Crossref

# Ursus gr. spelaeus from Grotta del Bandito (Piedmont, Northern Italy).1. Morphodynamics of teeth and indications of an evolutionary step

Giuseppe Santi\*,1 and Mario Rossi2

<sup>1</sup> University of Pavia, Dipartimento di Scienze della Terra e dell'Ambiente, Via Ferrata 1, I-27100 Pavia, Italy; (\*corresponding author: gsanti@unipv.it) <sup>2</sup> Museo Civico di Storia Naturale, Lungadige di Porta Vittoria 9, I-37100 Verona, Italy; (mario.rush@tiscali.it)

doi: 10.4154/gc.2020.03

#### Article history:

Manuscript received Juny 24, 2019 Revised manuscript accepted January 23, 2020 Available online February 29, 2020

Keywords: Ursus, teeth, Grotta del Bandito, Italy, Late Pleistocene, evolution

#### Abstract

This study is focused on cave bears from the Grotta del Bandito (Cuneo Province, Piedmont Region, Northern Italy), especially their teeth. The morphodynamic analyses have been elaborated and compared with other cave bears from Northern Italy, and other cave bear taxa from particular European sites. The Grotta del Bandito bears are similar in size to other cave bears from Italy, and no differences were observed with the other cave bear species or subspecies (e.g. *U. ingressus, U. s. ladinicus, U. s. eremus*). Thus their inclusion in the *U. gr. spelaeus* is the most appropriate classification, and they show a simpler dental surface than the "modern" cave bears (i.e. *ingressus*). The question of whether a single species of *spelaeus* lived in North Italy, is also introduced. In fact, the differences in size are probably the result of population variability, and no clear evidence of other spelaeoid species and/or subspecies, i.e. *ingressus, s. ladinicus* and *s. eremus*, was discovered.

## **1. INTRODUCTION**

Ursus gr. spelaeus is one of the most important members of the faunal assemblage during the continental Late Pleistocene in Europe and, consequently has been the subject of many publications. In order to establish the correct relationship among cave bears, genetic analyses have been recently addressed by morphometric analyses with the result of creating some confusion in the elaboration of an accurate phyletic tree. In Italy the greatest number of contributions to this debate have been based on morphometric and morphodynamic analyses, although lately genetic and chronological studies have gained attention, albeit in a lesser number with respect to those from foreign populations of cave bears (PEREGO et al., 2001; ORLANDO et al., 2002; BONA, 2004; QUILES, 2004; ROSSI et al., 2006; ROSSI & SANTI, 2005, 2007, 2011, 2012, 2013, 2015; ROSSI et al., 2018; SANTI & ROSSI, 2007, 2008, 2014; ZUNINO & PAVIA, 2005; MARTINI et al., 2014; TER-LATO et al., 2017, 2018). The most previously studied caves are those from Lombardy and Veneto in Italy, whereas those from Piedmont (Sambughetto Valstrona, Grotta del Bandito among the most important ones) have been only superficially analysed (e.g. ZUN-INO & PAVIA, 2005; SANTI et al., 2005; SANTI & ROSSI, 2018). The aim of this study therefore is to analyse in detail the morphodynamics of cave bear teeth from the Grotta del Bandito (Cuneo Province) (bearing in mind that the morphodynamic indices are useful only to give an indication of the evolutionary level ROBU, 2016). This will also expand our knowledge on cave bears in an area of Piedmont near the cave of Basura (Liguria) where more definitely "modern" bears have been observed with respect to those of other cave bear populations in Northern Italy (QUILES, 2004).

### 2. GROTTA DEL BANDITO

The Grotta del Bandito (Cuneo Province) along with the other caves located in Valstrona (the most important being the Grotta delle Streghe) and in Mount Fenera, is an important site of cave bear remains in the Piedmont region near the boundary with France. In the past, ZUNINO & PAVIA (2005) conducted a superficial survey of this cave which is geographically located on the right side of the Valley of Gesso (Fig. 1A). Its entrance is at 726 m a.s.l. and it is formed in the Jurassic limestone. The cave is composed of an E-W corridor (217 m) and three major cavities along with others of smaller dimensions. ZUNINO & PAVIA (2005) subdivided this cave into two parts with the same sedimentary infills: the first, called the "eastern branch" is composed of a sand-clay with sedimentary pebbles, and the second one, very similar in the first part of the corridor to the "eastern branch", occupies the western end (Fig. 1B). These authors also conducted three profiles (called L, M and N respectively) (Fig. 1C) in three different areas of the cave and discovered a vertebrate association listed in Table 1.

## 3. MATERIALS AND METHODS

The studied teeth (Table 2) are stored in the Museo Civico di Storia Naturale of Milan (Lombardy). All dentition types are present in the sample: incisors, canines, premolars and molars. This study uses the morphodynamics developed by RABEDER (1999) and GRANDAL D'ANGLADE & LÓPEZ GONZÁLEZ (2004). In his paper RABEDER (1991) conceived and applied the morphodynamic analysis on the P4/p4 only, and later elaborated it for the other teeth typologies, after having applied this method for the first time to the Arvicolidae of the Pliocene-Pleistocene (RABEDER, 1981). It was subsequently also proposed for the incisors, premolars and molars of cave bears. The most important concept on which this morphodynamic method is based, is the evaluation over time of the development of the complication of the dental surface (from the simpler forms to the most complicated and assigning each one a particular morphotype labelled

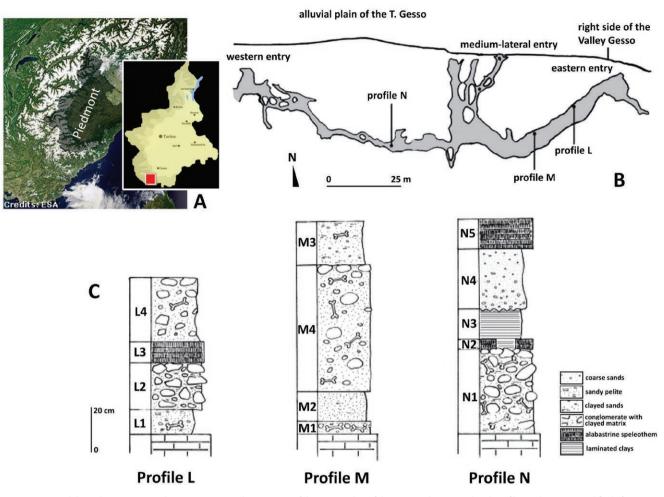


Figure 1. Grotta del Bandito (Cuneo, Piedmont): A. geographic position of the site. B. plan of the cave and C. generalized profiles in the cave (modified after ZUNI-NO & PAVIA, 2005).

with a letter from A to F which is associated with a morphodynamic factor), and to correlate it with the cave bears evolutionary line (RABEDER, 1991; 1999; RABEDER & TSOUKALA, 1990;

Table 1. Faunal list of the Grotta del Bandito (modified after: ZUNINO & PAVIA, 2005).

