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Observations on the *Ursus gr. spelaeus* remains from the Pocala cave (Trieste, Friuli Venezia Giulia, N. Italy)

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Abstract

Using the fossils of skulls, P⁴/₄, M₁ stored in the Geological and Paleontological Museum of the University of Padua (Veneto region), the most modern considerations on cave bear remains from the Pocala cave (Friuli Venezia Giulia region), are advanced. These bears belong to the *U. spelaeus* Rosenmüller, 1794 species and both the morphological-morphometrical and the morphodynamic characters, seem to be intermediate between those typical of the ancestral forms observed in the “*deningeri*” bears, and the more modern forms of “*ingressus*”, as in the other Italian populations recently examined (Covoli di Velo, San Donà di Lamon – Veneto region – and Buco del Frate – Lombardy).

Keywords

Ursus, Pocala, evolution, Eastern Italy, Pleistocene.

1. INTRODUCTION

In the last decade the phylogenetic tree of the cave bear has changed deeply, and has been complicated as a consequence of the great amount of new data, especially in the field of genetics (Hänni *et al.*, 1994; Hofreiter *et al.*, 2002, 2007; Orlando *et al.*, 2002; Knapp *et al.*, 2009; Stiller *et al.*, 2010; Baca *et al.*, 2012, 2013) and of the evidence of new discoveries. Since then, the distribution of the cave bear has been extended toward the east to Korea and to Western Siberia as well (Baryshnikov, 2007; Sher *et al.*, 2011).

The most important problems concern the taxonomical place occupied by some ancestral forms (*U. rossicus*, *U. savini*, *U. deningeri* and *U. kudarensis*) including the possibility that cave bear evolution could be characterized by a premature division into distinct phylogenetic lines. Despite the different interpretation given for the morphological, morphometric and genetic data (such as intraspecific variability or evidence of a specific division), the great polytypism that globally characterizes the cave bear in both its stratigraphic and geographic significance has become very clear.

The Pocala population is here re-assessed within this frame.

The Pocala bear was the object of previous research (Lazzaro, 2003; Rabeder, 2006 in Calligaris *et al.*, 2006); initially this bear was classified as *Ursus spelaeus*

Rosenmüller, 1794 (Lazzaro, 2003) and subsequently as *U. eremus* Rabeder *et al.*, 2004 (Calligaris *et al.*, 2006). Based on fossils stored in the Geological and Paleontological Museum of the University of Padua (Veneto region), the object of our study is to improve the knowledge about this population of bears, in order to better place them in the evolutionary frame of the Italian and foreign cave bears.

2. THE POCALA CAVE

The hole of the Pocala (cadastral n. 173/91VG of the Friuli Venezia Giulia Region) is surely one of the most famous caves not only of the Friuli Venezia Giulia region, but in Europe (Fig. 1A). A great amount of cave bear fossils were discovered at this site during numerous excavations that occurred during the 20th century (Calligaris, 2000; Lazzaro & Tremul, 2003). Initially Battaglia (1930) conducted a detailed search, but then the cave was abandoned for about 70 years (Lazzaro & Tremul, 2003). More recently, Lazzaro & Tremul (2003) provided a detailed description of the cave: the hole is located to the NNW of the Aurisina village (Trieste), its entry opens at 139 m. a.s.l. and it consists of a cavity of 6.5 m in width and 2 m height. Debris have certainly blocked and filled a part of the original area. A corridor of about 65 m long widens underneath to reach 27 m of width

