

## A STUDY OF THE EVOLUTION OF THE PLEISTOCENE CAVE BEAR BY A MORPHOMETRIC ANALYSIS OF THE LOWER CARNASSIAL

**Aurora GRANDAL-D'ANGLADE & Fernando LÓPEZ-GONZÁLEZ**

Instituto Universitario de Xeoloxía. Universidade da Coruña  
Campus da Zapateira s/n. E-15071 A CORUÑA. SPAIN  
E-mail xeauroa@udc.es

**Abstract :** In this contribution a morphometric study of the lower carnassial of the Cave Bear (*Ursus deningeri* and *Ursus spelaeus*) from several populations of diverse European localities and also different ages is carried out. This study includes a morphological analysis of the deployment of dental cusps and metric comparisons focused on general size and convergence of the cusps.

The morphologic study (by cluster analysis) presents a grouping trend of the populations according to their geographic position first, then to the chronology. This indicates that the expansion of the cave bear happened at a very early time, and that later did not exist great migratory movements that returned to put in contact remote populations. As for the metric analysis, differences in the degree of convergence of the cusps in the talonid and trigonid are only observed between the oldest sites (more convergent, smaller occlusal surface) and the modern ones (less convergent, larger occlusal surface) independently of their geographic location.

*Key words:* cave bear, lower carnassial, morphometry, evolution, Pleistocene, Europe

**Résumé :** Dans cette contribution une étude morphométrique de la première molaire inférieure de l'ours des cavernes (*Ursus deningeri* et *Ursus spelaeus*) de plusieurs populations de diverses localités européennes et d'âges différents, est effectuée. Cette étude inclut une analyse morphologique du déploiement des cuspidés dentaires et des comparaisons métriques centrées sur la taille générale et la convergence des cuspidés. Le résultat de l'étude morphologique (effectué par analyse de clade) présente une tendance groupant des populations selon leur position géographique d'abord, et selon leur chronologie ensuite. Ceci indique que l'expansion de l'ours des cavernes s'est produite très tôt, et que plus tard n'ont pas existé de grands mouvements migrants mettant en contact des populations éloignées. D'après l'analyse métrique, on observe seulement des différences du degré de convergence des cuspidés du talonide et du trigonide entre les sites les plus anciens (plus convergents, plus petite surface masticatrice) et les récents (moins convergents, plus grande surface masticatrice), indépendamment de leur emplacement géographique.

*Mots clés :* Ours des cavernes, étude morphométrique, première molaire inférieure, évolution, Pléistocène, Europe

## INTRODUCTION

The phylogenetic origin of the cave bear is at the moment under study. If traditionally it was considered arisen from *Ursus etruscus* CUVIER 1823 in the Upper Pliocene (Erdbrink, 1953; Thenius, 1959; Kurtén, 1968; Ficcarelli, 1979; Torres Pérez-Hidalgo, 1992), some authors attribute a more delayed origin, from the European lineage of brown bear (*Ursus arctos* LINNEUS 1758), at the end of the Lower Pleistocene (Mazza & Rustioni, 1994). Nevertheless, the recent studies based on DNA sequencing seem to demonstrate that the appearance of this species could have happened before the divergence between both lineages, European and Asian, of brown bear, that happened 850 Ky BP ago, (Hänni *et al.*, 1994), that is to say, approximately 1,2 million years ago (Loreille *et al.*, 2001).

The cave bear lineage is formed by two species, *U. deningeri* VON REICHENAU 1906 and *U. spelaeus* ROSENMÜLLER 1794, anteceded by a more primitive form, usually named *Ursus savini* ANDREWS 1922 (Kurtén, 1968), that sometimes is considered as a variety or subspecies of *U. deningeri* (Kurtén, 1969a; Bishop, 1982; Mazza & Rustioni, 1994). These three species are chronospecies. Unlike biological species, chronospecies are arbitrary divisions of a single evolutionary lineage, defined on the basis of morphological change. According to Simpson (1961) the morphologic differences between species should be at least as large as those between living species of the same taxonomic group.

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.