Species	L1	L4	M1	M3	M4	N1	N4
Ursus spelaeus Rosenmüller, 1794	XX	ΧХ	XXX	XX	ΧХ	XXX	Х
Canis sp.					Х		
Vulpes vulpes (Linnaeus, 1758)			Х				
Felis silvestris Schreber, 1777					Х		
Mustela putorius Linnaeus, 1758					Х		
Martes martes (Linnaeus, 1758)				Х			
Martes foina (Erxleben, 1777)					Х		
Capra ibex Linnaeus, 1758		Х					
Rupicapra rupicapra Linnaeus, 1758					Х		
Lepus sp.					Х		
Castor fiber Linnaeus, 1758					Х		
Microtus arvalis (Pallas, 1778)				XX			
<i>Microtus (Terricola</i> ) cf. <i>subterraneus</i> (de Sélys-Longchamps, 1836)			XX	XX		Х	
Clethrionomys glareolus (Schreber, 1780)	Х			XXX	Х		
Apodemus cf. sylvaticus (Linnaeus, 1758)	Х		Х	Х		Х	
Glis glis (Linnaeus, 1766)			Х	XX		Х	
Eliomys quercinus (Linnaeus, 1766)				Х			
Sorex araneus Linnaeus, 1758				XX			
Rhinolophus cf. ferrumequinum (Schreber, 1774)				Х	Х		

ROBU, 2016 etc.). Figure 2 clearly explains the morphotype concept for the P4/p4, the most important teeth in the evolutionary picture. Moreover, the methods do not give absolute results, but being a quantitative analysis advance an indication only of the evolutionary step reached by the studied specimens (RABEDER, 1991; ROBU, 2016). GRANDAL D'ANGLADE & LÓPEZ GONZÁLEZ (2004) proposed a similar morphodynamic elaboration to that of Rabeder for m1. For the different components of this kind of tooth (paraconid, trigonid cusplets and talonid one) the so called "Convergence Index" is evaluated. As well as the morphodynamic index *sensu* Rabeder, the main target of the

Table 2. Number of the cave bears tooth specimens from the Grotta del Bandito (Cuneo, Piedmont) analysed in this work. For explanation see the text.

tooth	n. of specimens (in this work)
12	10
i2	4
13	10
i3	8
P4	10
p4	6
M1	14
m1	27
M2	23
m2	28
m3	7
Total	147

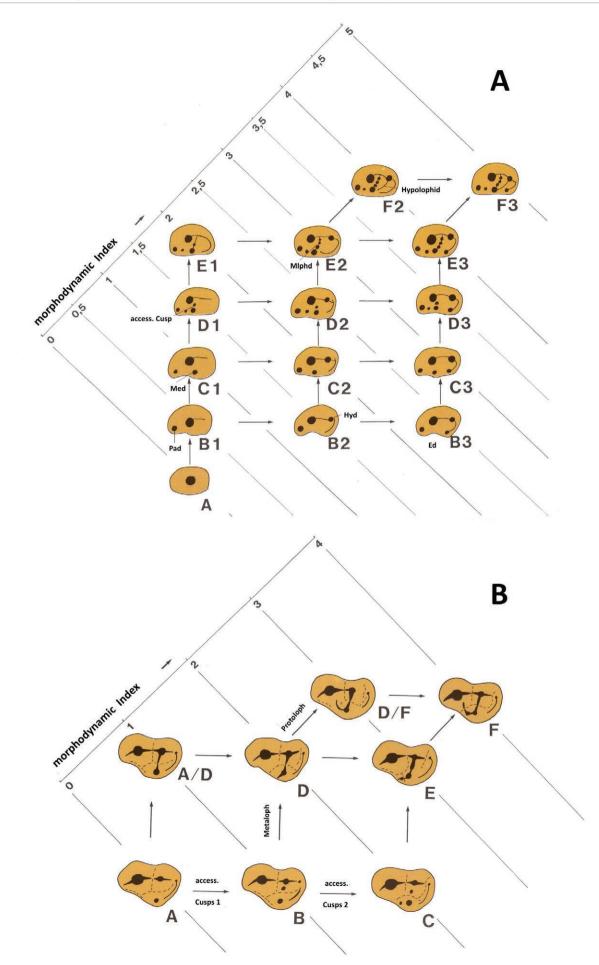


Figure 2. Morphodynamic indices of the P4/p4 (modified after RABEDER, 1991).

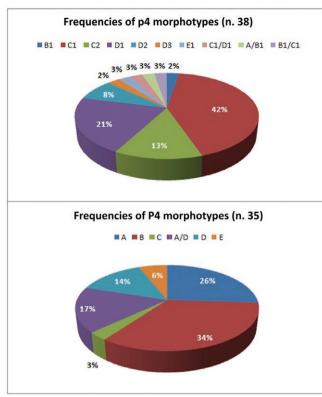


Figure 3. Frequencies (%) of the P4/p4 morphotypes from the Grotta del Bandito.

"Convergence Index" is to indicatively evaluate the evolutionary step reached by the cave bears.

For a more complete and detailed overview we included the data analysed by ZUNINO & PAVIA (2005) of part of the teeth discovered in this cave from and earlier preliminarily study. The following proposed considerations will be commented on and compared with the data of the cave bears from European caves in which recently different species and subspecies (*Ursus ingressus* RABEDER et al., 2004, *U. spelaeus eremus* RABEDER et al., 2004, *U. spelaeus ladinicus* RABEDER et al., 2004) have been identified.

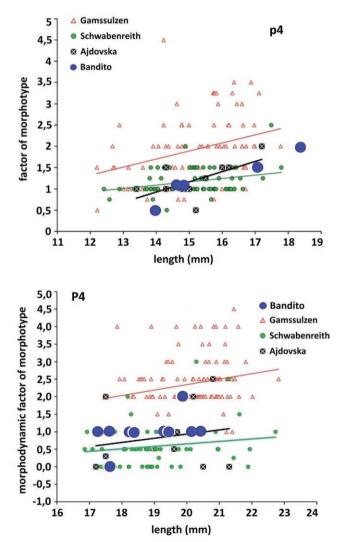
# 4. MORPHODYNAMICS OF TEETH

Incisors. Studies on incisors are rather rare; FRISCHAUF (2014) studied the incisors from Križna jama (Slovenia), FRISCHAUF et al. (2014) those from Drachenhöhle (Mixnitz-Styria) and BARYSHNIKOV et al. (2018) the incisors from the Urals-Caucasus Mts. In these three caves, remains of U. ingressus and U. kudarensis BARYSHNIKOV, 1985 (the latter is described in LUBINE et al., 1985) were discovered and examined in greater detail. Referring to the teeth from the Bandito cave the morphotype "p" for the *fossa lunaris-cingulum* of I2 is the only one observed; the standardized index (abbreviated "std") is low (58.91). (For meaning of the "morphotype" see above). This can be a consequence of a low number of specimens (n=10), which makes it impossible to indicate the evolutionary step of these teeth. Also for I3 the low number of specimens (n=10) prevents any definite conclusions on their evolutionary level. However, some considerations can be proposed: the kalyx distalis has "0" as the most frequent morphotype and only rarely (two teeth) the "1" one. The highest morphotypes are totally lacking. If this is confirmed, the evolutionary degree is rather low, but this deduction is thwarted by the scarcity of specimens. To conclude this short discussion

