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Fossil population structure and mortality analysis of the cave bears from Urşilor Cave, north-western Romania

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Research in cave bear palaeobiology focusing on population structure and mortality analysis may improve our understanding regarding the ecology of this species which vanished at the end of Marine Isotope Stage (MIS) 3, prior to Last Glacial Maximum (LGM), if assessed populations are large enough. Such population is available in Urşilor Cave, from north-western Romania, known as one of the most rich and complex European MIS3 cave bear sites. From the palaeontological excavation, situated at the lower level of the cave (= Scientific Reserve), more than 210 cave bear isolated lower molars, 160 mandibles and almost 180 canines were extracted and analyzed. The results obtained on the wear stages of the studied molars and mandibles indicated an "L"-shaped curve and suggest a non-attritional death pattern and a bone assemblage juvenile dominated. Moreover, the sex-ratio of upper and lower canines indicates a net dominance of females (5.4 females: 1 male). Although a "catastrophic" death pattern was obtained for cave bears, the animals seem to have died diachronically (non-simultaneously), over a time span of more than 6000 years. The triangular graph of age distribution is not appropriate for death assemblages from traps such as karst caves, where taphonomic processes like predation or scavenging would have played a less important role.

Key words: Mammalia, *Ursus spelaeus*, cave taphonomy, death pattern, sex-ratio, Romanian Carpathians, Urşilor Cave.

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Introduction

The aim of the present study is to emphasize the peculiarities of the fossil population structure and mortality of the cave bear bone assemblage from Urşilor Cave (= Urşilor), one of the most famous MIS 3 of Europe.

Questions regarding extinction, palaeodiet, and existence of several species/subspecies of *Ursus spelaeus* (Rosenmüller and Heinroth, 1794) during the Upper Pleistocene, are the most commonly debated issues within the cave bear scientific community, and the answers are often unsatisfactory, since the majority of researchers are trying to generalize their results to larger areas.

One of the keys to understanding cave bear life and death is knowledge of its palaeobiology (Kurtén 1976; Pacher and Stuart 2009). Age structure and the adult sex-ratio are generally considered to be the most important variables for understanding the biology of fossil species (Weinstock 2000; Pacher and Quilès 2013).

The study of cave bear population parameters has been undertaken in a detailed, systematic manner for at least six decades in order to explore how mortality profiles are related to age and sex, demographic parameters indicated by the fossils (e.g., Erdbrink 1953; Kurtén 1976; Stiner 1998; Germonpré and Sablin 2001; Weinstock 2000; Debeljak 2002; Pacher and Quilès 2013).

Through the study of the mode of death, various issues can be addressed regarding what type of accumulation resulted in the preservation of the studied remains (Lyman 2004): (i) active or passive, (ii) synchronic or diachronic, (iii) the number of organisms, and (iv) their demographic features. The study of the mortality pattern provides valuable information regarding the nature and the genesis of a bone bed, the population structure, the possible predators and the other palaeobiological parameters of a given cave bear population.

Typically, in order to assess the mortality pattern of a given population, taphonomists investigate age-frequency distributions. In such cases, the number of dead individuals per age class is tallied—usually, as MNI (Minimum Number of Individuals) values, which are plotted in a histogram. Each vertical bar represents an age class, while the height of a bar is scaled to the frequency of the individuals per age class (Lyman 2004).

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Classically, there are two basic mortality types: the first type is referred to as "attritional" or "normal" mortality. It is modeled as a frequency distribution of age classes in which very young and very old individuals are overrepresented relative to their living abundances, while reproductively active adults are underrepresented because of the varied mortality rates across age classes (Craig and Oertel 1966; Lyman 2004). Attritional mortality is selective. Those age classes most susceptible to natural (ecological) mortality (juveniles and older individuals) are more prone to die, whereas the healthy adults, in their first reproductive years, are less prone to vanish. This susceptibility to mortality results in a bimodal distribution. The frequency distribution is often referred to as "U"-shaped (e.g., Klein 1982; Lyman 2004). Attritional mortality results from normal to routine, ecologically-related deaths of population members. The "U"-shaped death model assumes that the mortality was slow and is reflective of the rate of biomass turnover (Voorhies 1969; Lyman 2004).

The "catastrophic" or "mass" mortality pattern is the second basic mortality type. It is modeled as a frequency distribution of age classes, in which successively older age classes are represented by fewer and fewer individuals; in other words, the frequency distribution is unimodal, with an extreme positive skewness, and it is referred to as "L"-shaped. Theoretically, because catastrophic mortality is non-selective, it will result in the death of proportionally more prime-age adults (Voorhies 1969; Lyman 2004).

