CATASTROPHIC DEATH ASSEMBLAGES FROM THE LATE PLEISTOCENE OF ITALY: THE CASE OF AVETRANA KARST FILLING (TARANTO, SOUTHERN ITALY)

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Abstract. New and detailed taphonomic and stratigraphical analyses have been carried out at the early Late Pleistocene site of "La Grave", nearby Avetrana (Taranto, Southern Italy). These, together with population analyses of the principal species represented (Bos primigenius, Dama dama, Cervus elaphus, Sus scrofa and Stephanorhinus hemitoechus), suggest that the fossiliferous deposits were probably accumulated rapidly, over a short time span, by exceptional events of heavy rainfall with overbank flooding. These results are supported particularly by comparison of the mammalian death assemblages from Avetrana with data from recent and Pleistocene catastrophic death assemblages documented in the literature. Furthermore, population analysis of species pinpoints the time of death between late autumn and winter. Periods with abundant and heavy rainfall are recorded in Late Pleistocene Mediterranean marine cores by the presence of sapropel levels, and in continental pollen diagrams covering the same time. Finally, observations on the morphometric variations in the bones of Bos primigenius reveal an increase in size of the species during the early Late Pleistocene and a decrease in size during the late Late Pleistocene and the Holocene.

Riassunto. Sono state effettuate nuove e dettagliate osservazioni tafonomiche e stratigrafiche sui depositi del Pleistocene Superiore antico di La Grave, nei pressi di Avetrana (Taranto, Italia meridionale). Tali osservazioni, insieme con analisi di popolazione delle principali specie (Bos primigenius, Dama dama, Cervus elaphus, Sus scrofa e Stephanorhinus hemitoechus), suggeriscono che il deposito fossilifero si è probabilmente formato in seguito ad eventi ravvicinati ed eccezionali, con forti precipitazioni e alluvionamenti. Questi risultati sono sostenuti in particolare dal confronto dell'età di morte dei principali mammiferi di Avetrana con i dati di letteratura relativi a "catastrophic death assemblages" attuali e pleistocenici. Le analisi di popolazione delle specie considerate, inoltre, suggeriscono che tali eventi eccezionali si sono verificati tra l'autunno inoltrato e l'inverno. Periodi di piogge abbondanti e concentrate nel Pleistocene Superiore sono riconosciuti nei livelli sapropelitici della stratigrafia marina e nei diagrammi pollinici continentali riferiti allo stesso intervallo cronologico. Sono discusse, infine, le variazioni morfometriche delle ossa di *Bos primigenius*. L'analisi mette in luce un aumento delle dimensioni della specie nel Pleistocene Superiore antico seguito da una diminuzione delle stesse nel tardo Pleistocene Superiore e nell'Olocene, tali variazioni risultano in accordo con la posizione biocronologica del deposito di Avetrana.

Foreword

The early Late Pleistocene mammal assemblage recovered from the karst cavity at "La Grave" near Avetrana (Taranto, Southern Italy) (Fig. 1) has been the subject of several previous papers (Sardella et al. 2005; Petronio et al. 2008; Salari & Sardella 2009; Pandolfi et al. 2011).

As described by Petronio et al. (2008), the fossiliferous deposit is found in an open-air karst cavity within Early Pleistocene limestone (called "Calcareniti di Gravina"). The "La Grave" cavity infilling is constituted by very abundant remains of large and small mammals, other vertebrates and fine sediments. Basing on biochronological data, the Avetrana mammal assemblage can be referred to the early Late Pleistocene (Melpignano Faunal Unit, according to Petronio et al. 2007, 2011), a time span between 0.110 and 0.080 Ma (Petronio et al. 2008). Useful biochronological information is provided by the occurrences of evolved forms of Cervus elaphus and Dama dama, which were first reported in Italy at the beginning of the Late Pleistocene (Petronio et al. 2007). The upper limit of the biochronological time span is provided by the occurrence of hippopotamus (Hippopotamus amphibius) and porcupine (Hystrix vinogradovi). The former is last recorded in Italy at the

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Fig. 1 - Location of the site.

beginning of the last glacial event (Bedetti et al. 2001; Petronio et al. 2008), whereas *H. vinogradovi* from Avetrana is the latest occurrence in Italy of the species (Salari & Sardella 2009). During the most recent investigations at the site of Avetrana (September, 2011), many new fossil remains was recovered and important new observations about the stratigraphy and taphonomy were made.

The aims of the present paper are therefore to reconstruct the detailed succession of events at the site and to establish the origin of the fossiliferous deposits through population analyses, palaeoclimatic and palaeoenvironmental considerations. Furthermore, on account of the exceptionally abundant remains of aurochs (*Bos primigenius*) discovered at the site, an exhaustive morphometric analysis of this species is reported. The aurochs assemblage from Avetrana may be considered one of the richest Pleistocene populations of this animal in Europe.

Remarks on the taphonomy and stratigraphy

Basing on stratigraphical observations, the deposit of Avetrana have been divided into nine beds and two discrete infillings or pockets (Fig. 2) by Sardella et al. (2005) and Petronio et al. (2008). The sedimentological, taphonomic and stratigraphical features of the deposit are summarised below. Over 80% of the fossiliferous remains are in a good state of preservation and approximately 60% of the vertebrate remains are ascribed to *Bos primigenius*.

The two pockets, named bed 0 in the previous papers, are filled with a yellow sandy clay with no evidence of bedding and capped by collapsed boulders. Fossil mammals from these pockets include *Erinaceus europaeus*, *Microtus (Terricola) savii*, *Hystrix vinogradovi*, *Lepus* sp., *Oryctolagus cuniculus* and *Felis silvestris*. All the remains are in a relatively well preserved state.

Bed 1 is composed of an uninterrupted stratum of calcareous pebbles, overlain by a thin deposit (30 cm) of argillaceous sand containing rare clayey pebbles (which are visibly altered) and a few fossil bones of *B. primigenius*. In all subsequent beds, the bones are generally chaotically disposed, with isolated long bones lying mainly parallel to the stratigraphic surface but without a predominant orientation.

Bed 2 comprises a thin (20 cm) deposit of sandy clay including numerous bone remains belonging to Aves, H. vinogradovi, Lepus sp., O. cuniculus, Vulpes vulpes, Canis lupus, Meles meles, Crocuta crocuta, Lynx lynx, Stephanorhinus hemitoechus, Sus scrofa, Hippopotamus amphibius, B. primigenius, Dama dama, Cervus elaphus, and a humerus of an undetermined Testudinata. The majority of the remains (about 83%) are very well preserved; a modest number of remains (about 12%) are slightly damaged through crushing or pressure and occasional bones have calcareous concretions (about 3%).