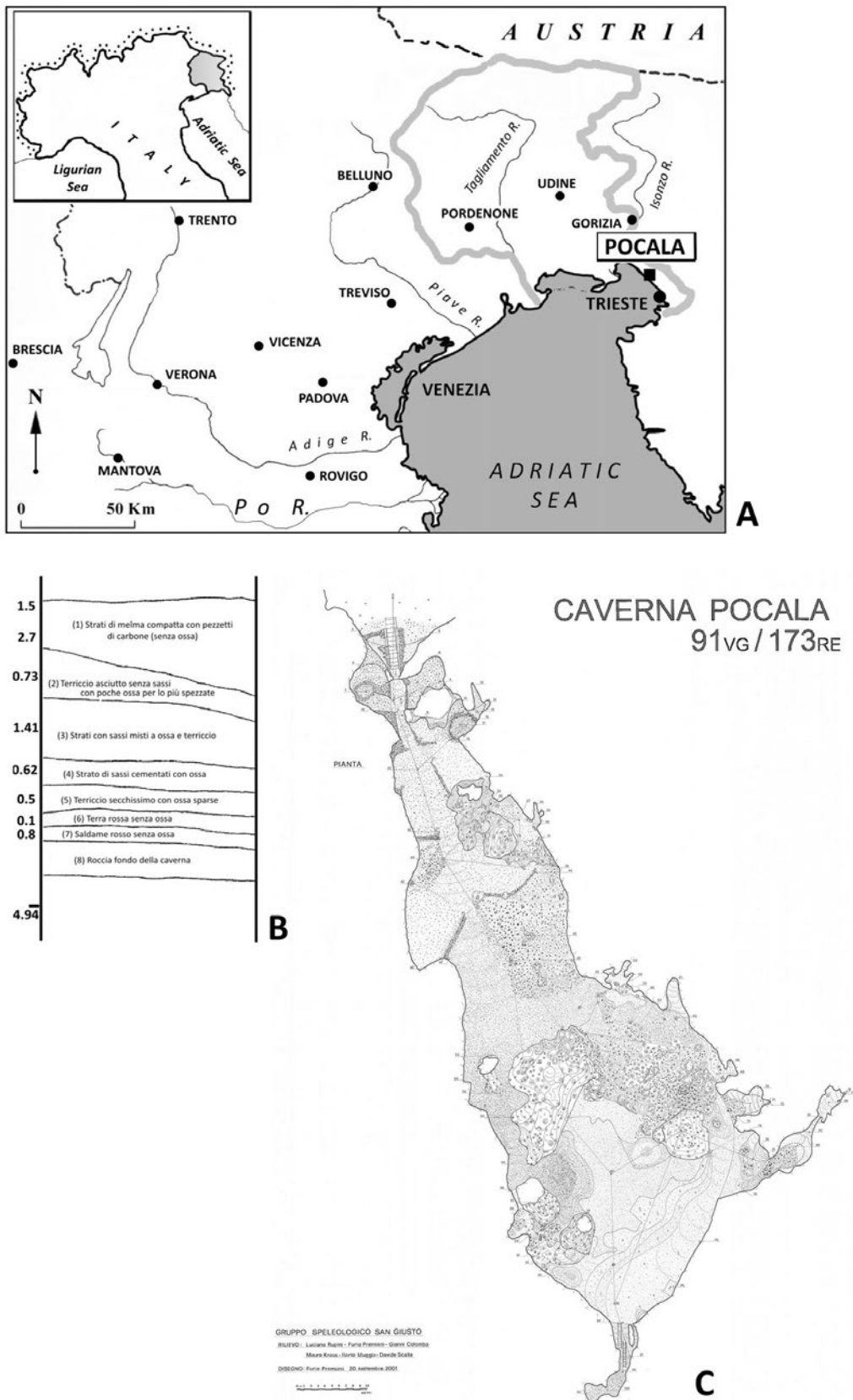


Fig. 1: Geographical position (A), a summary stratigraphy of the Pocala cave (B) (after Lazzaro & Tremul, 2003, mod.) and map of the cave (C) (GSSG in: www.gssg.it/wp-content/upload/download/2012/09/pianta-caverna-Pocalajpg, slightly modified).

at its extremity. The hole ends with a very large room, 45 m long, 50 m wide and 15 high. Marchesetti (1907) published a synthetic stratigraphy recently redrawn by Calligaris (2000, in: Lazzaro & Tremul, 2003) (Fig. 1B). A detailed map of the cave was recently elaborated by the GSSG (Gruppo Speleologico San Giusto - Trieste) (Fig. 1C).

3. MATERIAL AND METHODS

10 skulls, 9 of which are stored into the Geological and Paleontological Museum of the University of Padua and 1 which is preserved in the Museo di Storia Naturale of Milan, 28 P₄, 38 P₄ and 21 M₁ compose the samples under study. The parameters of the measurements of the skulls and teeth are those codified by Torres (1988a, b, c, d), and are presented in Table 1. On the P₄ and M₁ a morphodynamic analysis was also elaborated using methods of Rabeder (1999) and Grandal d'Anglade & López González (2004). The aim of these analyses is to show the presence of the different morphological types within a studied population. In fact, teeth in the more ancient forms (*U. deningeri*) were characterized by a very simple chewing surface, bicusps (p4) and tricusps (P4); successively with the formation of numerous accessorial cusps and crests, a gradual complication become evident, reaching the maximum complexity in *U. ingressus*. Both the number and position of these accessorial structures allows for the identification a series of morphotypes; the model that studies their distribution makes it possible to calculate the particular indices (morphodynamic indices) indicative of the evolutionary level of the population. The same is true for M₁ as well. For this tooth Grandal d'Anglade & López González (2004) have shown a decrease of the degree of convergence of the cusps from the forms of the Lower Pleistocene to those of the Upper Pleistocene. The degree of convergence is evaluated using certain indices: 1) the trigonid convergence index and 2) talonid convergence index.