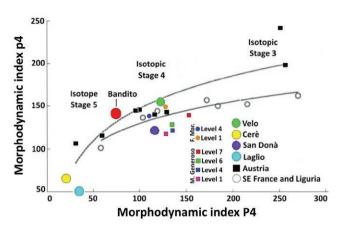


Figure 4. An example of morphotype "A" in P4 of the cave bears from the Grotta del Bandito.

on the morphodynamics of the incisors, all of the i2 have an "s" morphotype frequency typical of *spelaeus* (RABEDER, 1999). In i3 the lowest morphotype of the *sulcus mesialis* is B/C and in contrast to the other incisors, the main type most frequently observed is the "D" morphotype. In this case also the scarce specimens (n=8) prevents a definitive conclusion, but if this is con-



**Figure 5.** Relationship between the morphodynamic factor of morphotype and upper/lower fourth premolars (P4/p4) length from Grotta del Bandito, Adjovska jama, Schwabenreith and Gamssulzen caves (partly modified after: RABEDER, 2011).



**Figure 6.** Relationship between the morphodynamic indices of the upper/lower fourth premolars (P4/p4) from Grotta del Bandito and some caves in Italy, France and Austria (modified after: QUILES, 2004).

firmed in the future by the distribution of frequencies, it raises the possibility that at least two populations of bears (of different ages?) lived in the Bandito cave.

*Fourth upper/lower premolars (P4/p4).* Figure 3. shows the distribution of the frequency of the morphotypes in the upper and lower fourth premolars. Considering also the analysis undertaken by ZUNINO & PAVIA (2005) for the p4, the frequencies of the morphotypes (*sensu* RABEDER, 1999) are: 1 A/B1, 1 B1, 1 B1/C1, 1 C1/D1, 16 C1, 4 C2, 8 D1, 3 D2, 1 D3, 1 E1, while for P4 the morphotype frequencies are: 9 A (Fig. 4), 12 B, 1 C, 6 A/D, 5 D, 2 E. This distribution (the most frequent being that of the lowest morphotypes) is similar to that obtained for other cave bear populations in Northern Italy.

In summary, cave bear populations with variable sizes (from medium to large) lived in Northern Italy, but with very simple premolars; this is evidence that could indicate, a probable intermediate step in the evolutionary tree. In Figure 5 we only present the results of our measurements for the upper and lower fourth premolars, as well as the relationship between the morphodynamics and length of P4/p4 of bears from the Grotta del Bandito and other caves where different species and subspecies were found. Differences among the species are not noticed. A surprising view is shown in Fig. 6; in fact, the most important caves in Italy are placed in an interesting "cloud". A radiometric date of 29,130±90 yrs, was recently published for the Covoli di Velo by ROSSI et

al. (2018). In Figure 6, in which the morphodynamic index of P4 and p4 are in correlation, the Grotta del Bandito data are also inserted. We recall that the Fontana Marella and Mt. Generoso caves are located in western Lombardy near the boundary with Piedmont. In general, three aspects are noted: 1) both the Grotta del Bandito and Covoli di Velo (Veneto region) are placed along the "Austrian line", 2) the group composed by the levels FM an MG is substantially placed around the "French line", 3) the Grotta del Cerè (Veneto region) and the Grotta del Buco dell'Orso (Laglio, Lombardy region) are placed in a position in which the Austrian and French lines are not clearly separated. Data for Laglio (Buco dell'Orso Cave) premolars are too scarce to be able to advance any considerations. The exception is the S. Donà samples positioned along the "French line". Previously we indicated that the morphodynamic indices only give a relative indication of the evolutionary step reached by the bears (ROBU, 2016). The position of the Bandito is between the MIS 5 (80-130 Ky) and MIS 4 (Fig. 6) and to our surprise we can see that these bears occupy an evolutionary step similar to that of the early "populations" of cave bears. The contradiction between the bears of the younger age and the relative simplicity of their dentition, is confirmed. Consequently, we can also hypothesize that Italian territories were colonized by populations of bears coming from different areas of Europe, a mixed population that maybe separated rather early. Are the North Italian territories the zones of migration paths from west to east and vice versa? Is it possible that only a single phyletic line, the Austrian one, colonized Northern Italy and that the

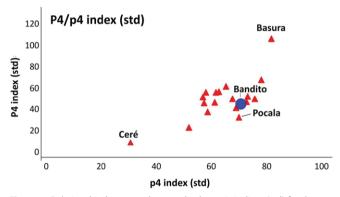


Figure 7. Relationship between the morphodynamic indices (std) for the upper/lower fourth premolars (P4/p4) from Grotta del Bandito and some other caves in Italy.

Table 3. Radiometric dating for some Italian cave bears (modified after: ROSSI et al., 2018).

#	SITE	Region	Radiometric dating k yr BP	Source
1	Conturines	Trentino Alto-Adige	107.2-115.8 to 41.9-47.5 (Uran series)	RABEDER et al. (1994)
2	Conturines	Trentino Alto-Adige	40.19±0.9	DÖPPES et al. (2018)
3	Conturines	Trentino Alto-Adige	>49	DÖPPES et al. (2018)
4	Conturines	Trentino Alto Adige	>50.579 to >46.435	SPÖTTL et al. (2018)
5	Grotta Generosa	Lombardy	38.2±1.4	BIANCHI-DEMICHELI & OPPIZZI (2001)
6	Grotta Generosa (Level 2)	Lombardy	39.2±1.0 to 51.2±4.0	BONA (2004)
7	Grotta Generosa (Level 4)	Lombardy	46.7±2.4	BONA (2004)
8	Grotta Generosa (Level 6)	Lombardy	47.8±2.6 to 50.8±5.0	BONA (2004)
9	Fontana Marella (FM1)	Lombardy	21.81±0.2	PEREGO et al. (2001)
10	Fontana Marella (FM2)	Lombardy	22.31±0.2	PEREGO et al. (2001)
11	Buse di Bernardo	Trentino Alto-Adige	25.78±0.22 to 25.1±0.3	AVANZINI et al. (2000)
12	Paina	Veneto	19.6±0.054	TERLATO et al. (2018)
13	Trene	Veneto	19.9±0.055	TERLATO et al. (2018)
14	Chiostraccio Cave	Tuscany	24.03±0.1	MARTINI et al. (2014)
15	Covoli di Velo	Veneto	29.131±0.9	ROSSI et al. (2018)

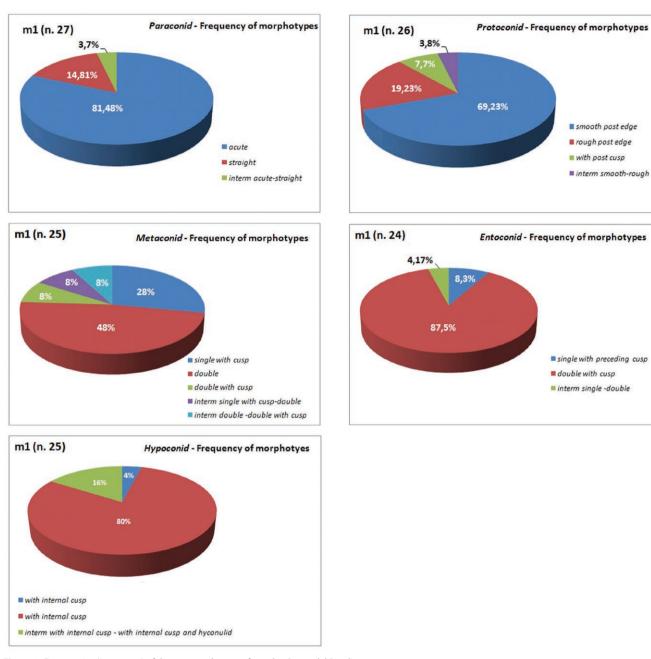


Figure 8. Frequencies (in percent) of the m1 morphotypes from the Grotta del Bandito.

influence of the "French line" (Basura (?) in the Liguria Region) may have arrived and tried to enlarge it in the last stages of evolution? We need more data to confirm or reject this hypothesis.

