The similar omnivorous diet of MIS 3 cave bears and extant brown bears in the Carpathians: Implications for a broadleaf-forest bear glacial refugia

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Introduction

The **cave bear** (*Ursus spelaeus*) went extinct at about 28 kyr B.P. in western Europe. A well-established theory suggests that their extinction can be attributed to the declining availability of plant-based resources (Pacher and Stuart, 2009). The **brown bear** (*U. arctos*), smaller-sized and with broad dietary habits, prevailed and occupied the ecological niche of the *U. spelaeus* after his extinction (Sommer and Benecke, 2005). The Romanian Carpathian cave bears have pointed towards a flexible omnivore diet suggested by a wide range of $\delta^{15}N$ values (Robu et al., 2013). A reliable method to infer short-term dietary patterns is **dental microwear analysis (DMA)**. Therefore, studying the diet of both *U. spelaeus* and *U. arctos* through DMA is crucial to understand its ecological balance throughout the Pleistocene and to infer the reasons for the prevalence of one species over the other.

Materials and Methods

We analysed **97 lower first molars** of ***U. spelaeus*** and contemporaneous ***U. arctos*** from eight cave sites in the **Romanian Carpathian** region (**Fig. 1**), using dental microwear analysis to reconstruct their pre-dormancy diets during MIS 3. The results of fossil bear species were compared to the reference dataset of extant bear species (Pappa et al., 2019). Furthermore, radiocarbon dating (AMS-UF) was applied on cave bears (n = 18) and brown bear (n = 1) from: Ursilor (n = 10), Oase (n = 3), Muierilor (n = 4) and Bisericuța (n = 2).

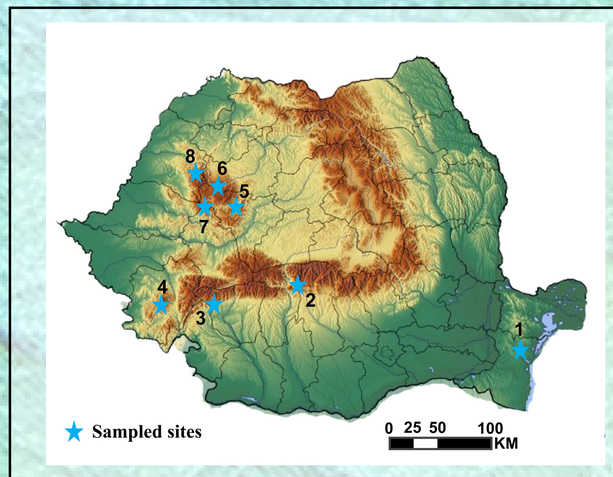


Fig. 1) Location of the sampled MIS 3 cave bear sites in the Romanian Carpathians. 1 – La Adam; 2 – Muierilor; 3 – P.-Aven nr. 2 din Cracul de la Cioaca Goală (ACCG; Cloșani); 4 – Oase; 5 – Cioclovina; 6 – Onceasa; 7 – Ursilor; 8 – Avenul Mățului.

Results

The **short-term** diet, i.e. the last days or weeks, of both *U. spelaeus* and *U. arctos* populations was identified as **omnivorous** (**Fig. 2**). Because they fall **within the range** of extant species that share a **highly variable** (including both hard and soft mast) **omnivorous diet**; *U. americanus*, as well as *U. arctos* from Kamchatka, Northern Europe, North America and Central Europe. In contrast, cave bears **significantly differentiate** from the **diet-specialized** *U. arctos* from Greece.

However, scratches of different width between the MIS 3 Carpathian cave bears and brown bears may suggest **divergent dietary niches**, with the brown bears displaying a propensity towards a more **specialized carnivorous diet** (**Fig. 4**). Furthermore, two **Holocene *U. arctos*** individuals from the Carpathians dated to 1007 cal kyr B.P., displayed a **scratch width pattern** more **similar** to that of the **Pleistocene *U. spelaeus***.

The presence of **puncture pits** (**Fig. 3**) on *U. spelaeus* populations suggested 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, an omnivorous diet mainly composed of **plant-based** resources with **sporadic meat consumption**, to store enough energy before **hibernation.** Moreover, an **early date of 27 cal kyr B.P.** was obtained from one individual from Ursilor Cave.

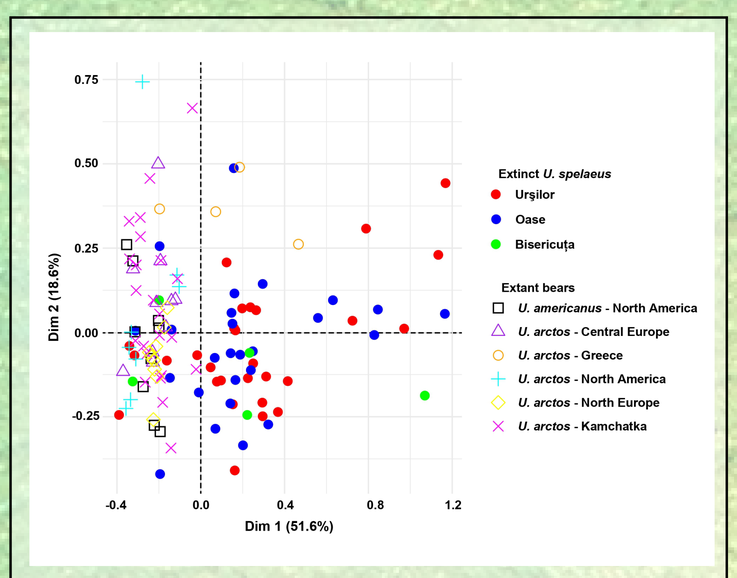


Fig. 2) Correspondence Analysis (CA) based on seven variables: number of fine and coarse scratches, small and large pits, gouges, puncture pits, and the scratch width score. Comparison of the fossil populations of *U. spelaeus* from Ursilor, Oase and Bisericuța with the extant bears.