4. MORPHOMETRY

In Figures 2-3 the comparisons between the “Basal length” of the Pocala population and those of some European cave bears (*U. spelaeus* and *U. ingressus*) are shown. In another comparison between the Pocala fossils and bears from the Conturines and Ramesch caves (Fig. 4) we can note that the Pocala population is characterized by larger sizes compared to the populations of these two caves which were inhabited by the species *U. ladinicus* and *U. eremus*. The range in size of the Pocala population is similar to those of typically advanced cave bears and, more in particular, of both *U. spelaeus* and *U. ingressus*. The analysis of the absolute length and the length of the dental row has also reached similar conclusions.

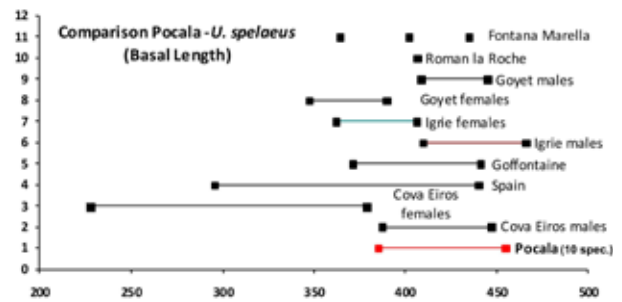


Fig. 2: Comparison of the “Basal Length” in skulls of cave bears from the Pocala (n. 10 specimens) and *U. spelaeus* from foreign caves.

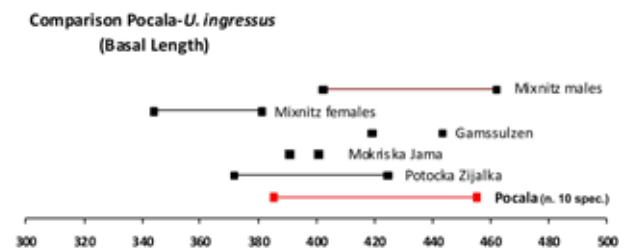


Fig. 3: Comparison of the “Basal Length” in skulls of cave bears from the Pocala (n. 10 specimens) and *U. ingressus* from foreign caves.

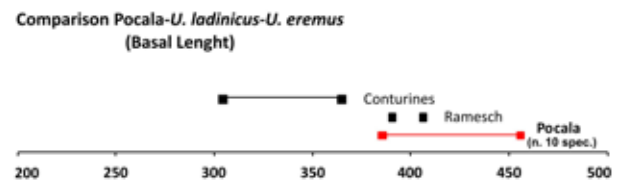


Fig. 4: Comparison of the “Basal Length” in skulls of cave bears from the Pocala (n. 10 specimens) and *U. ladinicus* – *U. eremus* from Conturines and Ramesch caves.

The graph in Figure 5 shows the relationship between the “Basal length” and the “Maximum frontal Width” of the skulls of different cave bears species. The points corresponding to the Pocala population are placed within the range of values of both the *U. spelaeus* and *U. ingressus* species. However, contrarily to these species which contain specimens of small and larger sizes, the Pocala population is characterized by peculiar proportions. In fact, the values of the basal length are similar to those of the individuals with a great size with respect to the populations referred to and the values of the maximum frontal width decreases faster than in both the *U. spelaeus* and *U. ingressus* populations, as can be seen by the regression line.

The relationship between the “Basal length” and the “Bizygomatic Width” is shown in Figure 6. Also in this case the cloud of the Pocala population falls inside the

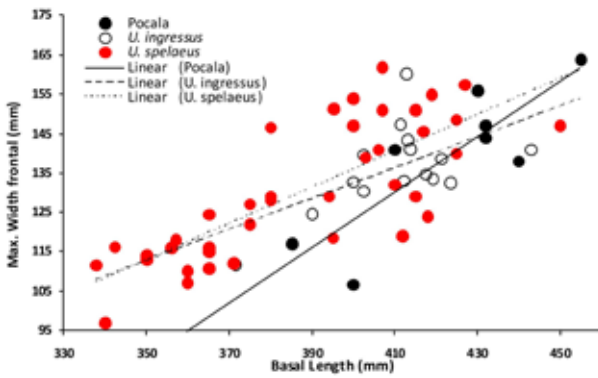


Fig. 5: Relationship between the “Basal Length-Maximum frontal Width” in bears from the Pocala and both the *U. ingressus* and *U. spelaeus*.

