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A new Pleistocene cave bear site in the high mountains of the Spanish Pyrenees: La Brecha del Rincón (Huesca, Spain)



Un nouveau gisement Pléistocène d'ours des cavernes de haute montagne dans les Pyrénées espagnoles : La Brecha del Rincón (Huesca, Espagne)

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ABSTRACT

In the Pleistocene fossil record, bear remains are common, especially in karstic sites due to their hibernation behaviour. However, these fossils are rare in the Spanish Pyrenees, and even more in a high mountain environment. Now, a new karstic site called La Brecha del Rincón has recently been discovered in the Spanish Pyrenees at an altitude of 2160 m. In a preliminary fieldwork, 105 bear fossil remains have been recovered, mostly corresponding to autopodial bones. Dental remains with taxonomic value are not available, so metapodial bones have been used for our taxonomic study. These bones are short and thick, typical of cave bears, and their morphometric analysis supports their assignment to a species of *Ursus deningeri* group. This makes La Brecha del Rincón the highest cave bear site in the Iberian Peninsula.

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RÉSUMÉ

Dans le registre fossile du Pléistocène, les restes d'ours sont fréquents, surtout dans les gisements karstiques, en raison du comportement d'hibernation de ces animaux. Cependant, ces fossiles sont rares dans les Pyrénées espagnoles, et encore plus dans un environnement de haute montagne. À présent, un nouveau site karstique appelé La Brecha del Rincón a été récemment découvert dans les Pyrénées espagnoles, à 2160 m d'altitude. Dans une recherche préliminaire sur le terrain, 105 restes fossiles d'ours ont été retrouvés, la plupart correspondant à des os de l'autopode. Des restes dentaires à valeur taxonomique n'étant pas disponibles, des os métapodes ont été utilisés pour l'étude taxonomique. Ils sont courts et larges, typiques de l'ours des cavernes, et leur analyse morphométrique plaide en faveur de leur attribution à une espèce du groupe d'*Ursus deningeri*. De ce fait, La Brecha del Rincón est la caverne d'ours la plus élevée de la péninsule Ibérique.

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1. Introduction

At the moment, there are very few bear sites of Pleistocene-Holocene age located in the Spanish Pyrenees and only one in the high mountains, the cave bear site of Coro Tracito (Huesca) (Rabal-Garcés, 2013; Rabal-Garcés et al., 2012), a cave situated at 1580 m. Other sites located at lower height in the Pyrenean region are: Abauntz, (Navarra), Gabasa 1 (Huesca) and Erinya (Lleida) with *Ursus spelaeus* remains, Les Muricers (Lleida) and Olopte (Girona) with *U. arctos* remains and Amutxate (Navarra) with remains of both species (see references in Rabal-Garcés, 2013 and Villaluenga, 2009). These data are in contrast to the abundance of Pleistocene ursid sites in the French Pyrenees, especially localities with *U. spelaeus* (Fosse and Quiles, 2005; Fosse et al., 2001).

These two ursid species, *U. spelaeus* and *U. arctos*, are common in karstic sites of Late Pleistocene due to the use of caves as hibernacula, especially by *U. spelaeus* (Kurtén, 1958; Purroy, 2014; Torres Pérez-Hidalgo, 1988). Other ursid species also used caves during their winter dormancy, such as *Ursus deningeri*, which is the ancestor of *U. spelaeus*. *Ursus deningeri* habited the Iberian Peninsula during the Early and Middle Pleistocene with the most important site in Cueva Mayor, in the karst system of Atapuerca (Burgos) (García, 2003; Torres and Cervera, 1995; Torres Pérez-Hidalgo, 1988). However, this species is not so common in the fossil record of the Iberian Peninsula (Torres Pérez-Hidalgo, 1988). A subspecies of *U. spelaeus*, *U. s. parvilatipedis*, was defined in Troskaeta (Guipúzcoa) by Torres Pérez-Hidalgo et al. (1991). Other European taxa of the cave bear group are *U. ingressus*, *U. ladinicus*, *U. s. eremus* and *U. s. denigeroides*, some of which are related with alpine habitats (Rabeder and Hofreiter, 2004).

Cave bears represent an exclusively Eurasian lineage of 'spelaeoid' ursids (Baryshnikov, 2008; Kurtén, 1976; Rabeder et al., 2004, 2010) that appeared in the late Early Pleistocene (Madurell-Malapeira et al., 2009; Moullé, 1992) following their separation from the brown bear (arctoid) line (Kurtén, 1976; Rabeder et al., 2010; Torres Pérez-Hidalgo, 1992). There is no consensus about the moment of this divergence. A recent study establishes it at 2.8 My (Krause et al., 2008) and supports its conclusions with the age of fossil remains of brown bears and the common ancestor *U. etruscus*. However, Loreille et al. (2001) suggest a late divergence for the two lineages, around 1.2 My based on molecular data. Later, *U. deningeri* was replaced by Late Pleistocene cave bear taxa (Hofreiter et al., 2002, 2004; Knapp et al., 2009; Orlando et al., 2002; Rabeder and Hofreiter, 2004) toward the end of Middle Pleistocene (Rabeder et al., 2000 in Pacher and Stuart, 2009; Torres Pérez-Hidalgo, 1992). One of these taxa, *U. spelaeus*, persists until its extinction towards the final of the Late Pleistocene, with late accurate date ca. 24,000 ¹⁴C yr BP in Alps and adjacent areas (Pacher and Stuart, 2009) and 24,030 ± 100 ¹⁴C yr BP in Italy (Martini et al., 2014). It is generally accepted that both groups are chronospecies, that is to say, arbitrary divisions of a single evolutionary lineage defined on the basis of morphological change. For this reason, it is difficult to establish the difference between both groups since

the boundaries between them are fuzzy (Argant, 2001; Grandal-d'Anglade and López-González, 2004; Mazza and Rustioni, 1994).