Bed 3 consists of 20 cm of argillaceous sand with only a few bones of O. cuniculus, Lepus sp., V. vulpes, C. lupus, M. meles, B. primigenius, D. dama and C. elaphus.

Bed 4, again around 20 cm in depth, is separated from the underlying layer by a discontinuity, marked by a stratum containing calcareous pebbles and including fragmentary remains of *Lepus* sp., *V. vulpes*, *C. lupus*, *B. primigenius*, *D. dama*, and *C. elaphus*.

Bed 5, around 140 cm thick, is composed of argillaceous sand containing very abundant bones and rare calcareous pebbles (Fig. 3A). In this bed, the majority of the remains are in a very good state of preservation (about 88%) and several bones are still articulated (Fig. 3B, D); about 11% of the remains are slightly crushed. Mammal remains are represented by O. cuniculus, Lepus sp., V. vulpes, C. lupus, L. lynx, M. meles, C. crocuta, H. amphibius, S. scrofa, Capreolus capreolus, D. dama, C. elaphus and above all, by B. primigenius.

The subsequent bed 6 is formed by about 20 cm of argillaceous sandy matrix and yielded several mam-

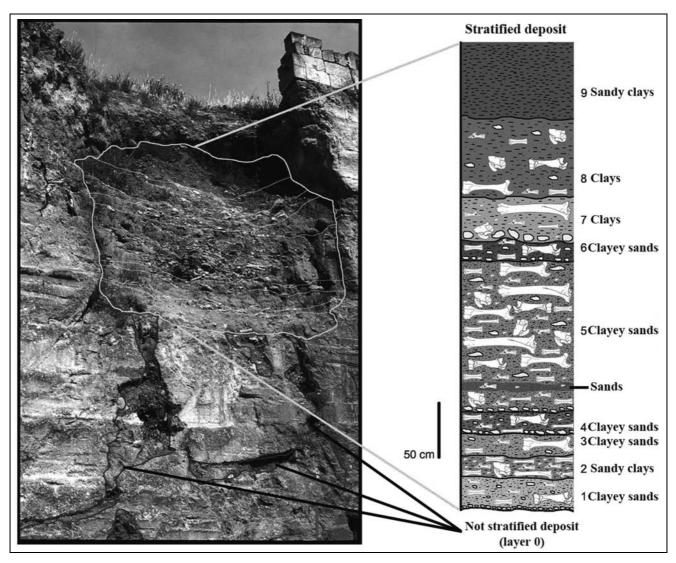


Fig. 2 - Avetrana (Southern Italy), Late Pleistocene: stratigraphy of the "La Grave" karst filling (by Petronio et al. 2011, modified).

mal remains. The bones in a good state of preservation (about 73%) are fewer than in the previous bed, whereas there is an increase in the percentage of damaged and concreted bones. The most representative taxa are O. cuniculus, V. vulpes, C. lupus, S. scrofa, H. amphibius, B. primigenius, D. dama, C. elaphus, and S. hemitoechus. A single Mousterian lithic artifact was also discovered in this layer.

In bed 7, around 40 cm thick, the abundance of fossil remains is similar to that in bed 5 (Fig. 3A). The percentage of well-preserved bones is relatively low (about 35%) and there is an increase in the percentage of damaged bones, although some are in anatomical connection (Fig. 3C). The species found in bed 7 are represented by remains of *O. cuniculus*, *V. vulpes*, *C. lupus*, *C. crocuta*, *S. hemitoechus*, abundant *B. primigenius*, *C. elaphus*, *D. dama* and a phalanx of *Megaloceros* sp.

Bed 8 is formed by about 75 cm of argillaceous sandy sediments with calcareous pebbles and scattered

remains of M. (T.) savii, H. vinogradovi, Lepus sp., O. cuniculus, M. meles, Mustela putorius, V. vulpes, C. lupus, F. silvestris, L. lynx, Panthera spelaea, C. crocuta, S. hemitoechus, S. scrofa, B. primigenius, C. elaphus and D. dama. Well preserved remains are very scarce in comparison with older beds and represent about 14% of the total assemblage from this horizon. Concreted remains are abundant (about 57%), as are damaged remains (about 21%). A few lithic artefacts, which are still being studied, have been recovered from this bed.

The highest argillaceous bed 9 is 70 cm thick and contains very rare bones, which are frequently partially decalcified and concreted.

New taxa from the Avetrana karst filling

Testudinata

A proximal portion of the humerus of a turtle from bed 2 is the only indication of a reptile occurrence at the site. At present, it is not possible to establish

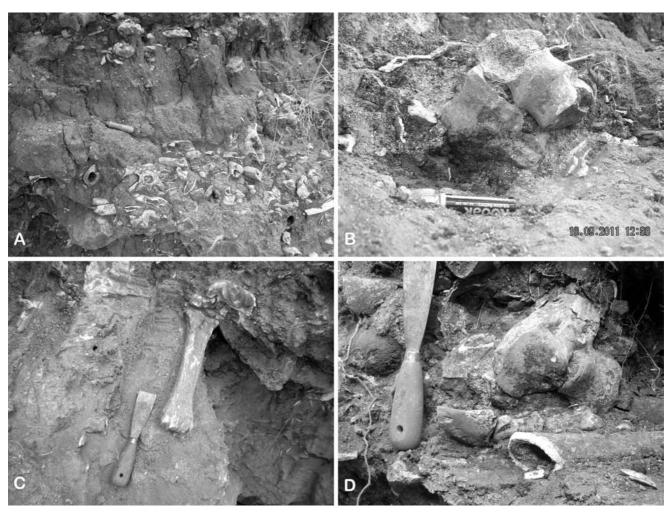


Fig. 3 - Avetrana (Southern Italy), Late Pleistocene: a) upper part of bed 5, bed 6 and lower part of bed 7; b) articulated distal humerus and proximal radius of *Bos primigenius*; c) articulated distal radius, carpal bones and metacarpus of *Bos primigenius*; d) articulated first, second and third phalanx of *Bos primigenius*.

whether this represents Pond terrapin (*Emys orbicularis*), or the Greek (*Testudo graeca*) or Hermann's tortoise (*Eurotestudo hermanni*).

Capreolus capreolus

The roe deer is represented by a few remains from bed 5, including a basal portion and a few fragments of antler and some fragmented postcranial remains (metapodial bones and phalanges) (Pl. 1, fig. 1). *C. capreolus* is a typical woodland species and prefers hardwood forests with a combination of scrub and clearings (Boitani et al. 2003); it is a common species in the Late Pleistocene of Italy but is invariably represented by only a few remains at each site (Petronio et al. 2007; 2011).