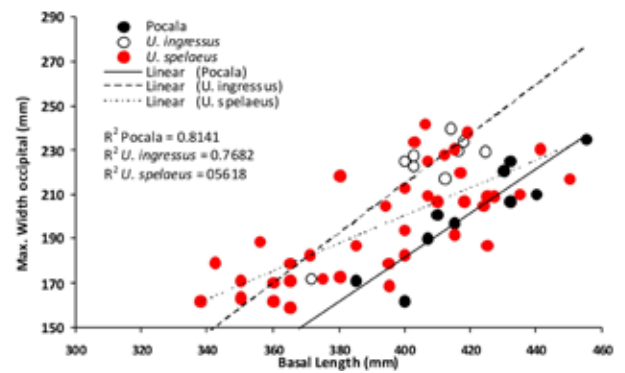


Fig. 7: Relationship between the “Basal Length-Maximum occipital Width” in bears from the Pocala and both the *U. ingressus* and *U. spelaeus*.

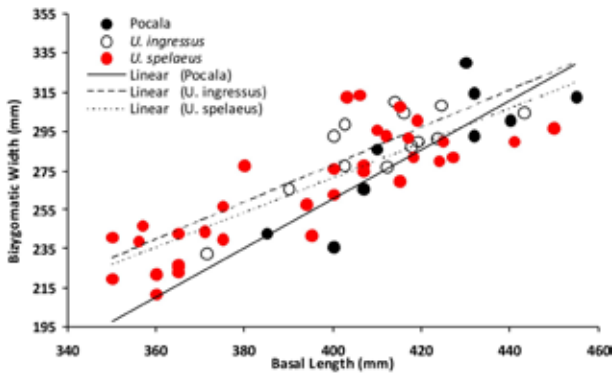


Fig. 6: Relationship between the “Basal Length-Bizygomatic Width” in bears from the Pocala and both the *U. ingressus* and *U. spelaeus*.

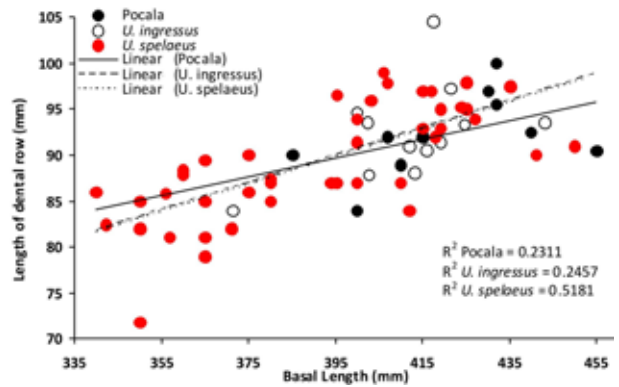


Fig. 8: Relationship between the “Basal Length-Length of dental row” in bears from the Pocala and both the *U. ingressus* and *U. spelaeus*.

range of the referred populations, but the bizygomatic width is always proportionally inferior than that observed for both *U. spelaeus* and *U. ingressus* species, as the regression lines show.

Figure 7 shows the “Basal Length” against the “Maximum occipital Width”. In this case the basal length is also proportionally longer for the Pocala population, but the difference with the *U. ingressus* species, is very strong. Lastly, the graph in Figure 8 shows the “Basal Length-Length of the dental row” relationship. The cloud of the Pocala bears falls inside the typical distribution range of the referred populations, and the regression lines clearly show that the three species have very similar morphometrical features relatively to regarding these parameters.

5. MORPHODYNAMIC DATA

The graphic in Figure 9 shows the relationship between the $P^4/4$ morphodynamic index. The point of the Pocala bears falls next to those of both the Conturines (in which the *U. ladinicus* holotype is present) and the layers containing *U. eremus* of the Herdengelh cave. The values of the morphodynamic indices of $P^4/4$ are significantly lower compared with those of *U. ingressus* from the Gamsulzen (GS), Nixloch (NL) and Liegloch (LL). The most complicated morphotypes are completely lacking. Consequently there is a relatively higher frequency of the simples ones. More in particular among the $P4$ morphotypes with indices from 3 to 4, and among $p4$, those with indices from 3.5 to 5 are completely lacking. This is typical of less evolved forms. Therefore this graph shows the conservation of archaic traits in the Pocala population.