Finally, Figure 7 shows that the Bandito bears are placed within the "cloud" of the other Italian cave bears with the only exceptions of Cerè (most ancient deposit) and Basura (more advanced bears) which are separated from the main distribution. In Northern Italy we have a scarcity of radiometric dating, and only some populations of cave bears have been dated. In Table 3 we reported the radiometric data calculated up to the present.

*First lower molars (m1)*. Considering the morphotypes proposed by GRANDAL D'ANGLADE & LÓPEZ-GONZÁLEZ (2004) (Fig. 8), the m1s from the Grotta del Bandito correspond to those of advanced cave bears; the paraconids are equally subdivided in acute and straight and the protoconid from smooth posterior edge to rough posterior edge. Metaconids fall between the single with cusplet, to double, while the entoconids are frequently double with cusplets and rarely, single with preceding cusplets (morphotype 13 sensu GRANDAL D'ANGLADE & LÓPEZ-GONZÁLEZ, 2004). Finally, the hypoconids exhibit an internal cusplet and hypoconulid. In the Bandito bears, teeth with only one metastylid (sensu RABEDER, 1999) are the most frequent, although more derived morphotypes (with two or three metastylids) are also present. The entoconid area is composed of cusplets of about the same size, along with another of small size (most frequent) or two (one specimen). Regarding the enthypoconids only the simpler ones are found; comprising morphotype A (the simple one), A/B (with an enthypoconid but not yet divided from the hypoconid by a furrow) and B (enthypoconid clearly divided from the hypoconid by a furrow). RABEDER (2014) studied the teeth from Križna jama (Slovenia) and classified them as U. ingressus; the simplicity of construction of the m1s from Bandito prevents their attribution to this species. The distribution of the main "Convergence Indices" (sensu GRANDAL

**Geologia Croatica** 

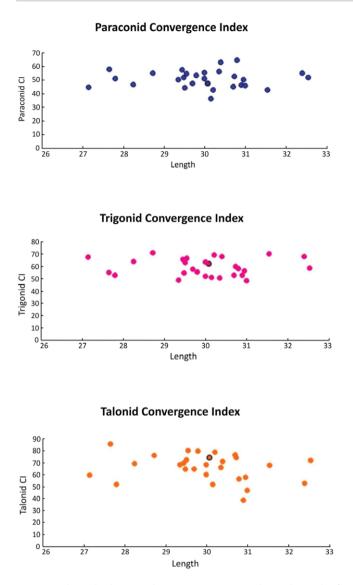


Figure 9. Relationship between the main "Convergence Index" and "Length" of the first lower molars (m1) from Grotta del Bandito.

D'ANGLADE & LÓPEZ-GONZÁLEZ, 2004) for the paraconid, trigonid cusplets and the talonid one, are shown in Fig. 9; these are rather homogenous, independent of the absolute length of the tooth. Also among these teeth a mix of "old" and advance features has also been noted; for example, considering the relationship between the "Total length – Talonid breadth" (Fig. 10) the point of the Bandito bears falls in the field of the "primitive" bears. In contrast, their relationship among the "Paraconid convergence index – Total length", the "Trigonid convergence index – Total length" and the "Talonid convergence index-Total length" suggests the Bandito bears be placed among the "advanced" cave bears. This is a confirmation that in Italy cave bears have a mix of features of tooth elements present in the finds of Middle and Late Pleistocene age.

Second lower molars (m2). Metrical data are reported in Fig. 11, while the calculated indices are shown in Fig. 12. A greater frequency of medium-low indices for the development of the metalophids is observed (Fig. 12) (on 26 specimens, 11 have a "B" morphotype), whereas in the trigonid construction, the simpler form is lacking. The mesolophid area is characterized by morphotypes A (with a central crest and a first formation of a mesolophid) and B (with a continuous mesolophid developed as a crest

or a line). Referring to the enthypoconids area, in the sequence of morphotypes, only the A (without enthypoconids) and the D (subdivision in three main parts) types are lacking. Intermediate indices are hence present in the Bandito "population", similar to that for others. Generally, a comparison with teeth from other caves shows, as in the Bandito specimens, that they have a low morphodynamic index; in the study on the cave bears from Križna jama (Slovenia), RABEDER (2014) calculated for the enthypoconid morphotype an index of 181.82 (std 98.12) from 11 specimens, and for the teeth from Risovača (Late Pleistocene, Serbia: CVETKOVIĆ & DIMITRIJEVIĆ, 2014)) the index is 181.3 (std 97.8). Also for the bears from Loutrá Aridéas (Greece) the enthypoconid index is 144.67 (std 78.08) (TSOUKALA et al., 2006). Furthermore, the "palaeopopulation" from Ajdovska jama (Slovenia) shows a very high morphodynamic index for the enthypoconid (std 166.03) that RABEDER (2011) considers attributable to U. s. ladinicus, but in a followed control, the value of 166.03, (Tab. 7 in RABEDER 2011) is a mistake. In fact, RABEDER (2011: p. 36) quoted: "The enthypoconid-index is astonishingly high and even supersedes the Gamssulzen population by more than 17%)". There is a mistakenly given standard value of 133 (instead of 185.3) so the correct standardized value is 117.4, which corresponds to the statement in the text (more than 17%, not more than 66%)". Here, considering the 28 elements in the specimens, it is difficult to distinguish these two species U. ingressus and/or U. s. ladinicus at the species or subspecies level for the Bandito bears.

*Third lower molars (m3).* A scarcity of specimens does not enable definite conclusions to be drawn, but observing the data the cave bears from the Bandito Cave have index values that are not completely low or high. The low number of specimens prevent further discussion as the sample is too small.

*First and second upper molars (M1–M2).* Also for these teeth (M1s) the morphodynamic indices (14 specimens and related to the paracone) are low (index is 75, std is 39.89); this is important because it confirms that for the cave bears in Italy, M1s were simple and that in the evolutionary position they occupied an intermediate place. The other morphodynamic indices are defined for the metacone (14 in specimens, index is 110.71, std is 62.90) and the proto?/metacone (14 specimens, index is 135.71, std is 43.43).