Mustela putorius

A fragmentary mandible of a small-sized carnivore with canine, three premolars and carnassial tooth (length C-M1 = 18.8 mm; length P2-M2 alveolar = 17.6 mm; length lower M1 = 8.4 mm) has been recovered from bed 8 (Pl. 2, fig. 1). It indicates the presence of polecat in the Avetrana karst filling. *M. putorius* prefers open woodland near water (Boitani et al. 2003), and it

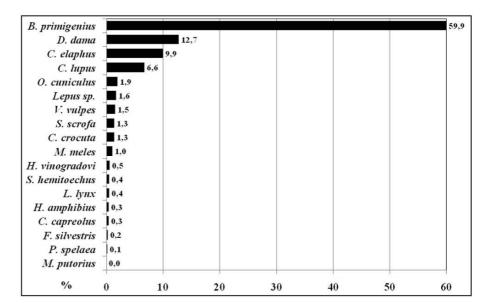
known from other Late Pleistocene sites in Italy (Petronio et al. 2011).

Materials and Methods

The most recent collections of fossil remains, made during September, 2011 came from all beds at the site "La Grave" nearby Avetrana, with the exception of beds 0 and 1, which were apparently sterile. The following taxa are recognized: Testudinata, Aves (in study), Rodentia (Microtus (Terricola) savii and Hystrix vinogradovi), Lagomorpha (Lepus sp. and Oryctologaus cuniculus), several Carnivora (Vulpes vulpes, Canis lupus, Mustela putorius, Meles meles, Felis silvestris, Lynx lynx and Crocuta crocuta), Perissodactyla (Stephanorhinus hemitoechus) and Artiodactyla (Hippopotamus amphibius, Sus scrofa, Cervus elaphus, Dama dama, Capreolus capreolus and abundant Bos primigenius).

The data concerning percentages of the different taxa reported in Petronio et al. (2008) are slightly modified. Increases in the percentage of carnivores (in particular *Canis lupus*) and lagomorphs (*O. cuniculus* being particularly well represented) are noted here; furthermore, the percentages of *B. primigenius* (the dominant species at the site with a frequency of about 60%) and *C. elaphus* are slightly lower (Fig. 4). The pachyderms (*S. hemitoechus* and *H. amphibius*) are very rare. Together, the most recent and previous taphonomic and stratigra-

Fig. 4 - Avetrana (Southern Italy), Late Pleistocene: percentages of fossil remains of selected mammalian taxa.



phical analyses of the karst filling described above, taking into account the preservational state of the bones (well preserved, very or few damaged, concreted etc) (Fig. 5) and their position and orientation in the layers, represent the first stage in reconstructing the succession of events. Furthermore, population analyses of some representative species may be used to obtain information about the time span of depositional events, the seasonality of such events and palaeoenvironment.

For this purpose, the minimum number of individuals was calculated for each bed, taking into consideration the side of each bone (right or left) and the most frequent skeletal element from only one side. The results were integrated with the analysis of the metrical characters, sex and age profiles of the other skeletal elements.

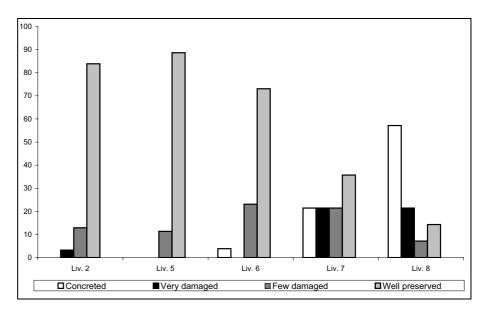
The estimated age of death was calculated according to the stage of fusion of the long bone epiphyses, and tooth eruption, replacement and wear stages according to Silver (1969), Barone (1974a,b) and Grant (1982) for present-day domestic cattle (as a proxy for *B. primigenius*), Hillman-Smith et al. (1986) for the white rhinoceros (*Ceratotherium simum*) and Goddard (1970) for the black rhinoceros (*Diceros bicornis*) (for *S. hemitoechus*), Bull & Payne (1982) for *S. scrofa* from Turkey, and

Mariezkurrena (1983) for *C. elaphus* from Cantabria (Spain) for red deer and fallow deer.

The estimate body weight of *B. primigenius* was calculated according to the regression equation of De Gusta & Vrba (2005) for African bovids. The estimate of the withers height in *B. primigenius* was carried out by multiplying the length of the radius, tibia, metacarpus and metatarsus by the coefficients of Matolcsi (1969) for present domestic cattle. Even if the biology and ontogeny of *B. primigenius* were different from present-day domestic cattle, estimated relative ages, body weight and withers height can probably be reconstructed with confidence.

In addition, in order to examine size variation through time in *B. primigenius*, the morphometric values of specimens from Avetrana were obtained according to Driesch (1976). Following Pandolfi et al. (2011), the values were compared with those from several other Southern European sites, in particular from Italy, ranging from the late Middle Pleistocene to the early Holocene (see Pandolfi et al. 2011, and references therein). To compare morphometric change through time, box-plot graphs are utilized, showing the extreme values (minimum and maximum) and the 25 and 75 percentiles.

Fig. 5 - Percentages of preservation of the bones and teeth recovered in the different levels of Avetrana.



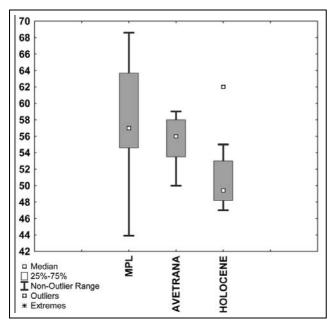


Fig. 6 - Box plot of variation in size of the antero-posterior diameter of the proximal epiphysis of the radius of *Bos primigenius* from Middle Pleistocene (N = 41) to Holocene (N = 9), including Avetrana (N = 8).

Remarks on the morphometrical variation of *Bos primigenius* during the Pleistocene and Holocene

Pandolfi et al. (2011) recognized a trend in the dimensional variations in female aurochs. In particular, the authors identified an increase in the maximum length and the distal transverse diameter of the metacarpus and of the metatarsus from the Middle Pleistocene to the beginning of the Late Pleistocene. This trend is followed by a decrease in the same measurements during Marine Oxygen Isotope Stages 4 and 3 (MIS 4-3) and the early Holocene. Furthermore, Pandolfi et al. (2011) noticed a general variation in shape of the metapodial bones from the Middle Pleistocene to Holocene. In particular, in the earliest population of the species (Middle Pleistocene) the metapodial bones are charac-

terized by a "clepsydra" shape. In these bones the epiphyses (especially the distal one) are more developed than the diaphysis so that the bones result slighter. The same shape in the metapodial bones of the Middle Pleistocene is recognized even during the Holocene. During the late Middle Pleistocene and the early Late Pleistocene the metapodial bones seem to have a more "columnar" shape. In these last specimens, the diaphysis is more developed than in the Middle Pleistocene and Holocene ones. Similar trends in other bones can also be examined and here, we consider the talus, tibia and radius, on account of their exceptional abundance in the assemblage and resulting large dataset for comparison. Furthermore, the metapodials, radius and tibia are more influenced by variation in size than the humerus and femur. Since it is very difficult to separate the talus, radius and tibia of males and females, in the analysis we consider these bones in toto.