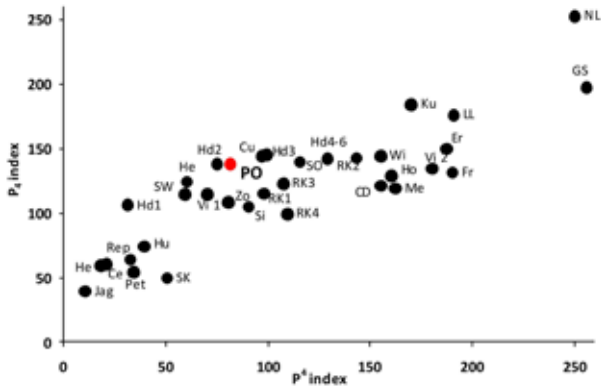


Fig. 9: Relationship between the “P⁴-P₄ index” in bears from the Pocala and foreign localities.

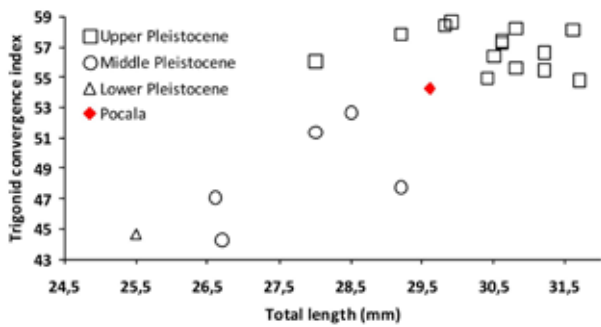


Fig. 10: Relationship between the “Total Length-Trigonid convergence index” in M₁ of bears from the Pocala and cave bears of the Pleistocene.

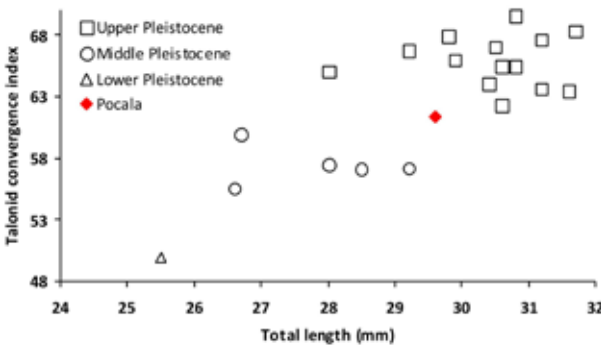


Fig. 11: Relationship between the “Total Length-Talonid convergence index” in M₁ of bears from the Pocala and cave bears of the Pleistocene.

The graphs in Figures 10-11 show the relationships between the “Total Length-Trigonid convergence index” and the “Total Length-Talonid convergence index” of the M₁ respectively. In both cases the points of the Pocala bears fall inside the cloud of the Upper Pleistocene deposits, and so the age hypothesized by Calligaris *et al.* (2006), is indirectly confirmed. The most interesting

aspect is that both the trigonid and talonid morphologies show a greater convergence of the cusps when compared with the M₁ of the same age. This trend is strengthened in the forms of the Middle-Lower Pleistocene perhaps indicating a more carnivorous diet in the primitive forms than in the modern ones. As for the fourth premolars, in the Pocala population as well, the M₁ is characterized by the preservation of archaic traits.

6. DISCUSSION AND CONCLUSIONS

Similarly to what has been observed in other Italian populations (*i.e.* Covoli di Velo, San Donà di Lamon, Buco del Frate, Buco dell’Orso and so on) (Santi & Rossi, 2006), the studied fossils from the Pocala cave show both archaic and advanced features. The more primitive ones are identified by the denture: 1) the more complicated morphotypes are totally absent while the frequency of simpler ones is very high (Tab. 1); 2) the morphodynamic index of P⁴/₄ has a middle-low value, similar to that calculated for the remains coming from both the Conturines and the lower layers of the Herdengelh caves from where the fossils belonging to the species: *U. ladinicus* and *U. eremus* (Rabeder *et al.*, 2004), come from 3) the M₁ is characterized by a greater convergence of both the trigonid and talonid with respect to the referred molars of the same age.