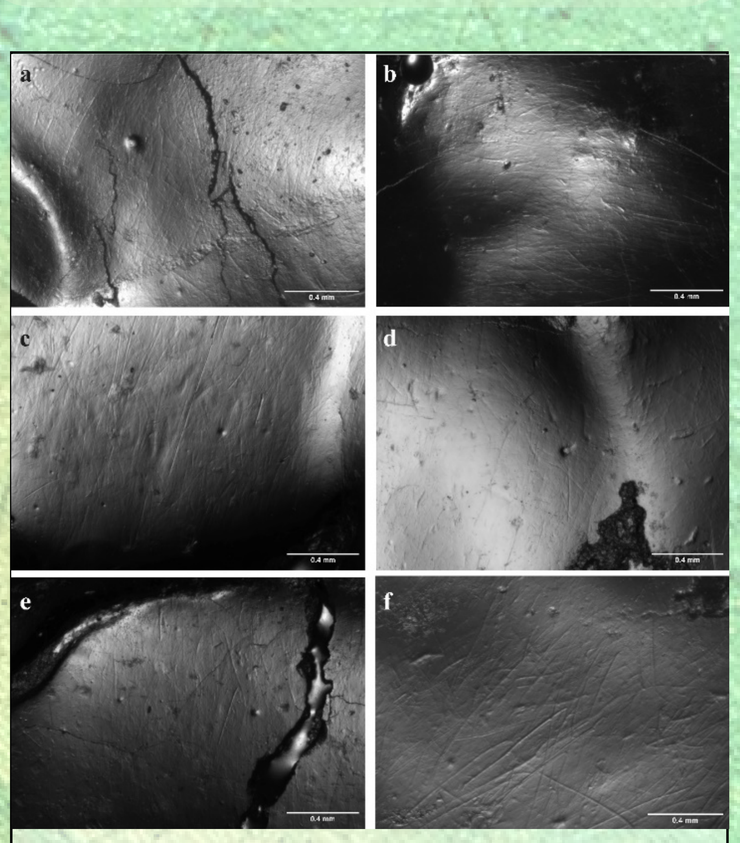
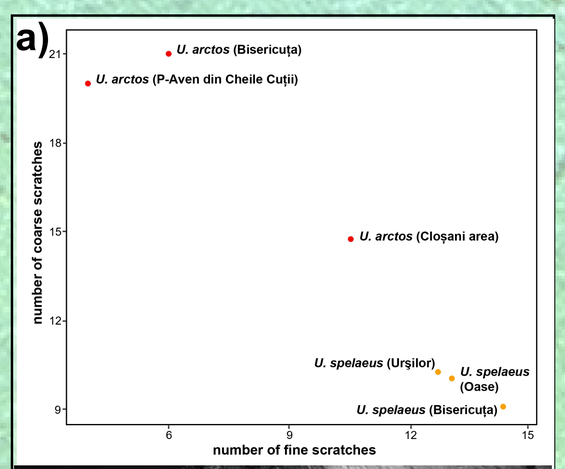


Fig. 3) a: Photomicrographs (×35 magnification) of the grinding non-faceted enamel surface of selected fossil individuals of *U. spelaeus* from the Carpathians. **a:** Ursilor (#PU/F); **b**: Ursilor (#PU/E2-III-1164); **c:** Oase (#O35.138); **d:** Bisericuța (#PB/C1-IX); **e:** Bisericuța (#PB/A1-I-II-1); **f:** Onceasa (#POc/016).



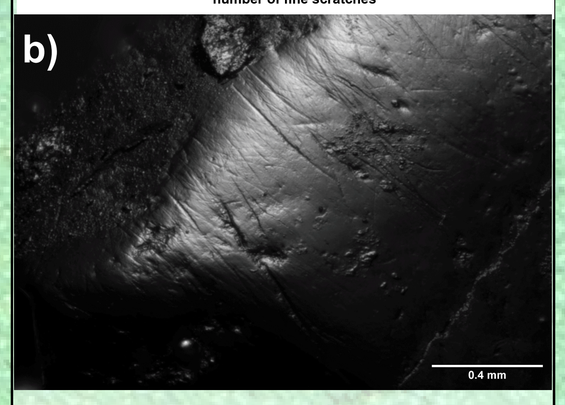


Fig. 4) a: Bivariate plot of the mean number of fine and coarse scratches for the fossil bear populations of *U. arctos* and *U. spelaeus* from the Romanian Carpathians. **b**: MIS 3 *U. arctos* from Bisericuța displaying coarse scratches (#PB/B1-X-XI).

Discussion and conclusions

These **dietary similarities** between *U. spelaeus* and extant *U. arctos* from the Carpathians, together with an early **27.1 cal kyr B.P.** date, suggest that the Carpathians served as an **ecological refuge** for cave bear population until their extinction. Moreover, **differences in the width of scratches** between MIS 3 brown bears and Holocene brown bears in the Carpathians could support the hypothesis of a **shift towards a more omnivorous diet** for the post-Last Glacial Maximum (LGM) *U. arctos*. This change might be attributed to the species occupying the **empty ecological niche** left due the **extinction of cave bear**. Finally, 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, reflecting the dietary adaptability of cave bear populations to specific ecological conditions.

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