For the radius, only the proximal transverse diameter (PTD) and the proximal anteroposterior diameter (PAPD) were measured (Fig. 6). The results demonstrate that PTD decreases from the Middle Pleistocene (MPL) to the late Late Pleistocene (LPL2), whereas it seems to increase slightly during the Holocene, although there is large variation in the dataset at that point. The specimens of Avetrana lie in an intermediate position between those from the Middle and the late Late Pleistocene. In Figure 6, a clear trend in the PAPD can be seen towards a decrease of size from the Middle Pleistocene to the Holocene. Data for the maximum length of the bones and the distal epiphysis are very scarce and the comparison between different periods is therefore very difficult. Standard Deviation (SD) and Coefficient of Variation (CV) values are relatively low for the aurochs population of Avetrana (SD = 3.07; CV = 5,53), whereas they are very high for other sites (for MPL and Holocene respectively SD = 7,81 and 4,83; CV = 13,45 and 9,4). This testified to the high

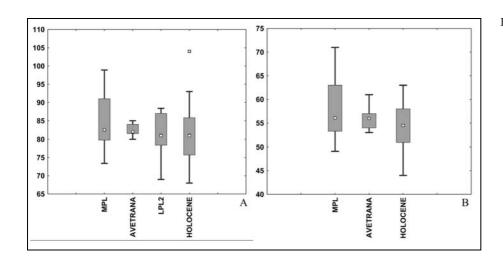
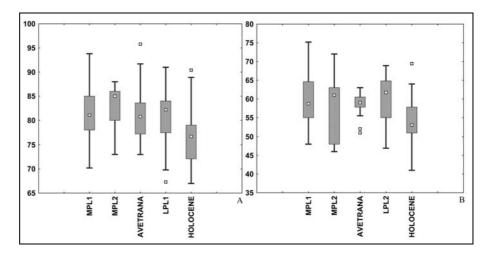


Fig. 7 - Box plot of variation in size of the distal epiphysis of tibia in *Bos primigenius* from Middle Pleistocene to Holocene. a) Distal transverse diameter (MPL N = 50; Avetrana N = 9; LPL2 N = 9; Holocene N = 31); b) Distal antero-posterior diameter) (MPL N = 8+Lunel Viel; Avetrana N = 5; Holocene N = 18).

Fig. 8 - Box plot of variation in size of the astragali of *Bos primigenius* from Middle Pleistocene to Holocene. a) Medial height (MPL1 N = 121; MPL2 N = 14; Avetrana N = 28; LPL1 N = 23; Holocene N = 26); b) Distal transverse diameter (MPL1 N = 121; MPL2 N = 15; Avetrana N = 21; LPL2 N = 29; Holocene N = 43).



morphological homogeneity of the adult remains of aurochs from Avetrana.

With respect to the tibia, a slight decrease of the distal transverse diameter (DTD) and the distal anteroposterior diameter (DAPD) is recorded from the Middle Pleistocene to Holocene (Fig. 7). As for the radius, the homogeneity of the Avetrana aurochs population is testified by the low values of the SD and of CV (for DTD, SD = 2,7 and CV = 1,99; for DAPD, SD = 3,11 and CV = 5,54), whereas they are very high for other sites (for DTD, MPL, LPL and Holocene are respectively SD = 7,32, 6,6 and 7,78; CV = 8,64, 8,15 and 9,57; for DAPD, MPL and Holocene are respectively SD = 6,19 and 5,32; CV = 10,66 and 9,88).

In the talus, a decrease in size during the Holocene is recorded (Fig. 8). The population of aurochs from Avetrana shows that the medial height (MH) is lower than in specimens from the Middle Pleistocene but higher than in those from the Holocene. A trend towards an increase in size from the Middle Pleistocene to the early Late Pleistocene, followed by a decrease during the Holocene, is observable in the antero-posterior medial diameter (MAPD). The other measurements (distal transverse diameter, DTD, and lateral height, LH) do not show clear variations or well-defined trends. As with the radius and tibia, the measurements of the talus show low values of SD and CV in the Avetrana population (for DDT of Avetrana specimens, SD = 3,37 and CV = 5,75; in the MPL1, MPL2, LPL2 and Holocene the values are respectively SD = 6,05, 8,60,6,21 and 5,81; CV = 10,12, 14,97, 10,37 and 10,77).

Population analysis

Population analyses were undertaken on certain species represented in the Avetrana fossil assemblage by both young and adult individuals. These are aurochs, steppe rhinoceros, wild boar, red deer and fallow deer. Again, even if it cannot be excluded that the biology of

these taxa and their ontogenetic ages were slightly different from the present-day representatives (in particular domestic cattle, the African rhinos, and modern wild boar, red deer and fallow deer), the estimated relative ages are probably similar.

Bos primigenius

The aurochs is very well represented in the site of Avetrana; remains of long bones, vertebrae, ribs, phalanges and teeth are present, and almost of them are to ascribe to adult and subadult individuals (see Petronio et al. 2008; Pandolfi et al. 2011) (Pl. 1, figs 2-12). The remains are in a good state of preservation, except for some concreted elements. Several remains were discovered in articulation, in particular from beds 2, 5 and 7 (Fig. 3B, C and D). Skull remains are apparently very rare in comparison to other elements and only one intact frontal bone with horn core was recovered. According to Pandolfi et al. (2011), the teeth and skeletal remains represent a minimum of 37 individuals, including 9 juveniles and at least 28 adults with upper and lower teeth in different stage of wear. New data pre-

layer	0-6 m	7-24 m	2-3 y	> 3 y	total
8	2			3	5
7	1	1	1	8	11
6		1		5	6
5	3	2	3	15	23
4				1	1
3				1	1
2			1	4	5
1				1	1
total	6	4	5	38	53

Tab. 1 - Avetrana (Southern Italy), Late Pleistocene: minimum number of individuals of *Bos primigenius* (m = months; y = years).