However, the variability of size and morphology is a constant in *U. deningeri* and *U. spelaeus*, even into the same population. This intraspecific variability is increased due to sex dimorphism or the existence of dwarf forms, like in high alpine populations. Moreover, some sites from the middle Pleistocene show intermediate forms between both species (Altuna, 1972; Rabeder & Tsoukala, 1990; Argant, 1991; Auguste, 1992). In occasions, these intermediate forms receive subspecific names, such as *Ursus*

*spelaeus deningeroides* MOTTI 1947 from Repolust, Austria (Mottl, 1947) and Azé, France (Argant, 1991; 2001).

The discrete features could be more conclusive. But the study of the jaws of the Savini's bear from Bacton reveals the lack of the first, second and third premolar as a general feature. And concerning *U. deningeri*, even some skulls and jaws from Mosbach's (the type- locality) present a long diastema with no anterior premolars. These ones are seldom present and, when present, the percent varies from one population to another (for a review, see Bishop, 1982).

Concerning the dentition, it was extensively described in the literature (see Kurtén, 1976 for a review) that the evolutionary trend in these species favors the appearance of cheek teeth with cusps more and more blunt and splitted into smaller ones, and progressively broader occlusal surfaces, produced by the smaller convergence of cusps, which is related to the herbivore type of feeding of this species.

This tendency was quantitatively studied under different approaches by some authors (Rabeder, 1983; 1999; Torres Pérez-Hidalgo, 1988a; Argant, 1995), although it is not well known if this process took place at the same rate in all the populations, or whether there are geographic or chronological differences.

In this work we try to such a study of this process in different European populations, separated in the time and/or the space, based on the lower carnassial (first lower molar), being the dental piece that, according to our previous work, better characterizes each population (Grandal d'Anglade, 1993a; 1993b).

## THE CAVE BEAR DENTITION

The cave bear displays a particular dental morphology with broad crushing surfaces, and muscular insertions in the skull and the jaw that reflect a great chewing power, reason why a basically herbivore diet is attributed to him (Kurtén, 1968; 1976). In the last years several approaches to the reconstruction of the diet of this species by means of the stable isotope analysis have been made, (generally <sup>13</sup>C and <sup>15</sup>N), preferably in bone collagen and dentine collagen and hydroxylapatite (Bocherens *et al.*, 1994; Bocherens *et al.*, 1997, Fernández Mosquera, 1998; Nelson *et*

al., 1998; Lidén & Angerbjörn, 1999; Vila Taboada *et al.*, 1999; Fernández Mosquera *et al.*, 2001).

According to the results of these studies, the cave bear was an herbivore feeding basically on C3 plants. The cheek teeth presents blunt and unfolded cusps, and broad occlusal surfaces, often covered by tubercles and small cusplets that increase the chewing surface in damage of the sharp function that the teeth of other carnivores have, or its predecessor *Ursavus* (fig 1).

the delay in the loss of the carnivorous characteristics, in comparison with the rest of cheek teeth. It could be assumed, then, that in the cave bear lineage the lower carnassial, more markedly than the other cheek teeth, underwent a process of reduction of the carnivorous character, that leads to an increase of the occlusal surface due to a widening of the tooth, and to the diminution of the convergence between the labial and lingual cusps, as well as a progressive deployment or splitting of these cusps (fig 2).

