acer*) managed to persist even during the most severe glacial periods, including the Last Glacial Maximum (LGM) (Magri et al., 2006; Jankovská and Pokorný, 2008). The consumption of fruits produced by these plant specimens, such as beechnuts, hazelnuts, acorns, and linden nutlets, is compatible with the microwear pattern found on cave bear individuals (Godfrey et al., 2004; Xafis et al., 2017), potentially suggesting the inclusion of these specific items in the diet of cave bears inhabiting the Carpathian region during MIS 3.

Our results are particularly intriguing as they suggest that the dietary patterns of Carpathian cave bears may exhibit similarities to those of extant brown bears inhabiting the same region. This is noteworthy considering that modern brown bears in the Carpathians predominantly consume seeded fruits as their primary food source during the hyperphagia period in autumn (Slobodyan, 1976; Štofik et al., 2013; García-Rodríguez et al., 2021). During autumn bears collect the remaining raspberries (*Rubus idaeus*) and whortleberries (*Vaccinium myrtillus*) from summer; they also eat mature blackberries (*Rubus fruticosus*), mountain-ash fruits (*Sorbus aucuparia*), fruits from wild apple (*Malus* spp.) and pear trees (*Pyrus* spp.), blackthorn (*Prunus spinosa*), and dog rose (*Rosa canina*), as well as beechnuts (*Fagus* spp.) and acorns (*Quercus* spp.) (Slobodyan, 1976; Kalabér et al., 1994).

The singular presence of hard items in the Carpathian cave bear diet during the Late Pleistocene, in contrast to other European regions, in conjunction with the observed similarities between the dietary patterns of cave bears and extant brown bears in the same region, yields valuable

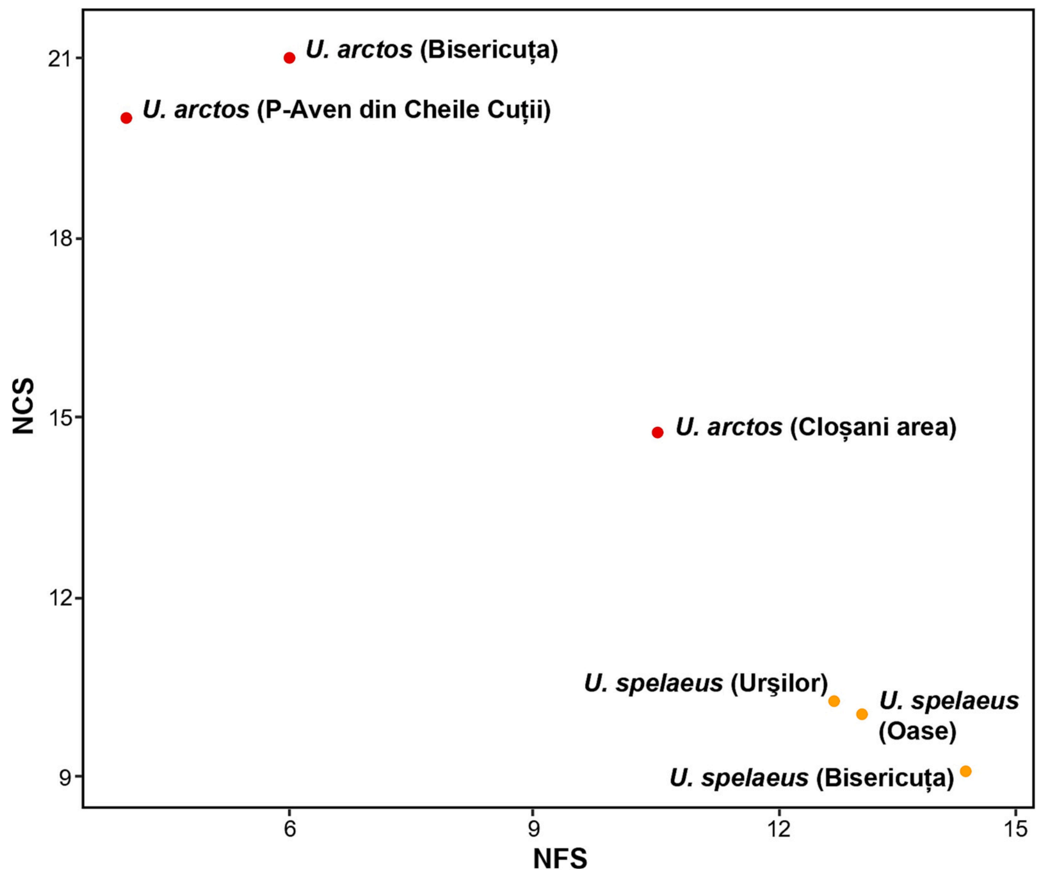

Fig. 6. Bivariate plot of the mean number of fine and coarse scratches for the fossil bear populations of *U. arctos* and *U. spelaeus* from the Romanian Carpathians.

insights into the enduring presence of specific tree species and their associated food resources within the Carpathian ecosystem over time. Moreover, a new unpublished date released in this article for an individual from Urşilor, calibrated to 27,056 cal yr B.P. (median age), which closely aligns with the species' extinction and stands as one of the earliest recorded dates for Eastern Europe, may suggest the prolonged existence of cave bears (*U. spelaeus*) in the Carpathians, owing to favourable ecological conditions and the availability of reliable herbivorous food resources. Consequently, the Carpathians may have functioned as a refuge for cave bears, sustaining a consistent availability of food sources for ursids, even during periods of severe glaciation.