Specimen	DB/L index	MB/L i	sex
metacarpus	macx	ndex	
ANS1	32,1	18,0	F
ANS2	30,4	18,1	F
ANS3	30,6	18,4	F
ANS4	31,8	18,9	F
ANS5	29,6	16,1	F
ANS7		18,6	F
ANS8		18,1	F
ANS9		17,7	F
ANS10		14,6	F
A6 8	31,3	18,1	F
A5 22	28,8	16,8	F
A8-1	32,5	17,9	F
A8-2	31,5	18,4	F
A7-1	32,1	20,2	M
A7-2	32,0	18,3	F
A5-1	28,4	15,8	F
A5-2	26,7	14,3	F
A3-1	30,6	18,2	F
A3-2	31,2	17,5	F
metatarsus			
ANS6	24,2	13,3	F
ANS11	24,7	14,3	F
A6 73	24,3	12,5	F
A5 23	25,3	15,3	M
Bos p. NC	24,8	13,2	F
A7-3	26,3	13,7	F
A7-4		12,9	F
A3-3	27,2	15,1	M
			

Tab. 2 - Avetrana (Southern Italy), Late Pleistocene: estimated sex ratio of *Bos primigenius*, according Howard (1963). F = female; M = male; L = length; DB = distal breadth; MB = minimum breadth of diaphysis.

sented here increase the minimum number of individuals (MNI) of aurochs at the site to at least 53 individuals (Tab. 1), including very young individuals. Young calves are represented in bed 5 by a lower D4 with a wear stage referable to between 3-4 and 5-6 months old. In bed 7, calves are represented by individuals with an estimated age of about 6 months and in bed 8, by individuals with an estimated age of 4-5 months. Furthermore, individuals are present with an estimate age of about 18 months in beds 5 and 7 and of about 12

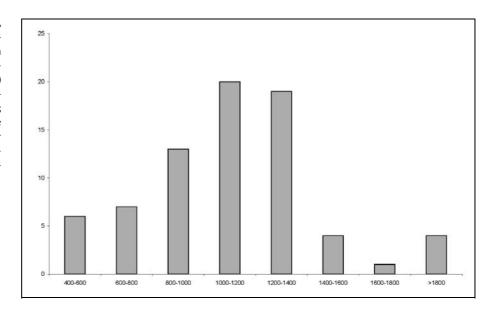
		Withers height			
Bone	Specimen	male	female	undet.	
Metacarpus	A7-1	157,0			
Metatarsus	A5 23	165,8			
Metatarsus	A3-3	160,2			
Metacarpus	ANS3		165,8		
Metacarpus	A5 22		165,8		
Metacarpus	ANS5		163,4		
Metacarpus	ANS2		161,6		
Metacarpus	ANS8		161,6		
Metacarpus	A8-1		161,6		
Metacarpus	A8-2		161,0		
Metacarpus	ANS7		159,8		
Metacarpus	ANS1		159,2		
Metacarpus	A3-1		158,6		
Metacarpus	ANS9		156,2		
Metacarpus	A7-2		156,2		
Metacarpus	A5-1		156,2		
Metacarpus	A5-2		155,6		
Metacarpus	A3-2		155,6		
Metacarpus	A6 8		152,6		
Metacarpus	ANS10		152,0		
Metacarpus	ANS4		151,4		
Metatarsus	NC		157,2		
Metatarsus	ANS11		153,5		
Metatarsus	A7-3		153,0		
Metatarsus	ANS6		161,0		
Metatarsus	A6 73		161,0		
Metatarsus	A7-4		148,2		
Radius	A5 20			163,4	
Radius	A5 21			159,1	
Tibia	A5 19			153,5	

Tab. 3 - Avetrana (Southern Italy), Late Pleistocene: estimated withers height (cm) of *Bos primigenius*.

months in bed 6 (lower D4 with different wear stages). Young adults are represented by several unworn lower M3 and by one mandible with the lower P4 erupting.

In agreement with Pandolfi et al. (2011), both the principal component analysis (PCA) of the metapodial bones and the Howard index (Tab. 2) show that the

Fig. 9 - Avetrana (Southern Italy),
Late Pleistocene Bos primigenius: distribution in
classes of the different estimate body weight (Kg)
using first phalanx (according De Gusta & Vrba 2005);
in abscissa are reported the
classes of estimate body
weight, in ordinate are reported the number of samples for each class.



adult aurochs of Avetrana are predominantly females. The new estimated withers height indicates a mean of about 158.2 cm (between 159.1 and 163.4 from radius, 153.5 cm from tibia, between 151.4 and 165.8 cm from metacarpus and between 148.2 and 165.8 cm from metatarsus) and 157.8 cm considering the females only and 161.0 cm considering the metapodial bones of males only (Tab. 3).

The estimate body weight of *B. primigenius*, calculated on the first phalanx (according to De Gusta & Vrba 2005), is between 411 and 2330 Kg with a mean of 1043 Kg. Only two phalanges suggest the presence of individuals with an estimate body weight over than 2000 Kg. The majority of the phalanges give an estimated body weight between 1500 and 1000 Kg and 26 phalanges give an estimation below 1000 Kg, between 900 and 400 Kg (Fig. 9). The results probably reflect the structure of the *B. primigenius* population revealed by the analysis of the teeth and the post-cranial remains, except for the individuals younger than 20-24 months (age of fusion of the first phalanx proximal epiphysis). At the present day, an adult male of the modern Chianina cattle breed weighs about 1700 Kg, an adult female about 1100 Kg, the calves of 20-24 months between 470-850 Kg (Borgioli 1979).

Stephanorhinus hemitoechus

Rhinoceros remains are relatively rare at Avetrana and are known from beds 3 and 6. The remains are referable to only two individuals, a very young and an adult individual. The latter is represented by a second and a third lower molar. The wear stages of these teeth give an estimated age of about 8-9 years old for the adult. The remains of a young individual is represented by several post-cranial elements and a first upper deciduous and a second lower deciduous premolar. Comparisons with the wear stages reported for the African rhi-

	Cerv	rus elaphus Dama dama			ıa	Sus scrofa			
layer	young	adult	total	young	adult	total	young	adult	total
8	1	2	3	2	3	5	2	2	4
7	1	1	2	3	2	5			0
6	1	3	4		1	1		1	1
5	1	2	3	3	1	4		1	1
4		1	1		1	1			0
3		1	1		1	1			0
2	1	1	2	1	1	2		1	1
1			0			0			0
total	5	11	16	9	10	19	2	5	7

Tab. 4 - Avetrana (Southern Italy), Late Pleistocene: minimum number of individuals of *Cervus elaphus*, *Dama dama* and *Sus scrofa*.

noceroses give an estimated age between 12 and 18 months old.