The advanced trait can be discerned in the absolute size increased of the individuals which corresponds to that observed in the biggest specimens of the *U. ingressus* species. Moreover, one of these features, a typically morphometric one, is peculiar: the width of the skull has a lesser value of the antero-posterior axis than the referred populations. This characteristic could be due to some local accommodation linked to diet, but we need a deeper analysis to confirm or to explain this affirmation. On the whole, the Pocala population shows an evolutionary trend very similar to that observed in other bears of the Italian peninsula, characterized by the presence of the archaic and modern traits forming a mosaic of features typical of these populations and which are scarcely observed in others cave bears of Europe.

The distribution of the morphologic, morphometric and morphodynamic characters in the Italian cave bear is characterized by the presence in the same cave or in close holes, of both archaic and advanced traits and by great differences in the morphodynamics when compared with other European populations. In our opinion this peculiar distribution is the consequence, over time, of the overlap of the conservative evolutionary trend that characterizes the Italian populations and, of the migration into the Italian peninsula of more advanced forms from the other European regions during the warm phases of the glaciation. Conversely, because of the presence of

the Alps, during the cool phases of the glaciation, the migratory flow was greatly limited or blocked. This migratory scheme characterized by a wide flow during the warm periods and a limited one during the cool phases, seems to be supported by genetic data (Orlando *et al.*, 2002).

In conclusion, at the present time we confirm that the fossils from the Pocala cave stored in the Geological and Paleontological Museum of the University of Padua belong to the *U. spelaeus* Rosenmüller, 1794 species as Lazzaro (2003) previously classified them for those remains preserved in the Museum of Storia Naturale of Trieste.

Table 1: Measurements of skulls, $P^4/4$ and M_1 , morphotypes and morphodynamic indices in bears population from the Pocala cave. The data concerning the morphotypes derive from both the study of the specimens stored in the Geological and Paleontological Museum of University of Padua and the literature (Lazzaro, 2003).

Skulls

N.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	20b	21
25416	540	455						235	97	36	313	96	164	131	75	90	155	90,5	71	23	64	68,8
25417	524	430		208		274		221	92	33,5	330	89	156	115	73	92	144	97	75	22	47	76,7
25419	501	432		212		243		207	90	39	293	86	147	114	71	84	147	100	77	23	46,5	67,8
25420	457	407		204		249		190	91	38	266				61	84	140	92	73	22	48	65,4
25422	462	400		173	93,5	210	105	162	81	33	236	75	107	82	60	73	128	84	63	16	43,5	59,0
25424	410	385		162		230	115	171	85	30	243	81	117	87	60	90	125	90	70	21	35	63,1
25425	490	440		201		270		210	85	35	301	86	138	105	63	85	153	92,5	72	23	60,5	68,4
25426	445	415		201		240	119	197	78	293					69	78	136	92	70	23	44	
25570	475	410		190		235		201	83	33	286	83	141	117	69	79	134	89	69	21	45	69,8
S.N.	477	432		202	106	252		225	86	35,9	315	81	144	101	70	89	147	95,6	71		51,4	72,9

Upper P4

P⁴	L	I	P⁴	L	I	MORPHOTYPES	
25416 r	20	13	25433 r	20	15		
25416 l	18	15	25570 r	20	14	A	11
25416 b	18,5	13	25570 l	18	13	A-A/D	7
25417 r	21	13	30967 r	18	12	A/B	7
25419 r	21	19	30967 l	20,5	13	B	13
25419 l	20	19	30968 r	20	13	A/D	8
25420 r	20	14	30968 l	18	14	A/C	5
25420 l	18	14	30969 r	21	14,5	C	3
25421 r	17	14	30969 l	19,5	15,5	D	4
25421 l	20	14	30970 r	20	13	TOT	58
25422 r	18	13	30970 l	18,5	13	P⁴ index	81,03
25422 l	13	12	30978 r	18	14		
25423 r	22	14	30978 l	19	15,5		
25423 l	22	14	30979 r	21	15		
25424 r	20	16	30979 l	19			
25424 l	20	14	30980 r	20	14		
25425 r	21	14	30980 l	20,5	15		
25426 r	19	13	30983 r	18	12		
25426 l	19	13	30983 l	18	12,5		