In recent years, several studies have been published about metapodial cave bear biometry (Athen, 2007; Athen et al., 2005; Rabeder et al., 2010; Withalm, 2001a,b, 2004, 2005), checking their usefulness in taxonomic identification (Athen, 2007; Withalm, 2001a, 2011), as well as in the chronological age determination of a cave bear population (Withalm, 2001a). Münzel and Athen (2009) performed a metapodial biometry study by means of discriminant analysis to separated two cave bear species, *U. spelaeus* and *U. ingressus*, with no satisfactory results. However, this could be because of a mixture of specimens of both species was taken as reference material of only one species.

The aim of the present paper is to present a new fossil bear site in the Spanish Pyrenees, providing a taxonomic assignment based on morphometric analysis of the metapodials. This will contribute to extend the knowledge of the geographic distribution of the ursids during the Pleistocene.

2. La Brecha del Rincón site

The cave of La Brecha del Rincón is located in the Sierra de Secús, in the municipality of Valle de Hecho (Huesca, España) (Datum ED50; X=692325, Y=4741635) at an altitude of 2160 m (Fig. 1). Geologically, the cave is developed in limestones of the Upper Cretaceous (Coniacian-Santonian). In the Pyrenees, the Cretaceous and Paleogene limestones form a huge barrier known generically as the Inner Sierras, the Bisaurín being the highest peak (2670 m) around the cave.

In August 2013, speleologists of the Centro de Espeleología de Aragón (CEA) discovered fossil bones in the cave of La Brecha del Rincón during their speleological prospection of caves and karst systems in Sierra de Secús. Members of Aragosaurus group (University of Zaragoza) and Heritage section of the Government of Aragón were notified about this exceptional discovery. In September, members of the CEA, University of Zaragoza and Heritage Government of Aragón prospected the cave in order to observe the potential of the fossil site and collected at the surface bones in high risk of destruction.

The topography of the cave is under study and its total extent is unknown. The access to the cavity comprises of an entrance with an elongated subtriangular morphology, and is 1.20 m wide by 0.80 m high (Fig. 1c). Just behind this, there are two consecutive flatteners, the first 9 m long and the second 11 m long, with an average height of 0.40 m, although it is only 0.30 m at the narrowest section. Fig. 1d shows the topography that has been done so far, and the location of the bear fossil remains. Almost all the collected remains were located in an elongate gallery a few hundred meters from the cave entrance. Some remains are accumulated at the bottom of the gallery among blocks of about a decimetre or a meter. The other remains were found in the upper part of the gallery, on top of a sedimentary fill of reddish fine-grain sediment.

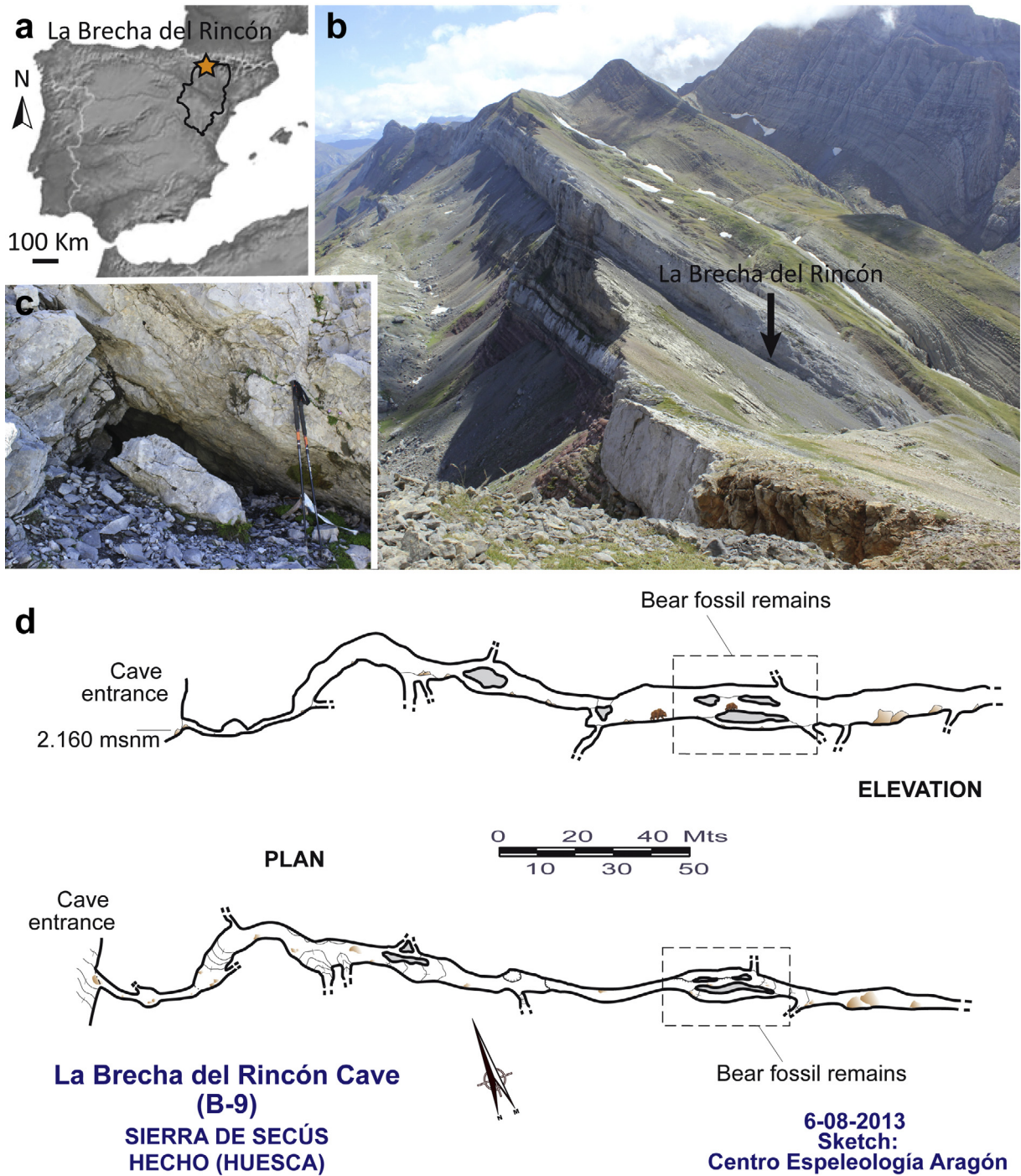


Fig. 1. (Color online.) Geographical situation of La Brecha del Rincón (a), showing a panoramic landscape (North is to the left) (b), and the cave entrance, 1.20 m wide by 0.80 m high (c). Topography of La Brecha del Rincón cave, still unfinished. The area where the fossil remains were found is shown. The topography was made by the Centro de Espeleología de Aragón (CEA) (d).