For Romanian Carpathians, although rich in Upper Pleistocene (MIS 3) cave bears sites, there were only few attempts (Quilès et al. 2006; Petrea 2009) for analyzing the mortality patterns of a given *Ursus spelaeus* population.

Abbreviations.—ASR, adult sex ratio; LS, Living age structure; MIS, Marine Isotopic Stage; NNVA, Normal Non-Violent Assemblage.

Material and methods

The site.—Urşilor Cave is situated in the North-Western part of Romania, Bihor Mountains, left slope of Craiasa Valley. The studied cave bear material was collected from the palaeontological excavation, situated at the lower level of the cave (Robu et al. 2011). The analyzed cave bear thanatocoenosis is a primary accumulation (deposition in situ for the fossil bones) situated at the bottom of a 17 m steep slope) derived mainly via pitfall entrapment, most probably during hibernation.

The excavations has not yet reach the bottom of the cave. The deepest point (relative to the 0 datum) is in the D3 and D4 quadrants (the longitudinal component of the excavation), almost 2.4 m deep. For both the longitudinal and transversal axis of the excavation, the first three bone layers (from top the bottom) are common and were analyzed together (Fig. 1). The cave bear remains found within the palaeontological excavation belong to the same climate period, ~45–40 calendar kyrs BP (median age) (Constantin et al. 2014).

Mortality and sex ratio analysis.—The mortality analysis of the cave bears from Urşilor were carried out using the first, second and third lower permanent molars (M_1, N = 82; M_2, N = 71; M_3, N = 50) and the lower jaws (N = 160) since they are the most often used skeletal elements for such analyses due to their regularity of the wear and damage patterns (Pacher and Quilès 2013). As only one age could be assigned to one mandible, the wear stage was determined for the entire mandible (and not independently for different molars of the same jaw bone). Nine age stages, defined according to Stiner (1994, 1998), on the basis of the crown wear pattern and root development have been distinguished. Stage I comprises germs and unworn teeth, with about 50% of root development completed and no visible wear. Stage II comprises teeth with more than 50% of root development completed and only slight abrasion of the enamel. Teeth of stage III have completely fused roots and show slight use wear on the cusps, but little or no dentine exposed. Stages IV to VII include teeth of adult individuals revealing different degrees of attrition on the occlusal surface. Stages VIII and IX are heavily worn teeth of older individuals, with completely worn crowns, which may have exposed pulp cavities. The use of wear stages do not give age in real years, nor is it assumed that single stages comprise equivalent time spans (Stiner 1998; Pacher and Quilès 2013).

Classically, the most frequently used method to calculate sex-ratios for cave bear assemblages is to assign canines to sex by measuring their crown widths, the labiolingual diameter at the base of the crown. The segregation of the two sexes, based on their marked sexual dimorphism (especially expressed in canines), is possible for almost all specimens with little or no overlap of the distributions. Based on crown width measurements, a bimodal frequency distribution was observed, and the two size groups could be assigned to females and males (Koby 1949; Kurtén 1955, 1958; Pacher and Quilès 2013).

For the sex ratio of the cave bear assemblage from Urşilor, the lower and upper canines of the cave bears (isolated and those still in the alveoli of mandibles and maxillary fragments or crania) were pooled together. Only the adult teeth were plotted (adult sex ratio of the lower and upper canines: ASR-Cinf and ASR-Csup; adult sex ratio of both lower and upper canines: ASR Combined-adults) in order to avoid biasing the results, although the total sex ratio (TSR) is often used (e.g., Pacher and Quilès 2013). All the measured lower (N = 74) and upper canines (N = 105) were examined morphologically and independently sexed.

Results and discussion

Mortality analysis.—For all of the analyzed lower molars (M_1, M_2, and M_3) and mandibles (left and right side), the cave bear bone assemblage has the same juvenile-dominated pattern, the highest peaks being mainly recorded for stages II and III (see SOM: table 1, 2, Supplementary