Sus scrofa

The wild boar is represented in Avetrana by only a few individuals (Pl. 2, fig. 10; Tab. 4), mostly by adult males but also, from bed 8, a very young individual of about 3-4 months old (on the basis of a lower fourth deciduous premolar) and a young animal of about 8-10 months old (erupting lower second molar).

Cervus elaphus

The red deer occurrence is indicated by at least 16 individuals, comprising 11 adults and 5 young (Pl. 2, figs 2-4; Tab. 4). They were recovered in almost all the beds, with maximum abundance in bed 6 (4 individuals). The juveniles have an estimated age younger than 18-24 months old and are represented particularly by long bones with unfused epiphyses, whereas a slightly worn lower D4 indicates the presence of an individual of about 8 months old. Among the adult

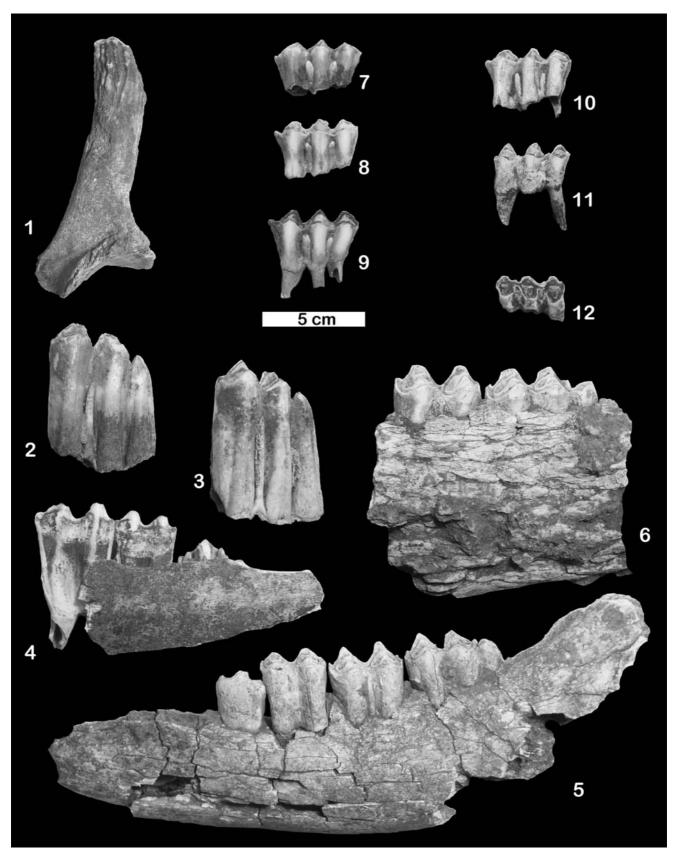


PLATE 1

Avetrana (Southern Italy), Late Pleistocene: Capreolus capreolus: 1) basal portion of antler; Bos primigenius: 2) - 3) lower M3 with unworn third lobe; 4) fragmented mandible with P4 erupting; 5) mandible with midwear M3; 6) fragmented mandible with very worn M3; 8) - 12) lower D4 in different status of attrition.

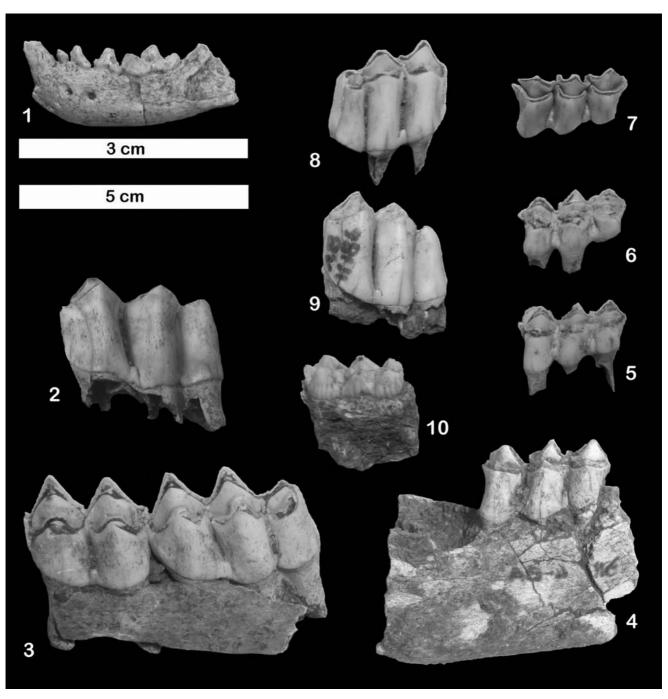


PLATE 2

Avetrana (Southern Italy), Late Pleistocene: *Mustela putorius*: 1) mandible; *Cervus elaphus*: 2) lower M3; 3) mandible portion with M2-M3; 4) mandible portion with D4; *Dama dama*: 5) - 7) lower D4 in different wear stages; 8) - 9) lower M3 in different wear stages; *Sus scrofa*: 10) mandible portion with D4.

remains from bed 6, two lower third molars are present; one of them has the third lobe unworn and it is referable to an individual of about 3-4 years old, while the other, with intermediate wear of the third lobe, is referable to an individual of about 5-6 years old.

Dama dama

At least 19 individuals of fallow deer are known from Avetrana, the second most abundant species after

B. primigenius, most frequent in beds 5, 7 and 8 (Pl. 2, figs 5-9; Tab. 4). The wear stages of teeth allow the recognition of adults of different estimated ages (according to the third lobe of the third lower molar, which has several wear stages). Moreover, juveniles present in bed 5 (indicated by the lower fourth deciduous premolar) show an estimated age of 8 to 20 months old. In bed 7, the juveniles have an estimated age younger than 8

months old and in bed 8, an estimated age between 8 and 20 months.

Discussion

Based on the reconstruction of the age classes present, the time of death of individuals of aurochs, red deer, fallow deer, wild boar and steppe rhino from Avetrana can be calculated. With respect to aurochs, the assemblages are constituted by calves with estimated ages of about 6, 12 and 18 months and by the dominance of adult individuals of approximately 3 years old. This population structure allows the hypothesis that the Avetrana aurochs died in a period between late autumn and winter. Aurochs calves were probably born in spring, as in the majority of modern free-range domestic cattle (Borgioli 1979). Thus, the absence of calves younger than 6 months precludes a season of death in

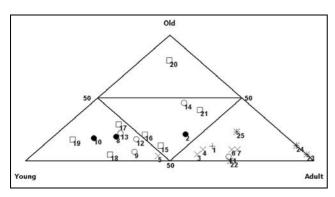


Fig. 10 - Ternary diagram of the population structure of aurochs from Avetrana and catastrophic and predation structures.