Lower P4

P_4	L	l	P_4	L	l	MORPHOTYPES	
25416 l	14	11	25570 r	14	10		
25417 r	15	11	25570 l	10	10,5	B1	4
25417 l	16	11	30967 r	15,5	11,5	C1	10
25419 r	17	11	30967 l	15,5	11,5	C1/D1	9
25419 l	17	11	30968 r	16	11	D1	4
25420 r	15	9,5	30968 l	17	11	C1/E1	1
25420 l	16	10	30969 r	17	13	C2	4
25423 l	19	15	30969 l	15,5	11,5	D1/D2	1
25424 r	16,5	11	30970 r	16	11	C2/D2	4
25424 l	14	10	30970 l	16	10	C3	1
25425 r	17	12	30980 r	16	11	TOT	38
25425 l	15	9,5	30980 l	17	11	P_4 index	138,8
25426 r	16	11	30983 r	14	9,5		
25426 l	16	10,5	30983 l	14	8,5		

M'	L	l	M_1	25422	25423 dx	25423 sx	25570	Mean
25416 r	28	19,5	TRIGON	A2	A2	A2	A2	
25416 l	28	20,5	TALON	B2	B2	B2	B2	
25417 r	30	21	PARACON	2	1	1	1	
25419 r	31,5	21,5	PROTOC	6	6	6	6	
25419 l	31	20,5	METAC	10	10	11	9	
25420 r	30	20	ENTOC	14	15	14	14	
25420 l	28,5	20,5	HYPOC	18	18	18	18	
25422 r	27	17,5	1	30	29,5	29	30	29,6
25422 l	28	17	2	18	17,5	16	17	17,1
25424 r	27	17,5	3	12	11,5	11,5	11,5	11,6
25424 l	26	19	4	15	15	14	14	14,5
25570 r	27	19	5	8	8	7,5		7,8
25570 l	29	20	6	6,5	6,5	6		6,3
30978 r	30	21	7	10	9	13	8	10,0
30978 l	30	21,5	PadCI	44,4	45,7	46,9	-	45,7
30979 r	28	19	TrdCI	54,2	56,5	52,2	-	54,3
30979 l	27	20	TadCI	66,7	60,0	62,9	57,1	61,68
30980 r	30	22						
30980 l	32	22,5						
30983 r	27,5	18						
30983 l	28	18						