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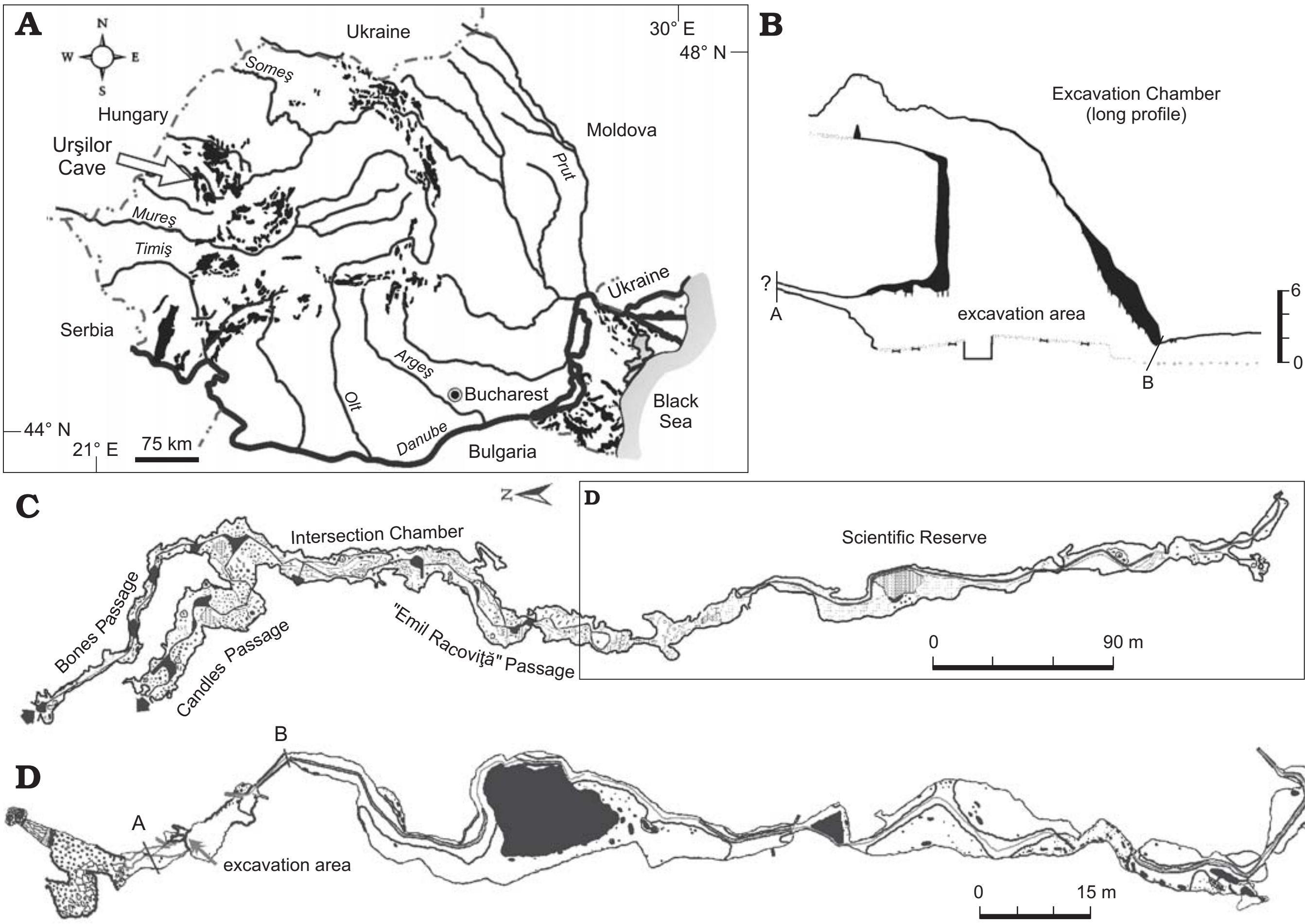

Fig. 1. Geographic localization (**A**) and plan (**C**) of Urşilor Cave of Chişcău. **B**. Long profile (section) of the Excavation Chamber from the Scientific Reserve. **D**. Plan of the lower level of the cave (= Scientific Reserve).

Online Material available at http://app.pan.pl/SOM/app61-Robu_SOM.pdf). The proportion of the other stages (IV to IX) uniformly decreases towards the last stage, which is the poorest represented.

For both the right and left side M_1, the bone assemblage from Urşilor is clearly juvenile-dominated: 61.36% and 60.52%, respectively. The first and the second use wear categories are underrepresented, while the highest peaks were recorded for the stage III. Adults are well represented, 38.63% (for the right M_1) and 36.84% (for the left M_1), although the highest proportion belongs to the prime-age adults (the first adult category). The old individuals (stages VIII and IX) are poorly represented, 0% and 2.63%, respectively (Fig. 2A).

The most numerous teeth in the assemblage are M_1 (M_1 is the first permanent tooth to erupt). As the assemblage is juvenile-dominated, with no considerable percentage of old adults, the mortality curve obtained for these teeth, almost unimodal, is typically “L”-shaped. This fact suggests a “violent” cause of death during or at the beginning of hibernation.

The mortality pattern obtained as a result of the M_2 analysis (right side; Fig. 2B) is almost the same as the one obtained for M_1; the juveniles (stages I–III) are the dominant age class (83.33% for right M_2 and 73.52% for left M_2), the adults have a lower representation (16.66% and 23.52%, respectively), while the old individuals are almost absent (0% and 2.94%, respectively). Since the stages I–III are the best represented (by teeth with open roots and germs) of all the age groups, and the old individuals are almost lacking, the mortality pattern is more similar to that of a living group. As observed for the lower M_1, the “L”-shaped curve obtained for M_2 suggests a “non-attritional” death pattern.