Fig. 1. (Couleur en ligne.) Situation géographique de La Brecha del Rincón (a), montrant un paysage panoramique (le nord est à gauche) (b); et l'entrée de la grotte, 1,20 m de large et 0,80 m de haut (c). Topographie de la grotte de La Brecha del Rincón, encore inachevée. La zone où les restes fossiles ont été trouvés est indiquée. La topographie a été effectuée par le Centro de Espeleología de Aragón (CEA) (d).

Table 1

List of skeletal elements recovered in La Brecha del Rincón, all belonging to bears.

Tableau 1

Liste des éléments du squelette retrouvé à La Brecha del Rincón, appartenant tous à des ours.

Skeletal element	Adult
Third lower incisor	2
Lower canine	2
Canine indet.	1
Ribs	19
Humerus	4
Ulna	3
Scapholunate	6
Pyramidal	2
Pisiform	2
Hamate	2
Capitate	1
Metacarpal I	3
Metacarpal II	3
Metacarpal III	2
Metacarpal IV	4
Metacarpal V	3
Sacrum	2
Femur	4
Fibula	2
Astragalus	2
Navicular	1
Metatarsal I	1
Metatarsal II	3
Metatarsal IV	3
Metatarsal V	3
Metapodial indet.	3
Phalanx 1	11
Phalanx 2	5
Phalanx 3	2
Patella	2
Baculum	2

At the moment, there are no radiometric datings of the fossil site, awaiting future excavations in the cave and to take samples for this purpose.

3. Materials and methods

The material recovered so far in La Brecha del Rincón site consists of 105 identified remains, all belonging to ursids (Table 1). Almost all of the remains belong to the postcranium. Most correspond to metapodials, carpals, tarsals and phalanges, and several fragments of limb bones, two sacral vertebrae, rib fragments, a patella and a baculum. Only five cranial remains have been recovered (three canines and two incisors). All the material is deposited in the Museum of Palaeontology of the University of Zaragoza (with reference codes from MPZ 2013/1201 to MPZ 2013/1305).

Because there are no dental remains with taxonomic value, metapodials have been used to compare the bears of La Brecha del Rincón to other ursids of the Iberian Peninsula and to make a taxonomic assignment. The work of Torres Pérez-Hidalgo (1988) has been followed for morphologic descriptions. For the metrical analysis we have taken eight metric variables following Withalm (2001a,b; Fig. 2): total length (tl), proximal width (pw), proximal depth (pd), smallest diaphyseal width (sdw), smallest diaphyseal depth (sdd), distal width (dw), distal epicondyleal width (dew) and distal depth (dd). Only specimens with fused epiphyses were included in the

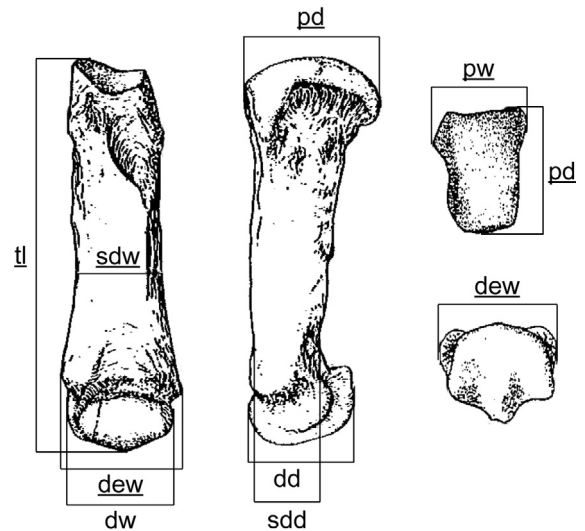


Fig. 2. Measurements taken on the metapodials of La Brecha del Rincón; the five ones for the morphometric comparison to other bear sites of the Iberian Peninsula are underlined.

Fig. 2. Mesures prises sur les métapodes de La Brecha del Rincón ; les cinq mesures utilisées pour la comparaison morphométrique avec d'autres gisements d'ours de la péninsule Ibérique sont soulignées.

Modified from Withalm, 2001b.

analysis. The measurements were taken with a digital caliper (Mitutoyo Digimatic Caliper CD-8" CX, Japan). Five metric variables have been chosen for comparative analysis because they reflect the general morphology of the bone and since many data from literature are available; these are: tl, pw, pd, sdw and dew (indicated on Fig. 2). Principal component analysis (PCA) have been performed for each complete metapodial recovered in La Brecha del Rincón, comparing them to other populations of the Iberian Peninsula ursids: *U. deningeri* from Cueva Mayor (Torres, pers. comm., 2014), *U. spelaeus* from Coro Tracito (Rabal-Garcés, 2013) and El Reguerillo (Torres pers. comm., 2014) and *U. arctos* from Illobi (Villaluenga, 2013), Los Rincones (Sauqué et al., 2014) and other sites of the Iberian Peninsula (Torres Pérez-Hidalgo, 1988). The software package PAST version 2.00 (Hammer et al., 2001) have been used for the PCA analysis.

4. Morphological and metrical analysis

Metapodials from La Brecha del Rincón (Fig. 3) are relatively short and thick, which are characteristics of the speloid lineage (*U. deningeri* and *U. spelaeus*); however, they are not as thick as those of *U. spelaeus*. Distal epiphysis from La Brecha del Rincón show similar values for distal width (dw) and distal depth (dd), like *U. deningeri* and *U. arctos*, but different from *U. spelaeus*, which shows a relatively large distal width (dw) with respect to the distal depth (dd).