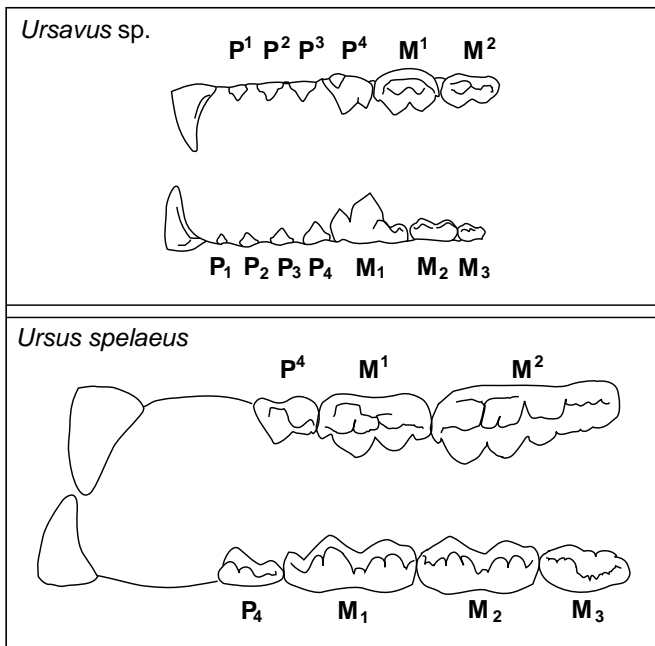


Figure 1. Schematic dental rows (right, lingual view) of *Ursavus* sp. (from the specimens MB.Ma.29323, MB.Ma.29321-1 and MB.Ma.29321-2 in the Museum für Naturkunde, Berlin) and *Ursus spelaeus* (from the specimen LXL-E-T-2708, in the Laboratorio Xeolóxico de Laxe, A Coruña)

Figure 1. Lignes dentaires schématiques (droite, vue linguale) de *Ursavus* sp. (spécimens MB.Ma.29323, MB.Ma.29321-1 et MB.Ma.29321-2 du Museum für Naturkunde, Berlin) et de *Ursus spelaeus* (spécimen LXL-E-T-2708, du Laboratorio Xeolóxico de Laxe, A Coruña).

Previous studies on the evolution in the cave bear lineage (Torres Pérez-Hidalgo, 1988a; Argant, 1995) focused on the morphology of the lower carnassial as a good criteria to distinguish between the species that form this lineage, and also to distinguish between *Ursus deningeri* and *Ursus spelaeus*, or to establish the evolutionary level reached by a given cave bear population. This is due to the very constant morphology that are observed in this piece, and to

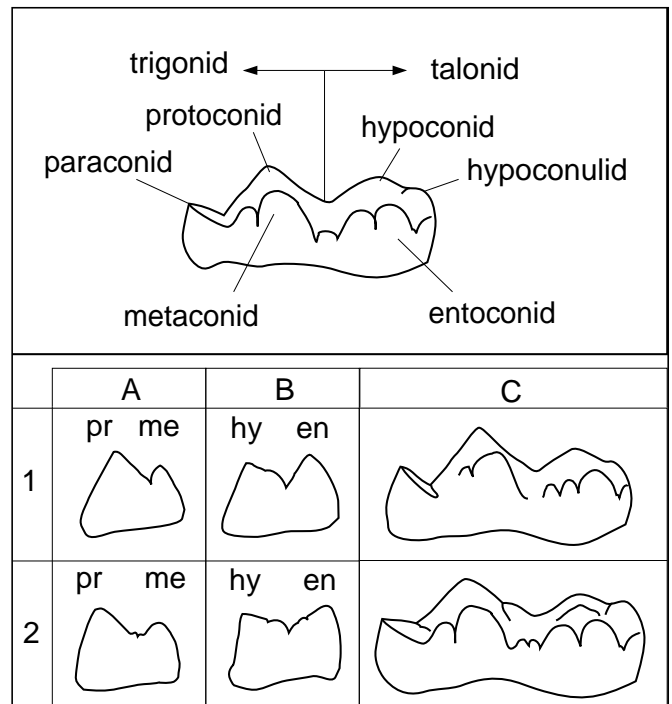


Figure 2.- a, Morphological sketch of the cave bear lower carnassial and denomination of the cusps (Lingual view, anterior part to the left); and b, Hypothetic section of the trigonid (A) and the talonid (B), and theoretical splitting of the cusps (C) in the lower carnassial of an "old" cave bear (1) and a "modern" one (2)

Figure 2.- a, Schéma morphologique de la première molaire inférieure d'ours des cavernes et de la dénomination des cuspides (vue linguale, partie antérieure vers la gauche). b, Section hypothétique du trigonide (A) et du talonide (B), et déploiement théorique des cuspides (C) dans la première molaire inférieure d'un ours des cavernes type "ancien" (1) et de type "moderne" (2)

## MATERIAL

The material used for this morphometric study consists of **316** first lower molars (lower carnassials) of cave bears from different sites (Fig. 3). The studied collections are enumerated in Table I, together with the number of pieces studied in each one of them and their chronology when known, most relevant references and the institutions where the collections are kept.