Considering the main components of the tooth, the morphodynamic indices most frequently have an intermediate range; in general the indices for the Bandito M2s are low when compared with those from the other caves, aligning them with the other analysed teeth.

In conclusion we propose in Fig. 13 a summary of the morphodynamics of the teeth from the Bandito cave compared with other species of bears (RABEDER et al., 2005). In fact, the premolars of the Bandito Cave fall inside the cloud formed by *U. spelaeus*, *U. s. eremus* and *U. s. ladinicus*; with only *U. ingressus* being well separated from the cloud (Fig. 13A). With these morphodynamic indices, it is difficult to subdivide the different species with the exclusion of *ingressus*, and consequently in our opinion it is better to indicate this distribution (with the Bandito bears) as gr. *spelaeus*. The same consideration can be advanced observing the Fig. 13B. The separation of the different species, however, is greater compared to that of the Fig. 13A, as well as the third one. Having utilised different indices for the different kind of teeth it remains uncertain whether the Bandito bears belong to one species or another.

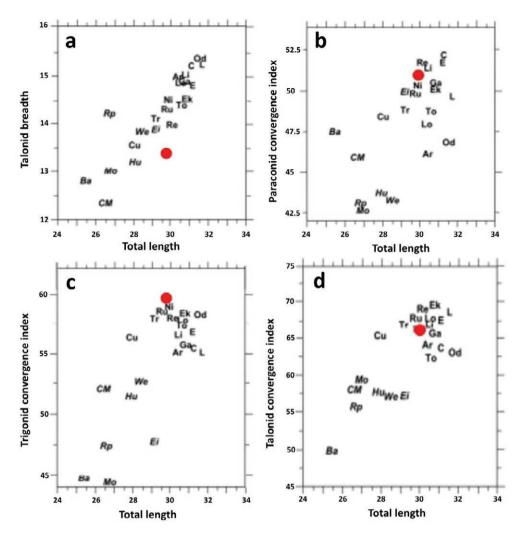
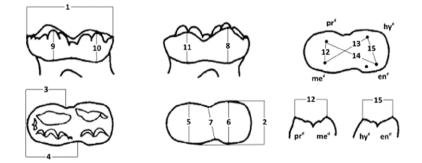


Figure 10. Position of the first lower molars (m1) from the Grotta del Bandito (red point) utilizing the relationships between the main convergence indices and "Length". Iberian Peninsula: E: Eirós; C: A Ceza; L: Liñares; Ar: Arrikrutz; Tr: Troskaeta; Ek: Ekain; To: Toll; Re: Reguerillo; CM: Atapuerca (Cueva Major); British Islands: Ba: Bacton; We: Westbury; Central Europe: Ei: Einhornhöhle (Scharzfeld); Ru: Rubeland; Ga: Gailenreuther (Zoolithenhöhle); Hu: Hundsheim; Ni: Nixloch; Li: Lieglloch; Cu: Conturines; Eastern Europe: Lo: Loutraki (Greece); Od: Odessa (Ukraina) (modified after: GRANDAL D'ANGLADE & LÓPEZ-GONZÁLEZ, 2004).



1 – length; 2 – breadth; 3 – trigonid length (lingual); 4 – trigonid length (labial); 5 – trigonid breadth; 6 – talonid breadth; 7 – constriction length; 8 – protoconid height; 9 – metaconid height; 10 – endoconid height; 11 – hypoconid height; 12 – protoconid-metaconid length; 13 – metaconid-hypoconid length; 14 – protoconid-endoconid length; 15 – hypoconid-endoconid length.

Teeth (n. 27)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Mean	29.45	16.96	14.94	17.02	15.75	15.74	13.48	10.39	9.47	8.07	10.27	10.93	17.19	19.15	12.09
Min	26.13	15.01	10.49	13.05	13.08	12.93	9.48	6.07	6.96	5.72	5.61	9.31	14.55	16.87	10.11
Max	33.04	18.95	17.82	22.5	18.23	18.93	17.99	12.51	11.49	10.95	11.89	12.64	20.47	22.31	14.37
Stand. Dev.	1.82	1.15	1.77	1.88	1.36	1.6	2.05	1.17	0.95	0.93	1.31	0.92	1.5	1.65	1.13
Coeff. Var.	6.18	6.79	11.83	11.04	8.63	10.15	15.25	11.29	10.06	11.53	12.79	8.39	8.72	8.6	9.33

Figure 11. Parameters (modified after: TOSUKALA & GRANDAL D'ANGLADE, 1997) and metrical data of the m2 from Grotta del Bandito.

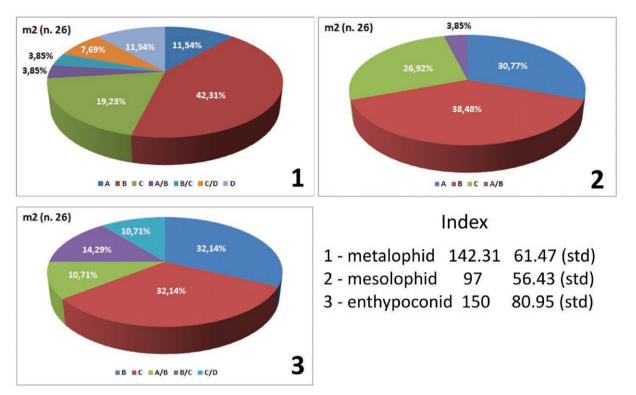


Figure 12. Frequencies, values and standardized values of the morphodynamic indices of the metalophid (1), mesolophid (2) and enthypoconid (3) of m2 from Grotta del Bandito.

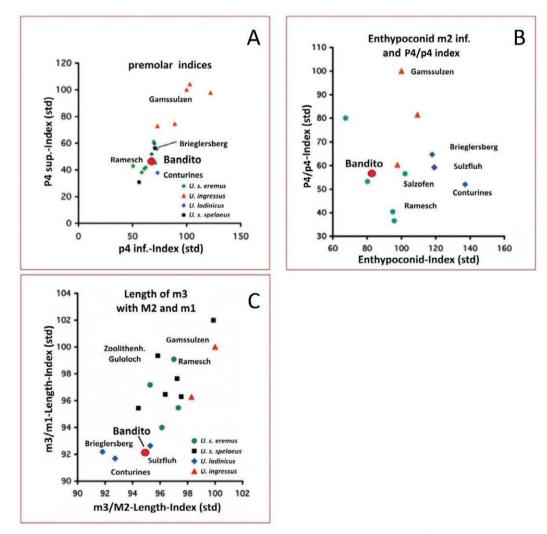
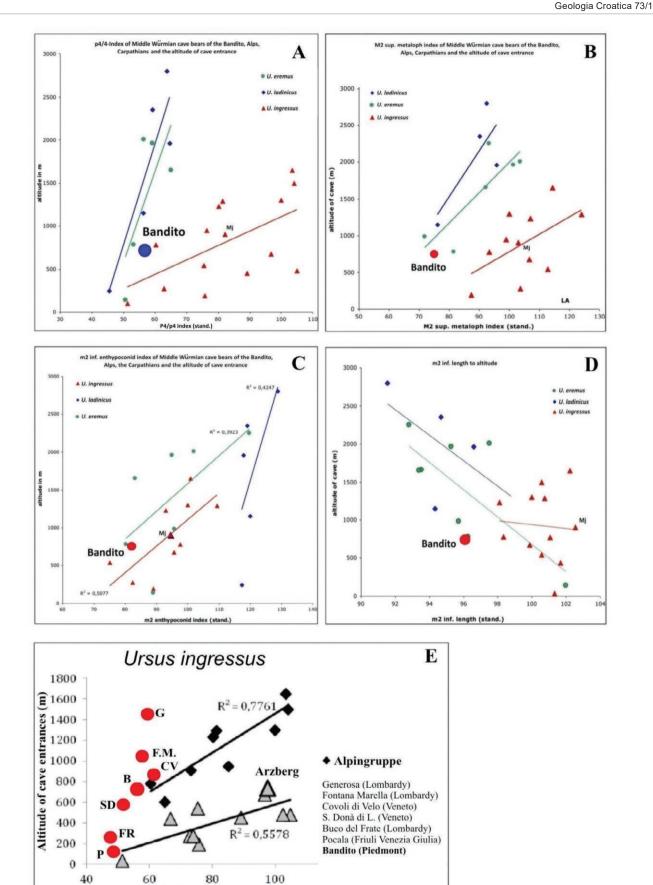