Although the fragile juvenile mandibles (wear stages I–II) have a lower structural density than the solid mandibles of adults (and old individuals) and they are generally underrepresented within cave bone assemblages, as mentioned for Oase Cave by Pacher and Quilès (2013), within the Urşilor thanatocoenosis juvenile mandibles are well represented.

More than 160 mandibles and mandible fragments (right and left side) were analyzed, in order to get better age-control on the death pattern previously obtained through the study of the lower molars. The results of this investigation point out that the mortality profile obtained for the mandibles is similar to the one recorded for the lower molars - an “L”-shaped profile (Fig. 2C; left mandible). The juveniles are the dominant age class (69.13% for the right mandible

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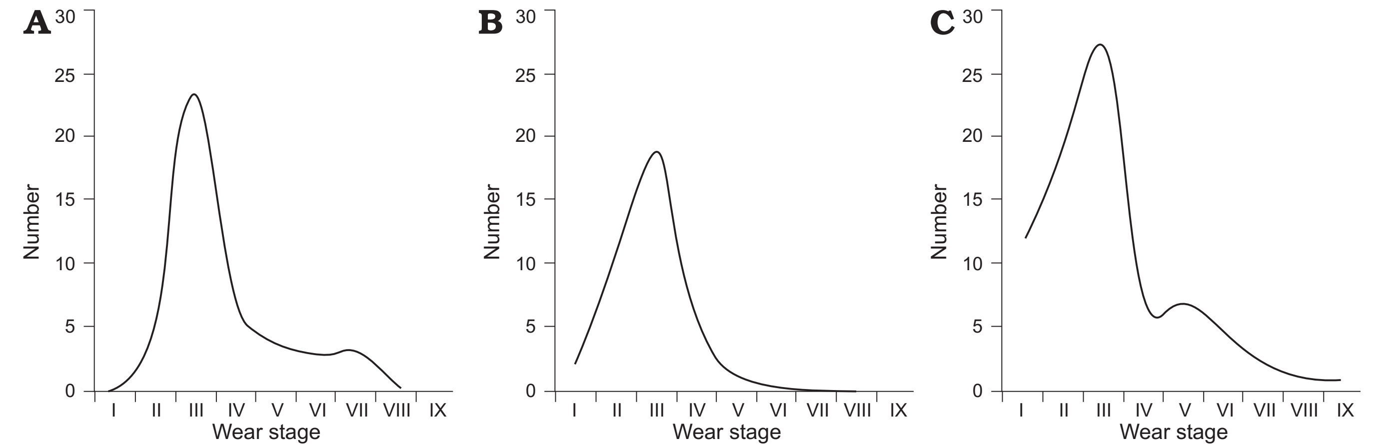

Fig. 2. Mortality profile of cave bears from Urşilor (~45–40 calendar kyrs BP). **A**. Right M1 (N = 44). **B**. Right M2 (N = 36). **C**. Left mandible (N = 82).

and 71.95% for the left mandible), the adults have lower percentages of specimens (28.39% and 25.60%, respectively), while the older individuals (2.46% and 2.43%, respectively) are almost absent. The death curves obtained for the mandibles, similar to those recorded for the lower molars, also suggest a "non-attritional" or "non-selective" death pattern.

All the age-at-death profiles obtained for the lower molars and mandibles collected from the palaeontological excavation within Urşilor, suggest a mortality pattern similar to a living population, typical for natural traps, probably enforced by the special stress of hibernation. Although it may be tempting to assume a catastrophic death for the entire bone assemblage, the radiocarbon data obtained for the cave bear bones suggests diachronic mortality over a time span of more than 6000 years. Moreover, as the bone assemblage is located at the base of a 17 m-deep shaft, we suggest that the majority of the cave bears bones found within the excavation accumulated via pitfall or cave entrapment. The mortality pattern „looks" catastrophic but, in fact, is a result of non-selective, diachronic deaths, spanning a long period of time.