Metacarpal I shows a strong shortening of the diaphysis and a certain curvature due to dorsal convexity and palmar concavity, typical of *U. deningeri* and *U. spelaeus*; in *U. arctos*, this element is longer and straighter. In the metacarpal II there is a subcircular protuberance situated below the proximal articulation on the dorsomedial edge,



Fig. 3. (Color online.) Metapodial bones of *Ursus cf. deningeri* from La Brecha del Rincón site. Right first metacarpal. Museum of Palaeontology of the University of Zaragoza (MPZ), Spain. MPZ 2013/1222: a: dorsal view; b: lateral view; c: right second metacarpal MPZ 2013/1232, dorsal view (the arrow indicates the well-defined circular protuberance); d: lateral view; e: right third metacarpal MPZ 2013/1218, dorsal view; f: medial view; g: right fourth metacarpal MPZ 2013/1217, dorsal view; h: medial view; i: right fifth metacarpal MPZ 2013/1236, dorsal view; j: medial view; k: right first metatarsal MPZ 2013/1229, dorsal view; l: lateral view; m: left second metatarsal MPZ 2013/1278, dorsal view; n: medial view; o: right fourth metatarsal MPZ 2013/1216, dorsal view; p: medial view; q: right fifth metatarsal MPZ 2013/1233, dorsal view; r: medial view.

Fig. 3. (Couleur en ligne.) Os métapodes d'*Ursus cf. deningeri* de La Brecha del Rincón. Premier métacarpien droit. Musée de paléontologie de l'université de Saragosse (MPZ), Espagne. MPZ 2013/1222 : a : vue dorsale ; b : vue latérale ; c : deuxième métacarpien droit MPZ 2013/1232, vue dorsale (la flèche indique la protubérance circulaire bien définie) ; d : vue latérale ; e : troisième métacarpien droit MPZ 2013/1218, vue dorsale ; f : vue médiale ; g : quatrième métacarpien droit MPZ 2013/1217, vue dorsale ; h : vue médiale ; i : cinquième métacarpien droit MPZ 2013/1236, vue dorsale ; j : vue médiale ; k : premier métatarsien droit MPZ 2013/1229, vue dorsale ; l : vue latérale ; m : deuxième métatarsien gauche MPZ 2013/1278, vue dorsale ; n : vue médiale ; o : quatrième métatarsien droit MPZ 2013/1216, vue dorsale ; p : vue médiale ; q : cinquième métatarsien droit MPZ 2013/1233, vue dorsale ; r : vue médiale.

well-defined in two specimens and smoother in another specimen. This protuberance is generally well-defined in *U. arctos*, being smoother in *U. deningeri* and *U. spelaeus*. The diaphysis section is slightly flattened at dorsopalmar direction, but not as pronounced as in *U. spelaeus*. Metatarsal I shows a strong shortening of the diaphysis, like in *U. deningeri* and *U. spelaeus*. The proximal articular surface is divided into two parts with an inflexion area in the middle: the anterior half is inclined forward and down and the posterior one almost horizontal. This is a very marked feature in *U. deningeri* and also in *U. spelaeus*. The proximal articular surface of the metatarsal IV presents a posterolateral obtuse angle, as in *U. spelaeus* and *U. deningeri*, being almost straight in *U. arctos*. The diaphysis is flattened in anteroposterior direction, showing a sub-ellipsoidal section with a flat anterior face and a blunt edge on the posterior face, typical features of *U. spelaeus* and *U. deningeri*, unlike *U. arctos*, of which the diaphysis shows a circular section.

Biometric data taken on the metapodials of La Brecha del Rincón are shown in Table 2. Five of these variables have

been taken for the comparative analysis to other sites of the Iberian Peninsula. The PCA of the analyzed metapodials reflects the variability among the three species (*U. spelaeus*, *U. deningeri* and *U. arctos*), including the 95% confidence ellipses. In all cases, the data of La Brecha del Rincón fall inside the variability of *U. deningeri*. Three different situations can be observed:

Mc I, Mc V, Mt I and Mt V (Fig. 4): data of La Brecha del Rincón fall inside the overlapping area of the convex hulls of *U. spelaeus* and *U. deningeri*, but outside of the convex hull of *U. arctos* and even outside of its 95% confidence ellipse in most cases.

Mc II, Mc III and Mt II (Fig. 5): data of La Brecha del Rincón fall inside the convex hull of *U. deningeri* (except for one of the two Mt II data), but also inside of the 95% confidence ellipses of *U. spelaeus* and *U. arctos*.

Mc IV (Fig. 6): data of La Brecha del Rincón fall inside the convex hull of *U. deningeri* (or almost) and outside of the 95% confidence ellipses of *U. spelaeus* and *U. arctos*.

The variability explained by each component (PC1 and PC2) and the loadings for each measurement are shown

Table 2

Biometric data taken on the metapodials of La Brecha del Rincón.

Tableau 2

Données biométriques prises sur le métapodes de La Brecha del Rincón.