Figure 13. Morphodynamics of the teeth from Grotta del Bandito compared with the other cave bears species (modified after: RABEDER et al., 2005).



**Figure 14. A.** Relationship between the P4/p4 index (std) from Grotta del Bandito and some caves in which different taxa of *Ursus* have been found and the altitude of the cave entrance. **B.** Relationship between the m2 metaloph index (std) from Grotta del Bandito and some caves in which different taxa of *Ursus* have been found and the altitude of the cave entrance. **C.** Relationship between the m2 enthypoconid index (std) from Grotta del Bandito and some caves in which different taxa of *Ursus* have been found and the altitude of the cave entrance **D.** Relationship between the length of m2 (std) from Grotta del Bandito and the caves entrance in which different taxa of *Ursus* have been found, and the altitude of the caves entrance (all diagrams modified after: RABEDER et al., 2005). **E.** Relationship between the upper/lower fourth premolars (P4/p4) indices and the the cave entrances altitudes of the Italian and Austrian sites (modified after: FASSL & RABEDER, 2015).

P4/p4 index (std)

#### 5. MORPHODYNAMICS-ALTITUDE RELATIONSHIP

A relationship between the altitude of the cave and the morphodynamics of the teeth has often been searched for in the past (RABEDER et al., 2005; LAUGHLAN, 2012). Here we investigate whether there is any possible relationship between the altitude and teeth (morphodynamic and morphometry) from the Bandito Cave. Fig. 14A-E shows the relationship between the premolar and molar indices and the altitude of the cave; the data of the Bandito bears falls in between the spelaeus eremus and ingressus taxa. Moreover, a hypothetical relationship between the m2 size and the altitude of the cave is also shown (Fig. 14 D); there is not an equal position of the Bandito bears; in fact in the Fig. 14A the mark is placed next to some of those belonging to s. eremus and s. ladinicus, while in the second one the Bandito bears are approximated to ingressus. The picture is confused and a relationship between the size of the tooth and the altitude of the cave cannot be demonstrated. The same considerations could be proposed when considering the enthypoconid of m2s and the total length of these teeth. On the basis of these data, a relationship between the distribution of the different species of cave bears and altitude also does not exist. Concerning the Bandito bears another consideration can be postulated. It is very difficult to determine which species of cave bear inhabited this area of Piedmont during the Late Pleistocene. Finally, a relationship between the P4/ p4 index and the altitude of the cave entrances referred to Ursus ingressus only, is also shown (Fig. 14E). Independently of the taxon considered (U. ingressus), the position of the Bandito point is interesting because it opens a discussion about the "migration path" and consequently about the colonization of the cave bears and also perhaps some phyletic considerations. In fact, the Bandito is placed at the beginning of the distribution of the "Alpingruppe" (sensu FASSL & RABEDER, 2015) nearly on the same altitude where the Arzberg cave is placed (the latter is included in their "colline gruppe" by FASSL & RABEDER, 2015). The distribution of the Italian localities is unexpected. From a common beginning, the lineage direction is very different to that of other bears. Is it true that the Italian cave bears are effectively a "separate" assemblage from others in Europe? Many signs would seem to confirm this (size, a low or medium morphodynamic index of the teeth, both the plumpness indices and the K-I for the metapodia are similar to those of other European "populations" etc.). Further studies are necessary to solve this dilemma.

# 6. IS URSUS SPELAEUS THE SINGLE SPECIES THAT LIVED IN ITALY?

Often in the past we have supported the thesis of the presence of a single species Ursus spelaeus in Northern Italy (e.g. SANTI & ROSSI, 2014). Previous studies on fossils from different caves of Northern Italy have shown a strong homogeneity among the Italian "populations". The Grotta del Cerè (Verona, Veneto) is the exception, where in fact, among the fossiliferous material, remains of U. deningeri VON REICHENAU, 1904 and U. arctos LINNAEUS, 1758 together with U. spelaeus have been found (ROSSI & SANTI, 2005). In their research on the metapodia from selected caves of Italy, SANTI & ROSSI (2014) have shown that morphometrically Ursus spelaeus ROSENMÜLLER, 1794 is the single species that lived in the Italian Alps. The differences in size are probably a result of population variability and no clear evidence of other spelaeoid species and/or subspecies, i.e. ingressus, s. ladinicus and s. eremus, has been discovered. A relationship between the size and the altitude of the cave is absent. In Italy therefore up to now, chronological data and mtDNA analyses are lacking, a complete study, that includes the morphometry, morphodynamics, chronology and genetics, is missing. Until now, only the Basura assemblage (Liguria Region) seems to be very different from the other cave bears in Northern Italy; in fact, the morphodynamic indices of the fourth premolars are higher compared with those of other Italian cave bears (QUILES, 2004; SANTI & ROSSI, 2014). For this assemblage a possible higher step in the evolutionary scale could be hypothesized. Contrary to the Basura population, in the Pocala Cave (Friuli Venezia Giulia, Eastern Italy), the cave bears have a large size, but the fourth premolars has a very simple structure (ROSSI & SANTI, 2015). Consequently, a confused picture on the morphodynamic indices is highlighted with the highest value (Basura) and the lowest ones for the Grotta delle Fate assemblage (Liguria). Two different explanations could be proposed: either this represents the presence of more taxa of Ursus, or an intraspecific variability of a single species. The discussion is, at the present time still open.

# 7. CONCLUSIONS

The study of the teeth of the cave bear from the Grotta del Bandito (Piedmont, Northern Italy) leads to the following conclusions. The teeth are generally of medium -size, although in some cases large specimens are also present; they are similar to other taxa of cave bears (ingressus, s. eremus, s. ladinicus). With these morphometric results the studied bears are determined as cave bears, but for the Bandito sample and the Italian cave bears in general it is not easy to distinguish which species they belonged to. The Bandito bears show the features of different "species"; in some cases these elements appear to be "primitive", in others they are more evolved. To indicate a dominant taxon is difficult, because the taxonomic determination sensu RABEDER et al. (2004) is mostly based on genetics, not on morphometrics. We prefer to indicate the Bandito cave bears as gr. spelaeus, not a single species, and no relationship with the altitude of the cave is noted.