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REFERENCES

- Baca M., Stankovic A., Stefaniak K., Marciszak A., Hofreiter M., Nadachowski A., Węgleński P. & Mackiewicz P. 2012. Genetic analysis of cave bear specimens from Niedźwiedzia Cave, Sudetes, Poland. *Palaeontologia Electronica*, 15 (2), 21A: 1-16.
- Baca M., Mackiewicz P., Stankovic A., Popovic D., Stefaniak K., Czarnogórska K., Nadachowski A., Gasiorowski M., Hercman H. & Weglenski P. 2013. Ancient DNA and dating of cave bear remains from Niedźwiedzia Cave suggest early appearance of *Ursus ingressus* in Sudetes. *Quaternary International*, 81: 1-7, <http://dx.doi.org/10.1016/j.quaint.2013.08.033>.
- Baryshnikov G.F. 2007. Bears Family (Carnivora, Ursidae). In: *Fauna Rossii isopredel'nykh stran. Novaya Seriya*, St. Petersburg, 147, Izdatel'stvo Nauka.
- Battaglia R. 1930. Notizie sulla stratigrafia del deposito Quaternario della caverna Pocala di Aurisina (campagna di scavo degli anni 1926-1929). *Le Grotte d'Italia*, 4: 17-44.
- Calligaris R. 2000. 1999 Ritorno in Pocala. Atti della Tavola Rotonda: Un importante sistema carsico dei Monti Lessini (Verona): I Covoli di Velo. Verona-Camposilvano 16-17 Aprile 1999: 87-100.
- Calligaris R., Rabeder G. & Salcher T. 2006. Neue paläontologische Grabungen in der Grotta Pocala bei Triest. In: Ambros D., Groppe C., Hilpert B. & Kaulich B. (Eds). *Neue Forschungenzum Höhlenbären in Europa. Naturforschenden Gesellschaft Nürnberg Abhandlungen*, 45 (2005): 49-56.
- Grandal d'Anglade A. & López González F. 2004. A study of the evolution of the Pleistocene cave bear by a morphometric analysis of the lower carnassial. *Oryctos*, 5: 83-94.
- Hänni C., Laudet V., Stehelin D. & Taberlet P. 1994. Tracking the origins of the cave bear (*Ursus spelaeus*) by mitochondrial DNA sequencing (ancient DNA/phylogeny). *Proceeding of the National Academy of Sciences USA*, 91: 12336-12340.
- Hofreiter M., Capelli C., Krings M., Waits L., Conard N., Münzel S., Rabeder G., Nagel D., Paunovic M., Jambresic G., Meyer S., Weiss G. & Pääbo S. 2002. Ancient DNA analyses reveal high mitochondrial DNA sequence diversity and parallel morphological evolution of Late Pleistocene cave bears. *Molecular Biology and Evolution*, 19 (8): 1244-1250.
- Hofreiter M., Münzel S., Conard N.J., Pollack J., Slatkin M., Weiss G. & Pääbo S. 2007. Sudden replacement of cave bear mitochondrial DNA in the late Pleistocene. *Current Biology* 17 (4): R122-R123.
- Knapp M., Nadin R., Weinstock J., Baryshnikov G., Sher A., Nagel D., Rabeder G., Pinhasi R., Schmidt H.A. & Hofreiter M. 2009. First DNA sequences from Asian cave bear fossils reveal deep divergences and complex phylogeographic patterns. *Molecular Ecology*, 18: 1225-1238.
- Lazzaro G. 2003. La popolazione di *Ursus spelaeus* della Grotta Pocala. *Atti Museo Civico Storia Naturale Trieste*, 49 (suppl.): 59-78.
- Lazzaro G. & Tremul A. 2003. La caverna Pocala di Aurisina. *Atti Museo Civico Storia Naturale Trieste*, Trieste, 49 (suppl.): 79-81.
- Marchesetti C. 1907. Relazione sugli scavi eseguiti nel 1905 dal dr. C. Marchesetti. *Bollettino della Società Adriatica di Scienze Naturali*, 27: 185-187.
- Orlando L., Bonjean D., Bocherens H., Thenot A., Argant A., Otte M. & Hänni C. 2002. Ancient DNA and the population genetics of cave bears (*Ursus spelaeus*) through space and time. *Molecular Biology and Evolution*, 19 (11): 1920-1933.
- Rabeder G. 1999. Die evolution des Höhlenbärengebisses. *Mitteilungen der Kommission für Quartärforschung der Österreichischen Akademie der Wissenschaften*, 11: 1-102.
- Rabeder G., Hofreiter M., Nagel D. & Withalm G. 2004. New taxa of Alpine Cave Bears (Ursidae, Carnivora). *Cahiers Scientifiques, Hors série*, 2: 49-67.
- Santi G. & Rossi M. 2006. New evidences from the bears of the Veneto region (Northern Italy) in the evolutionary picture of the Italian cave bears. *Scientific Annals, School of Geology Aristotle University of Thessaloniki (AUTH)*, 98: 179-186.
- Sher A.V., Weinstock J., Baryshnikov G.F., Davydov S.P., Boeskorov G.G., Zazhigin V.S. & Nikolskiy P.A. 2011. The first record of "spelaeoid" bears in Arctic Siberia. *Quaternary Science Reviews*, 30: 2238-2249.
- Stiller M., Baryshnikov G., Bocherens H., Grandal d'Anglade A., Hilpert B., Münzel S.C., Pinhasi R., Rabeder G., Rosendahl W., Trinkaus E., Hofreiter M. & Knapp M. 2010. Withering Away—25,000 Years of Genetic Decline Preceded Cave Bear Extinction. *Molecular Biology and Evolution*, 27 (5): 975-978.
- Torres P.H. 1988a. Osos (Mammalia, Carnivora, Ursidae) del Pleistocene Ibérico: Filogenia; Distribución estratigráfica y geográfica. Estudio anatómico y métrico del craneo. *Boletín Geológico y Minero*, 99 (I): 3-46.
- Torres P.H. 1988b. Osos (Mammalia, Carnivora, Ursidae) del Pleistocene Ibérico: Estudio anatómico y métrico de la mandíbula, hioides, atlas y axis. *Boletín Geológico y Minero*, 99 (II): 220-249.
- Torres P.H. 1988c. Osos (Mammalia, Carnivora, Ursidae) del Pleistocene Ibérico: Dentición decidual, fórmula dentaria y dentición superior. *Boletín Geológico y Minero*, 99 (V): 660-714.
- Torres P.H. 1988d. Osos (Mammalia, Carnivora, Ursidae) del Pleistocene Ibérico: Dentición inferior. *Boletín Geológico y Minero*, 99 (VI): 886-940.