1= Avetrana; 2= population model; 3-7 = catastrophic structures; 8 = predation model; 9-14 = predation structures (wolf); 15-21 = predation structures (hyaena); 22-25 = auroch population structures from prehistoric sites (data from Stiner 1990 and references therein).

spring or summer. The dominance of female individuals in the site of Avetrana is also in agreement with the general population structure in herds of living bovines, which have a hierarchical structure with one dominant male covering all the females (Hinshaw 1993; Walker et al. 1975). The population of aurochs of Avetrana comprises at least 15 young individuals (mainly represented by deciduous teeth) and 38 adults. Among the adults, at least 3 old individuals (represented by a very worn lower M3) are present. The majority of adult individuals are represented by a lower M3 with the third lobe unworn or slight worn. The percentage of young individuals (denoted by deciduous teeth), adults (denoted by unworn or slight worn lower M3) and old individuals (very worn lower M3) (in toto or from bed 5 only) is close to that reported for the dead white-tailed deer (Odocoileus virginianus) population from Mount St Helens (USA) after the 1980 volcanic eruption (Lyman 1989), for feral donkeys (*Equus asinus*) from the Mojave desert from a mass cull (Johnson et al. 1987), for the tahr (Hemitragus jemlahicus) from New Zealand documented by a live census (Schaller 1977) and for caribou herds (predominantly female) from Alaska (Miller 1975) (Fig. 10). The ratio of young individuals (with deciduous teeth) compared to adult individuals (with complete permanent teeth) is also close to those from the Early Pleistocene bison population from Untermassfeld in Germany, which is interpreted as the product of a catastrophic flood (Kahlke 2000) and other catastrophic death assemblages (Fig. 11).

The percentages differ markedly from those reported for prey assemblages accumulated by wolf, hyena, tiger, lion and humans (data from Stiner 1990, and references therein) (Fig. 10). Indeed, the carnivore accumulations show a U-shaped mortality pattern with dominance of very young and old individuals. This is the result of strategy of predation that focuses on the

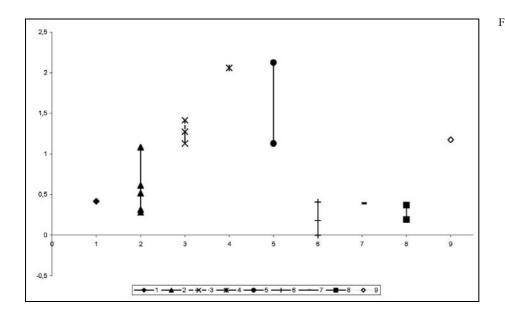


Fig. 11 - Ratio young/adult individuals of Bos primigenius. 1: Avetrana; 2: Range distribution of catastrophic structures; 3: Predation structures of herbivores killed by wolf; 4: Deceased population of fallow deer; 5: Predation structures of herbivores killed by hyaena; 6: Range of population of Bos primigenius from archaeological sites; 7: Population structure of Bison from Untermassfeld; 8: Predation structures of bovids killed by lion; 9: Predation structure of Bos killed by tiger. For references see the text and Stiner, (1990 and references therein).

most vulnerable prey. In the archaeological sites, human accumulations show a prime-dominated mortality pattern; this pattern is uncommon in nature and it is the result of selective ambush hunting. Finally, in the livingstructure death pattern the distribution is the result of non-selective actions. In these cases, all animals in a population have an equal probability of dying irrespective of age and the mortality is age-independent (Stiner 1990). The living-structure death pattern can be the result of several causes, such as large-scale floods, volcanic eruptions etc. Furthermore, living-structure death pattern reflects the population composition living in the considered area during a considered time. Thus, the composition of the population is not constant through time and is variable with the season and the population phases of growth, stability and decline.

In contrast, the population analysis of the rhino assemblage does not allow a precise indication of the season of death because of differences in lifeway in the modern species. Births in white rhino occur between December and June with the majority during the month of March, whereas in black and Indian rhinos, births are evenly spaced throughout the year (Laurie 1982; Kretzschmar 2002). Typically, black and white rhinos are relatively solitary. Males are solitary until it is time to mate, whereas females reside with their young in a solitary family unit, although females without young sometimes associate with other females. In the Indian rhino, weaning usually occurs after one year but may last up to 18 months. Rhinoceros unicornis is usually solitary except for females with young (Hillman-Smith & Groves 1994; Garnier et al. 2001; Grzimek 2005; Massicot 2006).

In wild boar, births occur during spring and, usually, sounders are composed of numerous individuals (Hopf 1979; Nowak 1991). In the site of Avetrana, remains attributable to wild boar are relatively scarce and are mostly from bed 8. The remains represent 2 juveniles and 2 adults (a few isolated teeth, fragmentary maxilla, fragmentary mandible and a few postcranial bones). The presence of the wild boar in bed 8 may be the result of carnivore accumulation or of the various taphonomic processes described for the previous beds (see later). In beds 5 and 6, wild boar is represented only by few isolated remains attributable to 2 adult males. The males of the species usually leave the herd when sexually mature (approximately 9-10 months old) (Hopf 1979; Nowak 1991). The estimated age of the 2 adults from Avetrana is about 2.5 years (presence of unworn third lower molars). Considering the age of the individuals of Avetrana and that in the temperate regions wild boar females give birth to one litter in the spring (Hopf 1979; Nowak 1991), it is probable that the death of the 2 above-mentioned males occurred during late autumn or early winter.

In modern red deer, males begin to compete for females and to protect their harems in late September and early October (Nowak & Paradiso 1991). The births usually occur in late spring or early summer and males do not contribute to the care of their young; during this time, the herd is composed only of females and their calves (Nowak & Paradiso 1991). Both males and females reach sexual maturity at approximately 16 months old. The young red deer from Avetrana have an estimated age younger than 18-24 months and the calves have an estimated age of around 8 months. Taking that into account and considering the very limited remains of antlers below bed 8, the season of death of the Avetrana individuals can be hypothesised as occurring during the winter months and before spring.

Modern fallow deer mate generally between September and January and births occur usually during early June (Feldhamer et al. 1988; Nowak 1999). In the summer, the herd is made up of females and their calves. The females reach sexual maturity at approximately 16 months and the males at approximately 17 months (Feldhamer et al. 1988; Nowak 1999). In the site of Avetrana, the ratio of adult to young individuals of fallow deer is approximately equal. The young fallow deer have a minimum estimate age of about 18 months. In addition, it can be hypothesized that the death of the individuals from Avetrana probably occurred during the winter. This can be hypothesized considering that in the population of Avetrana very young individuals are not documented, thus the death of population occurred before the summer. Furthermore, the minimum estimate age of the young individuals is of about 18 months; considering that the birth occurs during the early June, a time span coincident with the winter can be supposed for the death of the population.