From a general point of view, these bears occupied probably, an intermediate evolutionary step, and therefore more evolved individuals are also present. In fact, in the fourth premolars, ZU-NINO & PAVIA (2005) found higher morphotypes than in the other "Italian" "populations" in which these are absent. The explanation is not clear, but the closeness of the Basura Cave (Liguria Region) in which more advanced bears are found (QUILES, 2004) can suggest postulation of for example, the hypothesis of the replacement of the "primitive" bears with "advanced" ones. If in the Basura Cave the disappearance of the primitive bears seems clearer, in the Bandito Cave it is less clear. In other words, during the Late Pleistocene, close to the cave bears extinction (in fact the assemblage of the Bandito Cave and that of Fontana Marella are very similar), two different "populations" probably cohabited for a short period in the Bandito Cave area, one of these composed of "primitive" bears and a second, formed of a few, but more evolved specimens. Therefore, the complete substitution did not occur at once because the cave bears vanished and became extinct. The problem is still open.

#### ACKNOWLEDGEMENT

The authors thank Dr. Alessandro GARASSINO (Milan) and Dr. Giorgio TERUZZI (Milan) for access to the Museo Civico di Storia Naturale of Milan collections, three anonymous reviewers, the guest editor that with their comments improved this work, and Dr. Nicki B. CHARLES-STAR (Cleveland) for the revision of the English language.

#### REFERENCES

- AVANZINI, M., BERTOLINI, M., BETTI, G., BORSATO, A., CALMIERI, G., DEL-LANTONIO, E., LAZINGER, M. & ZAMBOTTO, P. (2000): Resti di Ursus spelaeus dalle "Buse di Bernardo" e dal "Covelo di Rio Malo" (Trentino-Italia): alcune implicazioni paleo ambientali.– Studi Trentini di Scienze Naturali - Acta Geologica, 75(1998), 155–160.
- BARYSHNIKOV, G., GIMRANOV, D. & KOSINTSEV, P. (2018): Variability of the upper incisors in the cave bears (Carnivora, Ursidae) from the Caucasus and Urals.– Comptes Rendus Palevol, 18, 209–222. doi: 10.1016/j.crpv.2018.08.001.
- BIANCHI-DEMICHELI, F. & OPPIZZI, N. (2001): Ricerche speleologiche e paleontologiche nella regione del Monte Generoso: la Caverna Generosa.– Bolletino della Società Ticinese di Scienze Naturali, 89, 61–66.
- BONA, F. (2004): Preliminary analysis on Ursus spelaeus Rosenmüller et Heinroth, 1794 populations from ,,Caverna Generosa" (Lombardy–Italy).– Cahiers Scientifique du Muséum d'Histoire naturelle de Lyon Hors Série, 2, 87–98.
- CVETKOVIĆ, N.J. & DIMITRIJEVIĆ, V.M. (2014): Cave bears (Carnivora, Ursidae) from the Middle and Late Pleistocene of Serbia: A revision.– Quaternary International, 339–340, 197–208. doi: 10.1016/j.quaint.2013.10.045
- DÖPPES, D., RABEDER, G., FRISCHAUF, C., KAVCIK-GRAUMANN, N., KRO-MER, B., LINDAUER, S., FRIEDRICH, R. & ROSENDAHL, W. (2018): Extinction pattern of Alpine cave bears-new data and climatological interpretation.– Historical Biology. doi: 10.1080/08912963.2018.1487422.
- FASSL, S. & RABEDER. G. (2015): Die Höhlenbären der Arzberghöhle (1741/4) bei Wildalpen - Neue Daten und Forschungsergebnisse von Ursus ingressus. VHO – Verein für Höhlenkunde in Obersteier, 248–254.
- FRISCHAUF, C. (2014): The Cave Bear Incisors from Križna jama (Slovenia).– Mitteilungen der Kommission für Quartärforschung der Österreichischen Akademie der Wissenschaften, 21, 75–83.
- FRISCHAUF, C., LIEDL, M.P. & RABEDER, G. (2014): Revision der fossilen Bären der Drachenhöhle (Mixnitz, Stmk).– Die Höhle, 65/(1–4), 47–55.
- GRANDAL D'ANGLANDE, 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.
- LAUGHLAN, L. (2012): Metrik und Evolutionsniveau der Höhlenbärenzähne aus der Medvedia-Höhle im Slovenský raj (Slowakei).– Diplomarbeit angestrebter akademischer GradMagistra der Naturwissenschaften (Mag.rer.nat.) (Unpublished) Universität Wien, 96 p.
- LUBINE, V.P., TCHERNIACHOVSKI, A.G., BARYSHNIKOV, G.F., LEVKOVS-KAIA, G.M. & SELIVANOVA, N.B. (1985): La grotte de Koudaro q1 (resultants de recherches pluridisciplinaires).– L'Anthropologie, 89/2, 159–180.
- MARTINI, I., COLTORTI, M., MAZZA, P.P.A., RUSTIONI, M. & SANDRELLI, F. (2014): The latest Ursus spelaeus in Italy, a new contribution to the extinction chronology of the cave bear.– Quaternary Research, 81, 117–124. doi: 10.1016/j. yqres.2013.10.003.
- 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. doi: 10.1093/oxfordjournals.molbev.a004016
- PEREGO, C., ZANALDA, E. & TINTORI, A. (2001): Ursus spelaeus from Grotta Sopra Fontana Marella, Campo dei Fiori Massif (Varese, Italy): morphometry and paleoecology.– Rivista Italiana di Paleontologia e Stratigrafia, 107/3, 451–462.
- QUILES, J. (2004): Analyse morphodynamique de l'ours des caverne (Carnivora, Ursidae) de cinq sites du pourtour Méditerranéen.– Cahiers scientifique du Muséum d'Histoire naturelle de Lyon Hors Série, 2, 149–161.
- RABEDER, G. (1981): Die Arvicoliden (Rodentia, Mammalia) aus dem Pliozan und dem alteren Plieistozan von Niederösterreich.– Beiträge zur Paläontologie Österreichs, 8, 1–373.
- RABEDER, G. (1991): Die Höhlenbären der Conturines Entdeckung und Erforschung einer Dolomiten-Höhle in 2800 m Höhe. 124 p. Verlagsanstalt Athesia-Bozen.
- RABEDER, G. (1999): Die evolution des Höhlenbärengebisses. Mitteilungen der Kommission für Quartärforschung der Österreichischen Akademie der Wissenschaften, 11, 1–102.
- RABEDER, G. (2011): Metrical analysis and evolutionary level of the cave bear teeth from Ajdovska jama.– Mitteilungen der Kommission f
  ür Quart
  ärforschung der 
  Österreichischen Akademie der Wissenschaften, 20, 31–42.
- RABEDER, G. (2014): Metrics and Evolutionary Level of Teeth of the Bears from Križna jama (Slovenia).– Mitteilungen der Kommission f
  ür Quart
  ärforschung der Österreichischen Akademie der Wissenschaften, 21, 57–63. doi: 10.2307/j.ctv8mdn09.12
- RABEDER, G. & TSOUKALA, E. (1990): Morphometric analysis of some cave-bear teeth from Petralona (Chalkidiki, North Greece).– Beiträge zur Paläontologie Österreichs, 16, 103–109.
- RABEDER, G., HOFREITER, M., NAGEL, D. & WITHALM, G. (2004): New taxa of Alpine Cave Bears (Ursidae, Carnivora).– Cahiers scientifique du Muséum d'Histoire naturelle de Lyon Hors Série, 2, 49–67.