Element	MPZ label	Side	tl	pw	pd	sdw	sdd	dew	dw	dd
Mc I	MPZ 2013/1222	dex.	56.82	23.31	19.8	11.53	8.9	17.09	15.73	15.74
Mc I	MPZ 2013/1224	sin.	54.6	21.96	19.35	10.64	9.09	16.43	15.6	15.33
Mc I	MPZ 2013/1227	dex.	55.43	21.17	19.44	10.85	9.99	16.79	15.65	15.34
Mc II	MPZ 2013/1232	dex.	69.1	16.12	24.44	13.9	10.51	21.01	18.05	18.26
Mc II	MPZ 2013/1234	sin.	68.75	16.05	24.08	12.3	9.89	20.48	19.42	17.46
Mc II	MPZ 2013/1220	dex.	72.9	17.34	26.77	13.88	12.41	23.1	20.34	20
Mc III	MPZ 2013/1218	dex.	73.66	15.43	25.5	13.44	10.94	22.6	18.85	19.76
Mc III	MPZ 2013/1235	sin.	71.86	16.78	25.56	13.22	10.52	–	–	19.09
Mc IV	MPZ 2013/1217	dex.	79	19.98	26.82	14.4	12.02	22.68	21.25	21.2
Mc IV	MPZ 2013/1219	sin.	75.13	16.07	26.42	13.2	11.75	21.96	20.18	19.51
Mc IV	MPZ 2013/1231	sin.	–	17.1	28.16	12.86	–	–	–	–
Mc V	MPZ 2013/1277	dex.	78.42	24.36	30.17	13.34	12.38	22.86	22.58	–
Mc V	MPZ 2013/1236	dex.	75.84	23.81	28.2	14.53	11.79	23.09	22.01	17.9
Mc V	MPZ 2013/1237	dex.	77.1	26.9	29.3	14.5	10.69	24.85	23.8	20.15
Mt I	MPZ 2013/1229	dex.	49.24	21.27	22.55	9.67	8.3	15.8	15.4	13.59
Mt II	MPZ 2013/1278	sin.	63	12.46	22.74	11.77	9.48	18.36	16.19	14.86
Mt II	MPZ 2013/1209	dex.	67.76	12.51	24.21	12.64	10.2	20.28	–	–
Mt IV	MPZ 2013/1279	sin.	–	19.78	25.61	13.79	–	–	–	–
Mt IV	MPZ 2013/1216	dex.	–	17.22	26.94	12.66	–	–	–	–
Mt IV	MPZ 2013/1212	sin.	–	–	–	11.36	11.28	18.79	17.05	–
MT V	MPZ 2013/1233	dex.	79.09	24.74	26.95	11.59	11.65	21.49	21.43	16.45

MPZ: Museum of Palaeontology of the University of Zaragoza; tl: total length; pw: proximal width; pd: proximal depth; sdw: smallest diaphyseal width; sdd: smallest diaphyseal depth; dw: distal width; dew: distal epicondyleal width; dd: distal depth. The five metric variables used in comparative study are: tl, pw, pd, sdw and dew.

in Table 3. PC1 accounts for most of the variance within every PCA and it is strongly influenced by the total length measurement, i.e. the length of the metapodial, with positive correlation. In the case of PC2, it is mainly influenced

by the length of the metapodial too, but in negative correlation. However, the loading of the pw (proximal width) measurement is larger in the PC2 of some metapodials (Mc I, Mt I and Mt V).

Table 3

Variability explained by each component (PC1 and PC2) and the loadings of the principal component analysis (PCA) of metapodials from La Brecha del Rincón and other comparison sites.

Tableau 3

Variabilité expliquée par chaque composante (PC1 et PC2) et charges de l'analyse en composantes principales (ACP) de métapodes de La Brecha del Rincón et d'autres gisements pour comparaison.

	PC	Eigenvalue	% variance	Loadings				
				tl	pw	pd	sdw	dew
Mc I	1	40.1129	72.513	0.8886	0.2773	0.2544	0.1382	0.2228
	2	12.475	22.551	–0.4512	0.5704	0.3692	0.3952	0.4226
Mc II	1	36.4697	56.74	0.7493	0.2511	0.3984	0.274	0.3765
	2	23.1945	36.086	–0.6582	0.2699	0.3855	0.3976	0.4327
Mc III	1	59.2116	77.37	0.8006	0.2446	0.3586	0.2444	0.333
	2	14.1841	18.534	–0.5976	0.3209	0.4356	0.3838	0.4503
Mc IV	1	67.7846	75.34	0.7433	0.3172	0.3859	0.2788	0.3467
	2	19.5987	21.783	–0.6664	0.2802	0.4466	0.3048	0.4302
Mc V	1	68.3406	70.109	0.7758	0.3824	0.3296	0.2499	0.2844
	2	21.8891	22.455	–0.6266	0.4014	0.3912	0.309	0.4447
Mt I	1	50.1085	76.79	0.9569	0.1823	0.1464	0.06606	0.1593
	2	10.6902	16.382	–0.2834	0.5535	0.5377	0.3937	0.4114
Mt II	1	41.1484	70.616	0.7229	0.2693	0.405	0.2937	0.3932
	2	13.894	23.844	–0.6898	0.3273	0.392	0.3153	0.4049
Mt V	1	78.4941	73.443	0.8393	0.3895	0.3036	0.1168	0.1952
	2	18.9396	17.721	–0.5429	0.6213	0.4311	0.2146	0.2955