The age-at-death pattern obtained for the cave bear remains from Urşilor was plotted for all analyzed lower teeth and mandibles (Fig. 3A). The mortality patterns are clustered around the so-called "juvenile-dominated bone assemblage", with 57.69–83.33% being juveniles, 16.66–38.63% adults, and 0–3.84% old individuals. Excluding the limits of the method (Stiner 1994) due to the difficulty of clearly distinguishing between stages III and IV, and differences in the degree of wear resulting from varied diets and environmental grit (Pacher and Quilès 2013), the results point to the conclusion that the cave bear thanatocoenosis is juvenile-dominated. In other words, an „L"-shaped age profile with a high proportion of juveniles, lower proportions of adults and a very limited proportion of old individuals, looks like a living population structure. This is what happens with a biological trap; it gathers all the age categories and reflects

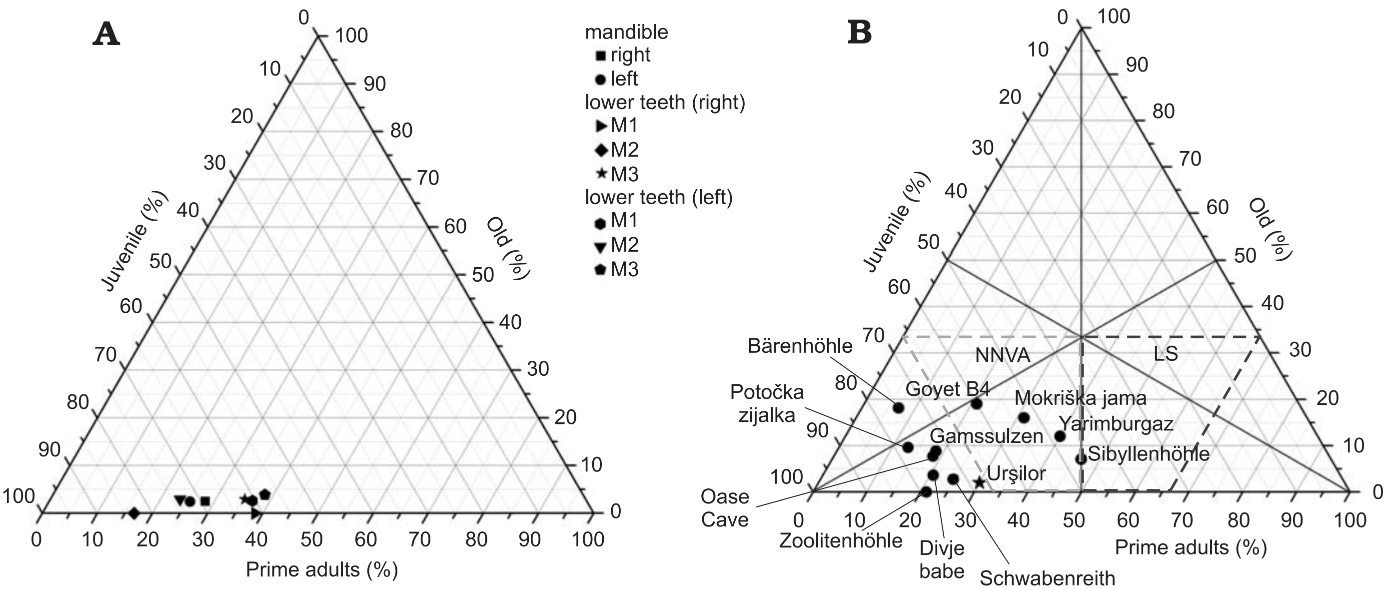

Fig. 3. Tripolar graphs showing the distribution of the teeth and mandibles (**A**) of cave bears from Urşilor (~45–40 calendar kyrs BP) in the three main age categories (according to Stiner 1994); and distribution of age classes (**B**) from different cave bear sites in the three main age categories, as proposed by Stiner (1994): NNVA (Normal Non-Violent Assemblage), grey dashed polygon; LS (Living age Structure), black dashed polygon.

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the age structure of a given population. Similarly, but used at another scale, is the cave trap case of Urşilor where all the age classes were „non-discriminatorily" collected.

The age-at-death model obtained for the cave bear remains from the Urşilor excavation was compared with the mortality profiles recorded for other European cave bear sites (Fig. 3B; SOM: table 3). Based on this, the Urşilor bone assemblage is close to Normal Non-Violent Assemblage (NNVA) area, which may lead to contradictions when compared with profiles obtained from the lower molars and mandibles. Using a population with known mortality profiles, on the tripolar graph, Stiner (1990) delineated areas that corresponded to the traditional "U"-shaped and "L"-shaped age frequency distributions. Stiner (1990, 1991a, b) employed a three pole graphic technique to assess the mortality patterns. She used this technique in order to distinguish, in a general way, the kinds of hunting methods that produced a particular kind of mortality. Cursorial predators tend to produce "U"-shaped mortality profiles, while predators which ambush their prey tend to produce "L"-shaped mortality profiles (Lyman 2004).