- RABEDER, G., STEFFAN, I. & WILD, E. (1994): The chronological position of the cave bears from Conturines cave: Abstract, 2nd International Cave Bears Symposium Alta Badia.
- RABEDER, G., HOFREITER, M. & WILD, E.M. (2005): Die Bären der Brieglersberghöhle (1625/24).– Die Höhle, 56/1–4, 36–43.
- ROBU, M. (2016): Age re-assessment of the cave bear assemblage from Urşilor Cave, north-western Romania.– International Journal of Speleology, 45/2, 123–133. doi: 10.5038/1827-806X.45.2.1947.
- ROSSI, M. & SANTI, G. (2005): First morphometric data about the metapodial bones of Ursus from Cerè Cave (Venetia Region, North Italy).– Cranium, 22/2, 13–25.
- ROSSI, M. & SANTI, G. (2007): Differentiation between Ursus deningeri Von Reichenau and Ursus spelaeus Rosenmüller based on mandibles from caves of the Veneto Region (Northern Italy). An overview.– Grzybowski Foundation Special Pubblication, 12, 73–78.
- ROSSI, M. & SANTI, G. (2011): Ursus deningeri-spelaeus group from Cerè Cave (Veneto, North Italy) in the new evolutionary frame of the cave bear. Part one: skulls and mandibles.– Annales Naturhistorische Museum Wien, Serie A, 113, 567–590.
- ROSSI, M. & SANTI, G. (2012): Morphometric and morphodynamic data on the mandibula and dental fossils of *Ursus spelaeus* Rosenmüller, 1794 from "Pale Rosse" cave (Passo Brocon, Trentino Alto Adige, Northern Italy).– Studi Trentini di Scienze Naturali, 92, 55–61.
- ROSSI, M. & SANTI, G. (2013): Studio morfometrico e morfodinamico di resti craniali, dentali e mandibolari di Ursus spelaeus dalla Grotta del Buco del Frate e dall'Altopiano di Cariadeghe (Brescia) nel quadro evolutivo degli orsi delle caverne.– Natura Bresciana, Annali del Museo Civico di Storia Naturale Brescia, 38, 33–43.
- ROSSI, M. & SANTI, G. (2015): Observations on the Ursus gr. spelaeus remains from the Pocala cave (Trieste, Friuli Venezia Giulia, N. Italy).– Revue de Paléobiologie Genève, 34/1, 77–84.
- ROSSI, M., ZORZIN, R. & SANTI, G. (2006): Morphometric observations about the Ursus fossils from Cerè cave (Venetia region, N. Italy).– Bulletin de la Société d'Histoire Naturelle de Toulouse et de Midi-Pyrenees, 141/1, 47–49.
- ROSSI, M., SANTI, G., ZORZIN, R., DÖPPES, D., FRIEDRICH, R., LINDAUER, S. & ROSENDAHL, W. (2018): The first directly dated cave bear from the Covoli di Velo cave (Verona Province, Veneto, Northern Italy) with some discussion of Italian cave bears.– Journal of Cave and Karst Studies, 80/3, 145–152. doi: 10.4311/2017PA0111.
- SANTI, G. & ROSSI, M. (2007): 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), Special Volume, 98, 179–186.
- SANTI, G. & ROSSI, M. (2008): Fossili craniali e mandibolari di Ursus da grotte del Veneto (Italia Settentrionale) nuove osservazioni sul quadro evolutivo degli orsi italiani.– Atti del Museo Civico di Storia Naturale di Trieste, suppl., 53, 3–12.
- SANTI, G. & ROSSI, M. (2014): Metapodial bones of Ursus gr. spelaeus from selected caves of the North Italy. A biometrical study and evolutionary trend.– Annales de Paléontologie, 100, 237–256. doi: 10.1016/j.annpal.2014.01.003.
- SANTI, G. & ROSSI, M. (2018): Evolutionary level of the cave bear from the Grotta del Bandito (Piedmont, N. Italy).– Slovenský Kras-Acta Carsologica Slovaca, 56/1, 5–14.
- SANTI, G., ROSSI, M. & FONTE, A. (2005): Morphometry of the limb bones of the Ursus spelaeus Rosenmüller-Heinroth, 1784 from Delle Streghe Cave (Sambughetto Valstrona, Piedmont–Northern Italy).– Revue de Paléobiologie Genève, 24/2, 597–616.
- SPÖTL, C., REIMER, P.J., RABEDER, G. & BRONK-RAMSEY, C. (2018): Radiocarbon constraints on the age of the world's highest-elevation cave-bear population, Conturines cave (Dolomites, Northern Italy).– Radiocarbon, 60, no 1, 299–307. doi: 10.1017/RDC.2017.60.
- TERLATO, G., ROMANDINI, M., NANNINI, N., PERESANI, M. & BOCHERENS, H. (2017): Cave bear (*Ursus spelaeus*) extinction in Northeastern Italy: anthropic impact, stable isotope evidence and extinction chronology.– Aragonit, 22/1, 26.
- TERLATO, G., BOCHERENS, H., ROMANDINI, M., NANNINI, N., HOBSO-NAND, K.A. & PERESANI, M. (2018): Chronological and Isotopic data support a revision for the timing of cave bear extinction in Mediterranean Europe.– Historical Biology, 1–11. Doi: 10.1080/08912963.2018.1448395.
- TSOUKALA, E. & GRANDAL D'ANGLADE, A. (1997): Système de mesures sur le squelette d'ursidae. Université Pierre Mendès France de Grenoble/Southern Methodist University – Symposium d'Auberives-en-Royans-Isère-France, 4-6 Novembre 1997, L'Ours et l'Homme, 265–287.
- TSOUKALA, E., CHATZOPOULOU, K., RABEDER, G., PAPPA, S., NAGEL, D. & WITHALM, G. (2006): Paleontological and stratigraphical research in Loutrá Aridéas bear cave (Almopia Speleopark, Pella, Macedonia, Greece).– Scientific Annals, School of Geology Aristotle University of Thessaloniki (AUTH), Special Volume, 98, 41–67.
- ZUNINO, M. & PAVIA, G. (2005): Il deposito a Ursus spelaeus della Grotta del Bandito (Roaschia, Cuneo, Italia): considerazioni stratigrafiche, tafonomiche e biocronologiche.– Rendiconti della Società Paleontologica Italiana, 2, 243–254.

**Geologia Croatica**