4.4. Dietary comparison between fossil U. spelaeus and U. arctos

Finally, the microwear results refute that the fossil populations from the Carpathians had a carnivorous diet, which is supported by the barely-present hyper-coarse scratches, which are only displayed by hyper-carnivores and bone-consumers such as polar bears (*U. maritimus*) (Pappa et al., 2019) and hyenas (*Crocuta* sp.) (Rivals et al., 2022). Nevertheless, the presence of certain fossil individuals overlapping with omnivorous ursids, known to consume both vertebrates and invertebrates, could suggest at least sporadic meat consumption among the cave bear individuals examined in this study. This could be explained as that towards the end of autumn, when winter approaches, resource availability diminishes, and diet becomes restricted; some individuals who have not been able to accumulate sufficient lipid reserves for the winter begin to consume meat to further supplement their stores, as recorded in extant *U. arctos* from the Carpathians (Slobodyan, 1976; Frackowiak, 1997). However, Carpathian cave bears did not have such a carnivorous diet during the pre-dormancy period, unlike some cave bear populations from the northern regions of the Iberian Peninsula (Pinto-Llona, 2013; Ramírez-Pedraza et al., 2020).

Additionally, *U. spelaeus* exhibited narrower scratches (lower SWS) in comparison to contemporaneous (pre-LGM) *U. arctos* specimens from the Carpathians. The brown bears, despite the limited sample size, displayed a clear trend of a higher number of coarse scratches relative to fine scratches. This distinction in the width of scratches between the Carpathian cave bears and brown bears may suggest divergent dietary niches, with the brown bears displaying a propensity towards a more specialized carnivorous diet. Pleistocene brown bears appear to have displayed a more carnivorous dietary behaviour compared to contemporary brown bears (Bocherens et al., 2011; Münzel et al., 2011), while modern brown bears from the Carpathians might exhibit more dietary similarities to cave bears from the same region during MIS 3. Furthermore, the two Holocene *U. arctos* individuals from the Carpathians (Cloșani area), dated to 1007 cal yr B.P., displayed a scratch width pattern more similar to that of Pleistocene *U. spelaeus*. These findings could support the hypothesis of a more omnivorous dietary change in the post-Last Glacial Maximum (LGM) *U. arctos*, potentially due to occupying the ecological niche of cave bears after their extinction. However, given the absence of statistical significance from two *U. arctos* Holocene individuals from the Carpathians, conducting further microwear studies with a significant sample size to compare its diet with the Late Pleistocene *U. spelaeus* populations of the same region becomes necessary. This will help to firmly establish dietary similarities and potential niche heredity continuities between Pleistocene cave bears and pre-LGM *U. arctos* populations in the Carpathians.

5. Conclusions

Overall, the highly omnivorous diet of cave bears from the Carpathians during the pre-dormancy period represents a dietary profile endemic to this region, which served as a refugium of fauna and flora ((Sommer and Nadachowski, 2006; Juřičková et al., 2019), and within which cave bears survived until at least 27.1 cal kyr B.P., close to the time of their extinction. Furthermore, the first observation of microwear features typical of hard-object consumers, i.e. fruit eaters, on cave bears provides more information about the uniqueness of the Carpathians in the context of European cave bears and suggests the possibility of niche heredity with the extant bears of this region. A high variability in their long-term diet is observed using stable isotopes, and the short-term diet of these individuals provides essential insights into the dietary uniqueness of Carpathian bears during the pre-dormancy period, and the high plasticity of their repertoire. This flexibility might explain the consumption of certain high nitrogen bulk items by some individuals while completely discarding the possibility of a meat-based diet for any of the cave bears analysed. These discoveries shed light on the ecological adaptations of cave bears in the Carpathian region during the Late Pleistocene and contribute to a deeper understanding of their dietary habits and responses to the unique environmental conditions of this region.

Ethics approval/declarations

Not applicable.

Consent to participate

Not applicable.

Consent for publication

Not applicable.

Credit authorship contribution statement

Paulo Duñó-Iglesias: Conceptualization, Data curation, Formal analysis, Investigation, Writing – original draft. **Iván Ramírez-Pedraza:** Data curation, Formal analysis, Investigation, Writing – original draft. **Florent Rivals:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Supervision, Writing – original draft. **Ionuț-Cornel Mirea:** Conceptualization, Funding acquisition, Writing – review & editing. **Luchiana-Maria Faur:** Conceptualization, Writing – review & editing. **Silviu Constantin:** Funding acquisition, Writing – review & editing. **Marius Robu:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Writing – original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

Data availability

Datasets related to this article can be found at https://doi.org/10.5281/zenodo.10076736, an open-source online data repository hosted at Zenodo (Duñó-Iglesias, 2023).

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