This three pole graphic representation, also used by Pacher and Quilès (2013) to describe cave bear mortality in karst settings, may be less relevant when analyzing a thanatocoenosis formed at the bottom of a shaft by pitfalling or drowning. Therefore, the use of a tripolar graph, in order to assess the mortality pattern of a cave bear population from a karst setting, is misleading, especially when studying the bone assemblages accumulated in special contexts (e.g., cave traps, pits).

Sex ratio.—There is no clear gap between apparent males and females for the labiolingual diameter of the adult lower canines (Fig. 4A). The frequency histogram of lower canine crown width indicates an almost unimodal curve, with a secondary small peak around 20–24 mm (probably males). Corroborating the measurements with morphological observations, I was able to calculate the mean value for females, 17.67 mm (min–max, 13.75–18.56 mm, N = 74) and for males, 21.72 mm (min–max, 19.23–24.33 mm, N = 14).

The transverse diameter of the adult upper canines (Fig. 4B) shows a similar pattern to that of the lower canines—an almost unimodal curve, with two small peaks, first around 11 mm (within the "female" range, with significantly smaller specimens) and the other, around 21–24 mm (probably males). The mean value for females is 15.78 mm (min–max, 9.73–19.57 mm, N = 91), while for males it is 20.88 mm (min–max, 15.23–21.81 mm, N = 16).

A better graphic representation of the sex ratio of the cave bears from Urşilor resulted (Fig. 5) when the maximum length and width of both the lower and upper canines were plotted.

The lower canines (Fig. 5A) are clearly separated in two clusters. The morphometric analysis allowed us to distinguish without any doubt between males and females. As can be observed, the females significantly outnumber the males. The

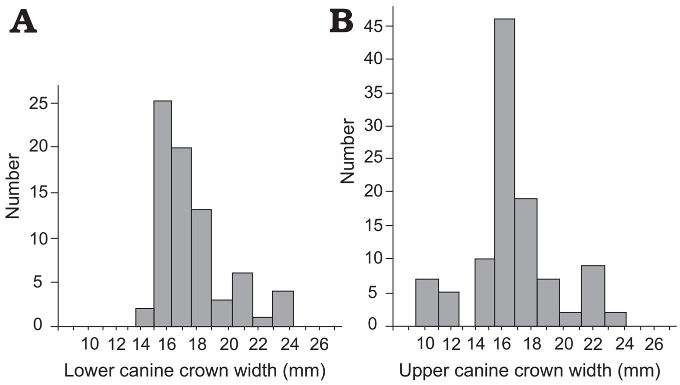

Fig. 4.Transverse diameters of all of the adult lower (**A**, N = 74) and upper (**B**, N = 105) cave bear canines from Urşilor (~45–40 calendar kyrs BP).

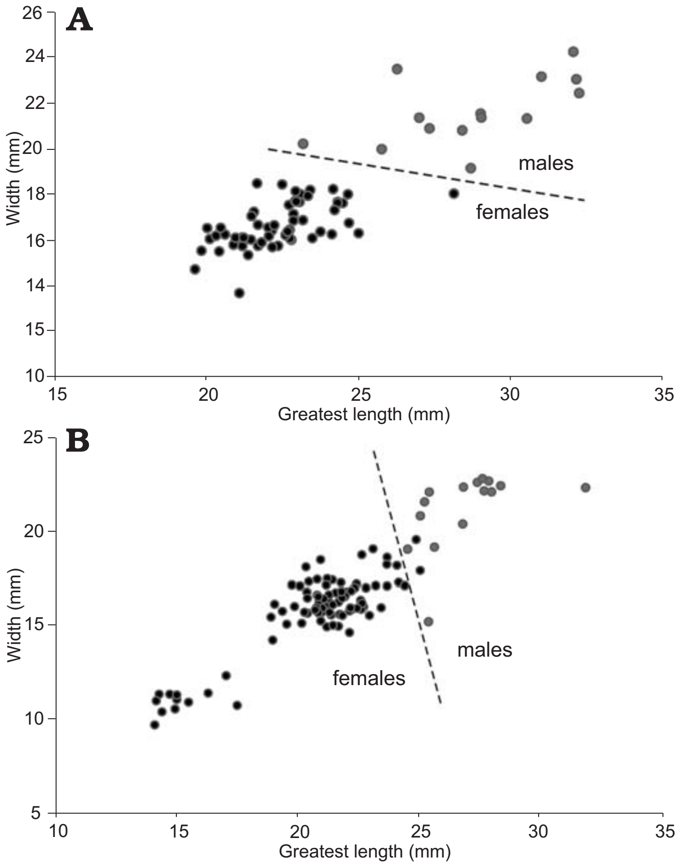

Fig. 5. Greatest length vs. width for the lower (**A**, N = 74) and upper (**B**, N = 105) cave bear canines from Urşilor (~45–40 calendar kyrs BP).

assemblage from Urşilor contains 74 lower canines: 60 belong to females (29 isolated and 31 attached to mandibles) and 14 belong to males (10 isolated and 4 attached to mandibles). For the isolated lower canines, the ASR is 29 females to 10 males, while for the attached lower canines it has a value of 31:4.