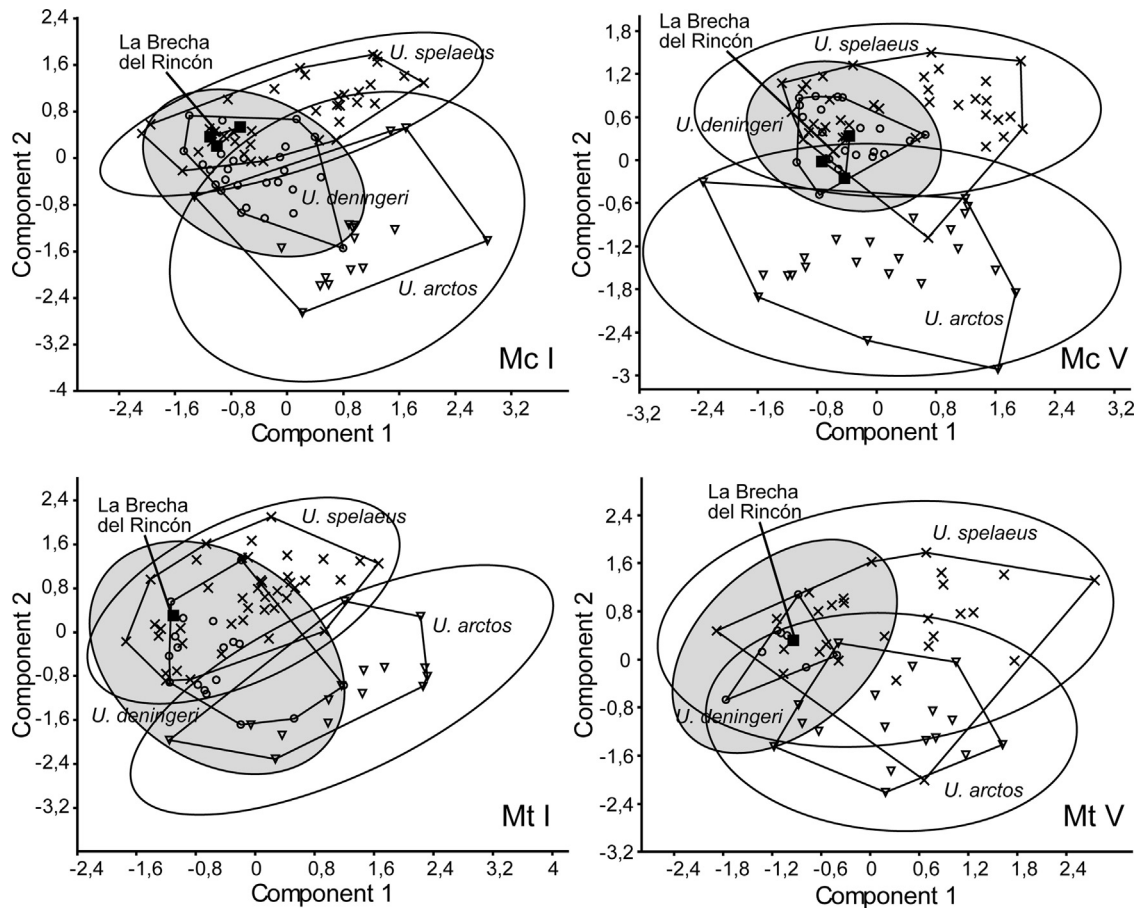


Fig. 4. Principal component analysis (PCA) of metapodials Mc I, Mc V, Mt I and Mt V showing plots of components 1 against 2. Measurements of Cueva Mayor (*Ursus deningeri*) and El Reguerillo (*U. spelaeus*) taken from Torres pers. com., 2014, Coro Tracito (*U. spelaeus*) taken from Rabal-Garcés, 2013, Illobi (*U. arctos*) taken from Villaluenga, 2013, Los Rincones (*U. arctos*) taken from Sauqué et al., 2014 and several sites of *U. arctos* of Iberian Peninsula taken from Torres Pérez-Hidalgo, 1988. Legend of symbols: *U. spelaeus* (cross); *U. deningeri* (circle); *U. arctos* (triangle) and La Brecha del Rincón (square). Ninety-five percent confidence ellipses are shown for each species, for *U. deningeri* grey.

Fig. 4. Analyse en composantes principales (ACP) des métapodes Mc I, Mc V, Mt I et V Mt montrant les points représentatifs des composantes 1 en fonction de ceux des composantes 2. Mesures de la Cueva Mayor (*Ursus deningeri*) et El Reguerillo (*U. spelaeus*) d'après Torres, com. perso., 2014, Coro Tracito (*U. spelaeus*) d'après Rabal-Garcés, 2013, Illobi (*Ursus arctos*), d'après Villaluenga, 2013, Los Rincones (*U. arctos*) d'après Sauqué et al., 2014 et de plusieurs gisements d'*U. arctos* de la péninsule Ibérique, d'après Torres Pérez-Hidalgo, 1988. Légende des symboles : *U. spelaeus* (croix) ; *U. deningeri* (cercle) ; *U. arctos* (triangle) et La Brecha del Rincón (carré). Des ellipses de confiance à 95% sont affichées pour chaque espèce, en gris pour *U. deningeri*.

5. Discussion

Morphological features of bear metapodials of La Brecha del Rincón reveal similarities to the species *U. deningeri*. They are shorter than *U. arctos* metapodials, but not as plump as those of *U. spelaeus*. Moreover, they show the typical dorsopalmar and dorsoplantar flattening of the speloid forms. The well-defined circular protuberance of Mc II, found in specimens from La Brecha del Rincón, is very marked in *U. arctos*, but is also found in spelaeoid forms, especially in *U. deningeri*.

Morphometric comparisons of metapodials from La Brecha del Rincón to Pleistocene bear taxa from Spain show their inclusion to the variability of the species *U. deningeri*. In some isolated cases, data are included inside the convex hull of *U. spelaeus* and inside the 95% confidence ellipse of *U. arctos*. Nevertheless, data of La Brecha del Rincón correspond to variability of *U. deningeri*, always falling inside the

convex hulls of this species, except in one case, where it is only within the 95% confidence ellipse (although very close to the convex hull). The Mc IV is the only element analyzed that is outside of the variability of *U. spelaeus*. Comparing their measurement data of *U. deningeri* from Hundsheim (Withalm, 2001a) we can see that the Mc IV from La Brecha del Rincón is very similar in total length (tl) and a bit smaller in epiphyses width (pw and dew) than the Mc IV from Hundsheim.

Therefore, remains found in La Brecha del Rincón site can be preliminary assigned to *Ursus* cf. *deningeri*, giving a Middle Pleistocene age. However, we hope future excavation campaigns provide us with cranial remains or isolated teeth that permit us to make a more precise characterization of this bear population. On the one hand, it is known that often the separation between *U. deningeri* and *U. spelaeus* (cave bear lineage) is difficult to establish (Grandal-d'Anglade and López-González,