In summary, the results of population analyses of the considered species suggest that several catastrophic events were responsible for the death of most of the individuals at Avetrana, probably occurring between late autumn and winter. The taphonomic and sedimentological characteristics of the site indicate that water was the principal agent of accumulation of the mammalian remains, probably rapidly deposited either as a single or successive multiple events. Moreover, it can be hypothesized that the accumulation of the remains in the site occurred during a period or periods of intense rainfall.

Today the plateau of tarantine Murgia is predominantly flat but with large basins, such as La Grave and the old town of Avetrana (62 m asl), then declining seawards through a series of slopes and terraces. Furthermore, between Avetrana and the coast, there are some elevated areas, such as the Monte dei Diavoli (117 m asl) and the Monte della Marina (100 m asl). Any heavy downpours would rapidly have flooded the area

or turned it into a swamp, thereby allowing the accumulation of animal carcasses in the karst cavity.

Periods with abundant and concentrate rainfalls during the MIS5 are recorded in the marine stratigraphy by the presence of sapropel levels. These are well studied and recognized in the eastern Mediterranean but are equally present in the western part (Balearic Islands, Tyrrhenian Sea, Strait of Sicily, Ionian Sea) (Rohling & Hilgen 1991; Capotondi & Vigliotti 1999; Cramp & O'Sullivan 1999). These records seem to be related to a monsoon-type climate in the Mediterranean Basin (Rossignol-Strick 1985; Rohling & Hilgen 1991). In particular, in the western Mediterranean Sea, the sapropel levels S5, S4 and S3 marks the warm peaks of MIS5 (respectively 5e, 5c and 5a) (Capotondi & Vigliotti 1999). Furthermore, in Italy, an increase in arboreal vegetation is recorded during the last interglacial and subsequent stadials/interstadials of MIS 5 (Follieri et al. 1995; Follieri & Magri 1998, 2001). The forest phases (the Eemian and St Germain I), respectively correlated with MIS5e and 5d, testify to a dominance of woodland characterized by different vegetation (Valle di Castiglione and Lagaccione in Central Italy; Follieri et al. 1995; Follieri & Magri 2001). In particular, during the Eemian (approximately 0.130-0.115 Ma), Mediterranean vegetation similar to that of MIS1 occurred, which suggests the occurrence of rainy winters and dry summers. During the St Germain I stadial (approximately 0.110-0.095 Ma), a montane vegetation profile is recorded, which suggests considerable general wetness and abundant rains in the summer as well as the winter (Follieri et al. 1995; Follieri & Magri 1998, 2001).

The ecological requirements of the large mammals allow reconstruction of the palaeoenvironment around Avetrana during the MIS5. The great quantity of aurochs, the presence of fallow deer and red deer, and scarce rhinoceros, suggest a landscape characterized by large wooded areas, rich in glades or localised open spaces (or diffuse Mediterranean "macchia"). Wild boar and hippopotamus suggest the presence of expanses of water and more humid conditions than prevail today, contra Petronio et al. (2008) who may have over-emphasised the scarce presence of Microtus (Terricola) savii and other taxa (essentially birds such as Otis tarda and Perdix perdix), which indicate open environments. The new data and analyses show that in the early Late Pleistocene, the area around Avetrana and probably the northern Ionian slope of Salento were more forested than the Southern Adriatic slope. The mammalian assemblages referred to the Melpignano Faunal Unit of the latter area, in contrast, indicate a more open environment dominated by equids and rhinos (see Di Stefano et al. 1992; Bologna et al. 1994; Petronio et al. 2007; Pandolfi & Petronio 2011).

Conclusion

The data obtained during the most recent excavations, integrated with previous information, have permitted a detailed analysis of the "La Grave" karst filling, nearby Avetrana. Analysis of variation in size in Pleistocene and early Holocene aurochs partially confirms the results obtained by Pandolfi et al. (2011); however, the metapodial bones are now revealed to be the most useful element for investigation of size variations in Bos primigenius. This species increases in size during the Middle and early Late Pleistocene and decreases in size during the late Late Pleistocene and early Holocene. Furthermore, in agreement with Petronio et al. (2008) several layers are recognized in the site of Avetrana, which were probably deposited rapidly during a short time span by exceptional events, resulting in the rapid incorporation of carcasses in the karst cavity. The abundance of the remains, many still in articulation, their state of preservation, the absence of skulls and the population analysis of some representative species strongly suggest that the remains were accumulated by water during several catastrophic events in the area.

In particular, beds 2, 5 and 7 were deposited over a short time and probably each one represents a single depositional event. In contrast, beds 3, 4, 6 and 8, which are characterized by scarce fossil remains and abundant clay-sandy matrix, are considered as deposited over a longer time span. Furthermore, the remains in beds 3, 4, 6 and 8 are often in a poor state of preservation, sometimes covered by calcareous crusts and with only few cases (in beds 6 and 8) of anatomical articulation. Finally, beds 3 and 4, being separated by a layer of calcareous pebbles, are assumed to represent two distinct sedimentary cycles.

The hypothesis of rapid infilling of the cavity through heavy rainfall and flash floods can be supported by the population analyses of the taxa recovered from the site. In particular, aurochs, fallow deer and red deer provide useful information about the season of death and consequently the probable time span of the aggradation. In beds 5 and 7, the estimated season of death of these three species suggests probable deposition between the autumn and the winter.

Finally, bed 8 shows some peculiar features with respect to the other beds, being here the percentage of concreted bones relatively high (Fig. 5). Furthermore, bed 8 is characterized by a very high percentage of carnivore remains (especially the wolf). These are often recovered entire and/or as articulated remains and are referred to young and adult individuals. The sedimentological characteristics of bed 8 suggest that it was probably deposited over a long time span, with frequently stagnant water (also suggested by the presence of calcareous concretions). The high percentage of wolf

in the bed 8 may be due to the presence of dens and/or simply by more common frequentation of the area. However, the role of a natural trap of the cavity, for the carnivores that were attracted by the presence of carcasses, cannot be ruled out.

In conclusion, the biochronological age previously suggested is in agreement with the inferred palaeoclimatological indications. Infilling of the karst cavity probably occurred during seasons (autumn – winter) with abundant rainfall, correlated with forest phases of

the aforementioned pollen diagrams and, in the marine stratigraphy, with the presence of sapropel levels.

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