The upper canines (Fig. 5B) are obviously concentrated in three clusters, and females significantly outnumber males. The ASR for the upper canines is 91 females to 14 males. A group of 12 female upper canines can be clearly distinguished from the main female cluster, having smaller di-

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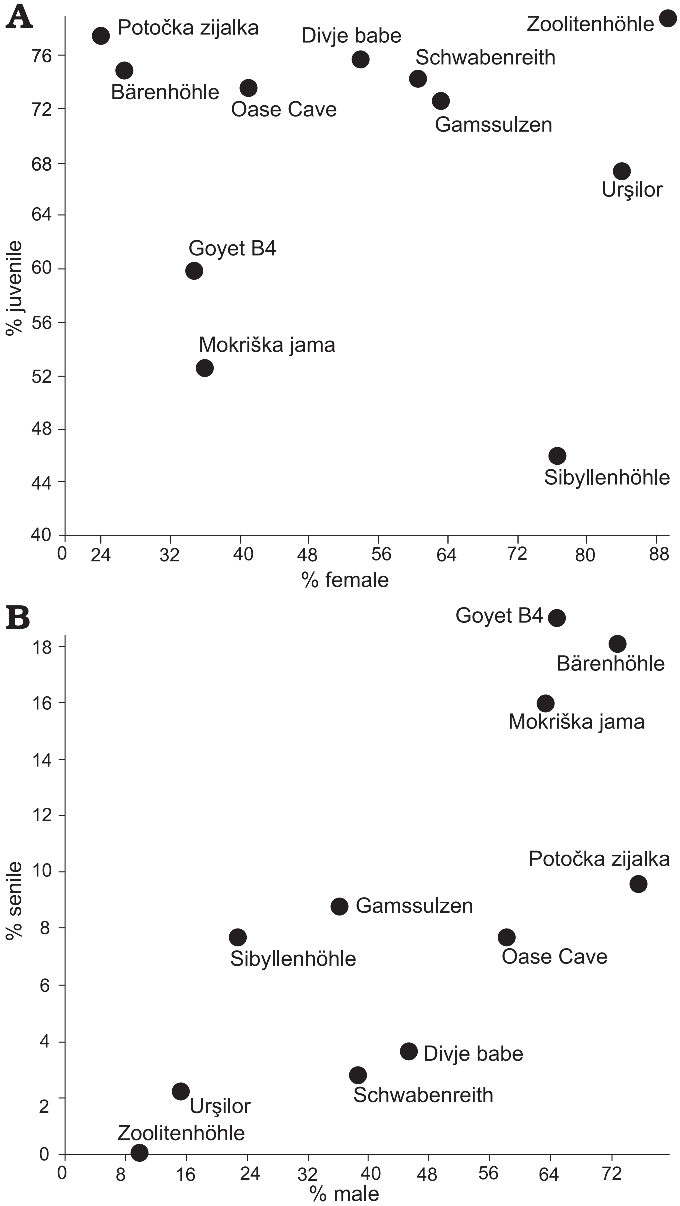

Fig. 6. Percentage of juveniles vs. females (**A**) and old individuals vs. males (**B**) of cave bears from Urşilor, (~45–40 calendar kyrs BP). Data derived from SOM: tables 3 and 4.

mensions (for both the maximum length and width measurements). The upper canines that belong to males form a distinct cluster as well, on the upper part of the graph (grey dots), with the highest values.

There were 91 female upper canines found within the excavated bone assemblage at Urşilor, 19 attached to skulls and skull fragments and 72 isolated, and 14 male upper canines, 5 attached to skulls and skull fragments and 9 isolated. Among the attached upper canines, the ratio is 19 females to 5 males, while among the isolated canines it is 72 females to 9 males.

Hence, the ASR for all of the adult cave bear lower and upper canines from Urşilor is 151:28, females to males (84.35% : 15.64%), giving a ratio 5.4:1, one of the highest recorded for all known European cave bear sites (Weinstock 2000; Debeljak 2004, 2007; Pacher 2004; Pacher and Quilès 2013; Germonpré 2004; Stiner et al. 1998). All three techniques (ASR-Cinf, ASR-Csup and Combined-adults) used to calculate the cave bear sex ratio point to the same result: the bone bed is clearly female-dominated. The sex ratio values obtained for Urşilor cluster around those calculated for Zoolithenhöhle, Sibyllenhöhle, Schwabenreith, Gamssulzen, and Divje babe (stratigraphic levels 2–10), where the females outnumber the males, while, at the other end, Bärenhöhle, Oase Cave, Potočka zijaka, Mokriška jama, and Goyet B-4 are male-dominated (SOM: table 4).