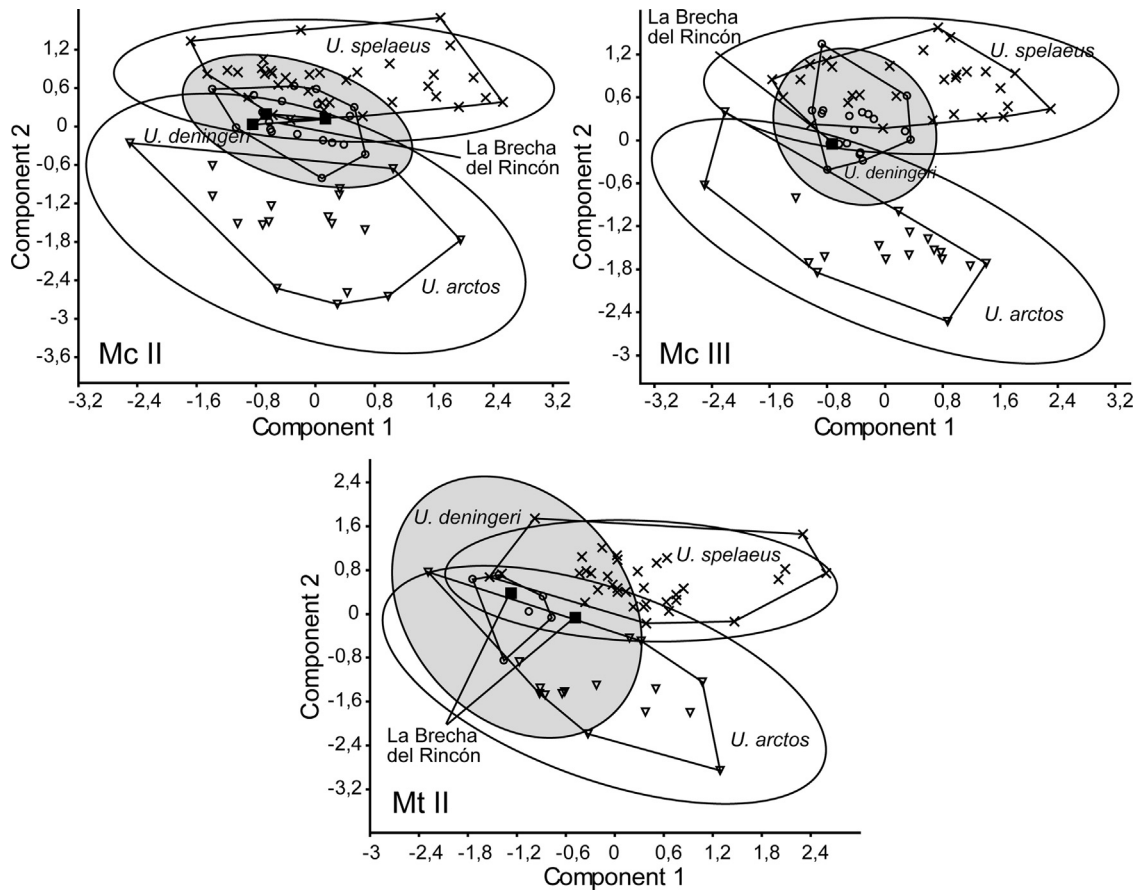


Fig. 5. Principal component analysis (PCA) of metapodials Mc II, Mc III and Mt II showing plots of components 1 against 2. Measurements of Cueva Mayor (*Ursus deningeri*) and El Reguerillo (*U. spelaeus*) taken from Torres pers. com., 2014, Coro Tracito (*U. spelaeus*) taken from Rabal-Garcés, 2013, Illobi (*U. arctos*) taken from Villaluenga, 2013, Los Rincones (*U. arctos*) taken from Sauqué et al., 2014 and several sites of *U. arctos* of Iberian Peninsula taken from Torres Pérez-Hidalgo, 1988. Legend of symbols: *U. spelaeus* (cross); *U. deningeri* (circle); *U. arctos* (triangle) and La Brecha del Rincón (square). Ninety-five percent confidence ellipses are shown for each species, for *U. deningeri* grey.

Fig. 5. Analyse en composantes principales (ACP) des métapodes Mc II, Mc III et Mt II, montrant les points représentatifs des composantes 1 en fonction de ceux des composantes 2. Mesures de la Cueva Mayor (*Ursus deningeri*) et El Reguerillo (*U. spelaeus*) d'après Torres, comm. pers., 2014, Coro Tracito (*U. spelaeus*), d'après Rabal-Garcés, 2013, Illobi (*U. arctos*), d'après Villaluenga, 2013, Los Rincones (*U. arctos*), d'après Sauqué et al., 2014 et de plusieurs gisements d'*U. arctos* de la péninsule Ibérique d'après Torres Pérez-Hidalgo, 1988. Légende des symboles : *U. spelaeus* (croix) ; *U. deningeri* (cercle) ; *U. arctos* (triangle) et La Brecha del Rincón (carré). Des ellipses de confiance à 95 % sont affichées pour chaque espèce, en gris pour *U. deningeri*.

2004). The morphological difference between *U. deningeri* and *U. spelaeus* is defined by the variation of some continuous features, like the progressive reinforcement and doming of the skull and the jaw, or discrete ones, like the loss of the three anterior upper and lower premolars (Grandal-d'Anglade and López-González, 2004). In fact, there are different authors that point out the existence of the intermediate forms between both species, like in Petralona, Greece (Rabeder and Tsoukala, 1990) or Azé I-3, France (Argant, 1991, 2009). Sometimes, e.g., in Azé I-3, this intermediate form receives a subspecific name, *U. spelaeus deningeroides*, proposed by Mottl for the Repolusthöhle population in Austria (Mottl, 1964). According to Withalm (2001b) bears from Repolusthöhle are really small and it is clear that they belong to the species *U. deningeri*. However, Withalm (2001b) recommends using the old terminus "deningeroides" from Mottl (1964) to separate this form from the other deninger bears on the subspecies level, calling

them *U. spelaeus* "deningeroides". Metapodial bones from La Brecha del Rincón are, in general, longer than those from Repolusthöhle, but they are more similar in terms of the widths of the epiphyses (comparison data from Withalm, 2001a). On the other hand, it is interesting to test the possibility that the remains from La Brecha del Rincón could show similarities with alpine cave bears: *U. ladinicus* and *U. s. eremus*, which inhabited the Alps during the Middle Würm (Rabeder et al., 2004, 2008). Metapodials from La Brecha del Rincón have a smaller size and they are less plump than those of alpine bears *U. ladinicus* and *U. s. eremus*, (Rabeder et al., 2004; Withalm, 2001a) and more similar to those of *U. deningeri* from Hundsheim and Repolusthöhle (Withalm, 2001a). Finally, another cave bear taxon defined in Spain is *U. spelaeus parvilatipedis* (Torres Pérez-Hidalgo et al., 1991). The principal diagnostic characters are short and quite plump metapodials, not so different from those of *U. deningeri* and shorter than *U. spelaeus*.