As modern brown bear females hibernate together with their cubs at least during their first two winters, it is expected for cave bear bone assemblages to have a good correlation between the sex ratio and the percentage of juveniles.

Fig. 6A shows, for the analyzed sites, there is no clear correlation ($R^2 = 0.0039$) between the percentage of females and the percentage of juveniles. A possible explanation for this weak correlation is that, besides a biased mortality pattern, all the cave bear sites typically have a high percentage of juveniles (Kurtén 1958; Boessneck and von der Driesch 1973; Baryshnikov and David 2000; Weinstock 2000; Sabol 2005) and female-versus-male-dominated sites are common throughout Europe (Pacher and Quilès 2013).

At Urşilor, the most numerous use wear categories are stages II, III, and IV (older juveniles and prime-adults) and it seems reasonable not to have a correlation between the females and the juveniles, since stages III and IV represent, most probably, young cave bears, during the first winter without their mothers. Therefore, for a relevant result, only the first two wear use stages should be correlated with the percentage of the females, since it is well known that during those stages (I–II) the cave bear cubs lived together with their mothers.

For the analyzed sites, there is a moderate correlation (Fig. 6B) between cave bear males and aged individuals ($R^2 = 0.5984$). At Urşilor, the frequency of old individuals is low, and the sex ratio is female-dominated. A similar situation was recorded for Zoolitenhöhle, Schwabenreith, and Divje babe caves. Other sites (e.g., Oase Cave and Potočka zijalka) are characterized by a higher percentage of old bears, and the caves are considered male-dominated. Therefore, in female-dominated cave bear assemblages (but not only for these thanatocoenoses), the percentage of males (% male) can be correlated with the percentage of older individuals (% senile).

Pacher and Quilès (2013) suggest the existence of two groups of cave bear sites, based on the available data: female-dominated (with a lower proportion of older individuals) and male-dominated (with a higher proportion of old adults), a pattern difficult to explain (Weinstock 2000), but thought to be explained by mortality and sex ratios (Grandal-d'Anglade and Vidal 1997; Weinstock 2000; Debeljak 2007; Germonpré and Sablin 2001), altitude (Rabeder et al. 2008) or climate change (Grandal-d'Anglade and Vidal 1997; Germonpré and Sablin 2001). Since all the cave bear bone

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assemblages have not been completely excavated (which is nearly impossible), it is difficult to categorize them as male/female-dominated, and the hypotheses based on altitude, climate change, or mortality pattern cannot be substantiated.

The fossil material excavated from Urşilor represents only a small part (~9 m^2) of a bone assemblage which extends across hundreds of square meters and over a depth of ca. 3–4 m of fossil-bearing sediments, throughout the cave system. Although a large number of cave bear bones have been excavated, there is no complete picture of the age-at-death profile and sex ratios for the entire cave system. At different scales, the same situation might be encountered for all the analyzed cave bear sites across Europe. Sometimes there are significant differences in sex-ratios even among various zones of a single site (Germonpré 2004; Pacher 2004; Pacher and Quilès 2013). And then, a question arises: are the death patterns and sex ratios we normally obtain from a small excavation area representative for an entire cave system? Fortunately, as the Excavation Chamber has acted as a natural trap, the age structure of the cave bears from the excavated bone assemblage should be close to the age structure of the MIS 3 thanathocoenosis from this cave.

Conclusions

More than 210 lower molars and more than 160 adult cave bear mandibles and mandible fragments were analyzed, in order to assess the age structure and sex ratio of the bone assemblage from the palaeontological excavation within Urşilor. The age-at-death pattern points to a „juvenile-dominated bone assemblage". The obtained sex ratio, one of the highest among the European cave bear sites, 5.4 females to one male, categorizes this site as "female-dominated" (with a lower proportion of older individuals).

As the age-at-death curve and radiocarbon data suggest that the bone assemblage has an "L"-shaped pattern ("catastrophic"), its "bone sources" were not selective and the death of the animals happened diachronically (non-simultaneously), over a time span of more than 6000 years.

The tripolar graph technique used to assess the pattern of death (NNVA or LS) in cave bear bone assemblages, especially in cave traps (like Urşilor), apparently does not help in understanding either the formation of the bone bed or the pattern of cave bear death.

The relevance of the data recorded from the partially excavated cave bear bone assemblages is of great concern for the sex ratio results. One cannot compare the sex ratio obtained from a small excavation within a site with the one obtained from a large-scale excavation.

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