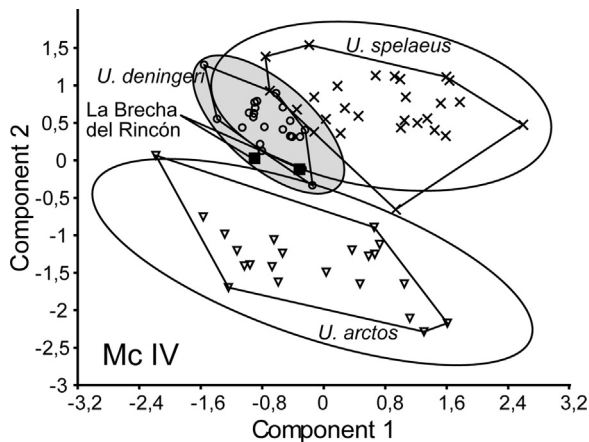


Fig. 6. Principal component analysis (PCA) of metapodial Mt IV showing plot of components 1 against 2. Measurements of Cueva Mayor (*Ursus deningeri*) and El Reguerillo (*U. spelaeus*) taken from Torres pers. com., 2014, Coro Tracito (*U. spelaeus*) taken from Rabal-Garcés, 2013, Illobi (*U. arctos*) taken from Villaluenga, 2013, Los Rincones (*U. arctos*) taken from Sauqué et al., 2014 and several sites of *U. arctos* of Iberian Peninsula taken from Torres Pérez-Hidalgo, 1988. Legend of symbols: *U. spelaeus* (cross); *U. deningeri* (circle); *U. arctos* (triangle) and La Brecha del Rincón (square). Ninety-five percent confidence ellipses are shown for each species, for *U. deningeri* grey.

Fig. 6. Analyse en composantes principales (ACP) du métapode Mt IV montrant les points représentatifs des composantes 1 en fonction de ceux des composantes 2. Mesures de la Cueva Mayor (*Ursus deningeri*) et El Reguerillo (*U. spelaeus*), d'après Torres com. perso., 2014, Coro Tracito (*U. spelaeus*), d'après Rabal-Garcés, 2013, Illobi (*U. arctos*), d'après Villaluenga, 2013, Los Rincones (*U. arctos*), d'après Sauqué et al., 2014 et de plusieurs gisements d'*U. arctos* de la péninsule Ibérique, d'après Torres Pérez-Hidalgo, 1988. Légende des symboles : *U. spelaeus* (croix); *U. deningeri* (cercle); *U. arctos* (triangle) et La Brecha del Rincón (carré). Des ellipses de confiance à 95 % sont affichées pour chaque espèce, en gris pour *U. deningeri*.

Metapodials from La Brecha del Rincón are shorter or of similar length, but comparatively much thinner than metapodials of *U. s. parvitatipedis*.

The location of La Brecha del Rincón is noteworthy due to its very high altitude (2160 m). There are some examples of high mountain sites of cave bears in the Alps, but only a few surpass La Brecha del Rincón in altitude, such as Conturines in Italy (2750 m), Drachenloch in Switzerland (2445 m), Schreiberwandhöhle in Austria (2250 m) or Sulzflunhöhlen also in Austria (2350 m) and Schneiberhöhle in Germany (2270 m) (Döppes et al., 2011; Fosse et al., 2001). However, none of these are *U. deningeri* sites. In the Iberian Peninsula, the highest cave bear site known until now was Coro Tracito, situated in the Pyrenees at 1580 m, followed by Liñares, in Galicia, at 1150 m, both sites containing *U. spelaeus* remains. In the case of *U. arctos*, dens of current populations have been found at an altitude of 2100 m in the Cantabrian Mountains, and grizzly bears in Yellowstone Park can establish their dens up to 2926 m altitude (Purroy, 2014). Therefore, La Brecha del Rincón is one of the highest cave bear sites in Europe and the highest in the Iberian Peninsula. This discovery is very important because of its paleoclimatic implications. As we can see in the work of Döppes et al. (2011), a great number of cave bear sites found in the High Alps are chronologically included in the Marine Isotope Stage 3 (MIS3), between

65 and 35 ka, a warm period. The authors said that only warmer climatic conditions could have facilitated habitat conditions necessary to sustain a viable bear population in the High Alps during this period, which was probably even warmer than today. This is based on, among other things, the fact that it would be impossible for bears to satisfy their nutritional needs by predominantly feeding on hard, grassy high-alpine vegetation. Therefore, bears that inhabited the area surrounding La Brecha del Rincón in the Pyrenees Mountains must have done so in a warm period that would enable a source of food needed for their survival. Possible future radiometric datings of the site will give more accurate data to provide a chronological context to these paleoclimatic and paleoecologic inferences.

A first taphonomic assessment of the site and its formation based on the small size of the remains and their good selection, suggests that these could have been transported from a higher zone and/or they have been brought to the gallery through a small conduct or drain. On the other hand, the small dimension of the cave entrance and the difficult access to the galleries containing bones, which is done through two flatteners only 0.30–0.40 m size, suggest that bears did not use this cave entrance, at least with the actual topography of the cave. The possibility of large bones have been stolen by illegal collectors is highly unlikely. La Brecha del Rincón cave was only known by another speleological group that discovered it in the 1990s and it is impossible that people without speleological equipment could gain access to the zone of the bone accumulation.

6. Conclusion

The discovery of La Brecha del Rincón site provides new data about geographic and altitudinal distribution of Pleistocene cave bears.

Based on morphologic and morphometric analysis of the metapodials, the fossil remains have been assigned to *Ursus cf. deningeri*, awaiting the recovery of new material (especially cranial remains), which permits a more precise characterization of this bear population.

If this hypothesis is confirmed, La Brecha del Rincón would be the first site of *U. deningeri* located in the Spanish Pyrenees and the highest cave bear site in the Iberian Peninsula, standing at 2160 m altitude.

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