In addition, two populations of the Iberian Peninsula have been included, whose data (both morphological and metrical) come from the bibliography: Reguerillo (Madrid), 90 to 60 ka BP (Reinhard *et al.*, 1996) and Cueva Mayor of Atapuerca (Burgos), 320 ka BP (Bischoff *et al.*, 1997).

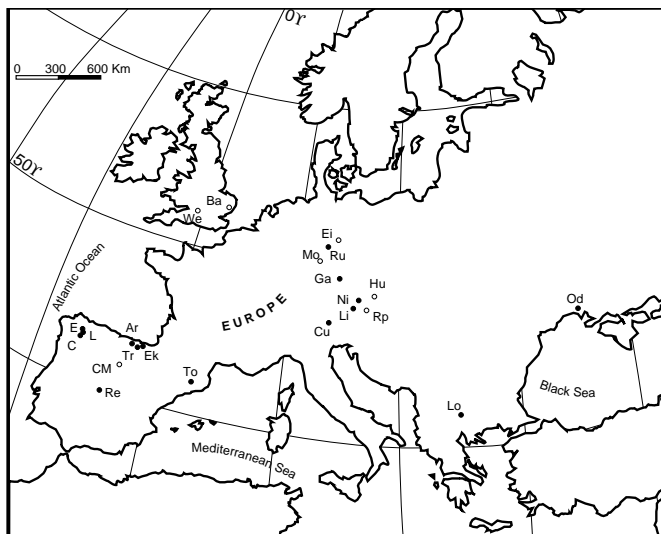


Figure 3.- Map of situation of the studied sites. White points represent “old” populations, black points, the “modern” ones.

Figure 3.- Carte de situation des sites étudiés. Les points blancs représentent les populations “anciennes”, les points noirs, les “modernes”:

IBERIAN PENINSULA: E, Eirós; C, A Ceza; L, Liñares; Ar, Arrikutz; Tr, Troskaeta; Ek, Ekain; To, Toll; Re, Reguerillo; CM, Atapuerca (Cueva Mayor). BRITISH ISLANDS: Ba, Bacton; We, Westbury. CENTRAL EUROPE: Ei, Einhornhöhle (Scharzfeld); Ru, Rubeland; Ga, Gailenreuther (Zoolithenhöhle); Hu, Hundsheim; Ni, Nixloch; Li, Lieglloch; Cu, Cunturines. EAST: Lo, Loutraki (Greece); Od, Odessa (Ukrania).

## MORPHOLOGICAL ANALYSIS

For the study of the morphological variability of the lower carnassial, certain morphotypes for each cusps have been predetermined, based on Torres Pérez-Hidalgo (1988b), Torres Pérez-Hidalgo *et al.* (1991) and Grandal d’Anglade (1993c). These morphotypes reflect a progressive deployment of the cusps (Fig. 4). However, we avoided to assign a polarity to these morphotypes, because of the lack of data concerning the sequence of their appearance in time, if any. The percentage of appearance of the morphotypes in each one of the studied populations was calculated. On the obtained data matrix (Table II) a cluster analysis (UPGMA, similarity index is Euclidean distance) was performed (Fig.5).

First of all, the data obtained allow us to reject a clear polarity in the proposed morphotypes. Otherwise, the dendrogram should present a grouping trend according to the age of the populations. In turn, in the obtained dendrogram the grouping of the populations is clearly related to their geographic situation. Two main groups are clearly emphasized: one formed by the populations of the Iberian Peninsula and a second one composed by the Central European populations, including those ones from the East (Loutraki and Odessa), and the British populations. Finally, two ancient populations from Central Europe lay apart from the others: Mosbach and Repolust, of Middle Pleistocene age.

In the table II the main differences between both geographic groups can be observed with detail.

The Iberian populations display very low percentages of acute paraconids (morphotype 1), whilst in the central European sites the incidence of this feature is higher, more markedly in the older ones (except Bacton).

In the case of the protoconid, there is a remarkable difference between the Iberian groups, in which there are high percents of protoconids with smooth posterior edge (morph. 4) that is almost absent in the Central European sites, independently of the age.

The metaconid is a cusp that can present a high variability, even locally. In the Iberian populations the metaconid vary from single with one cusplet (morph. 8), double (morph. 9), double with several cusplets (morph. 11) or triple (morph. 12), whilst the Central European sites the metaconids are less splitted,

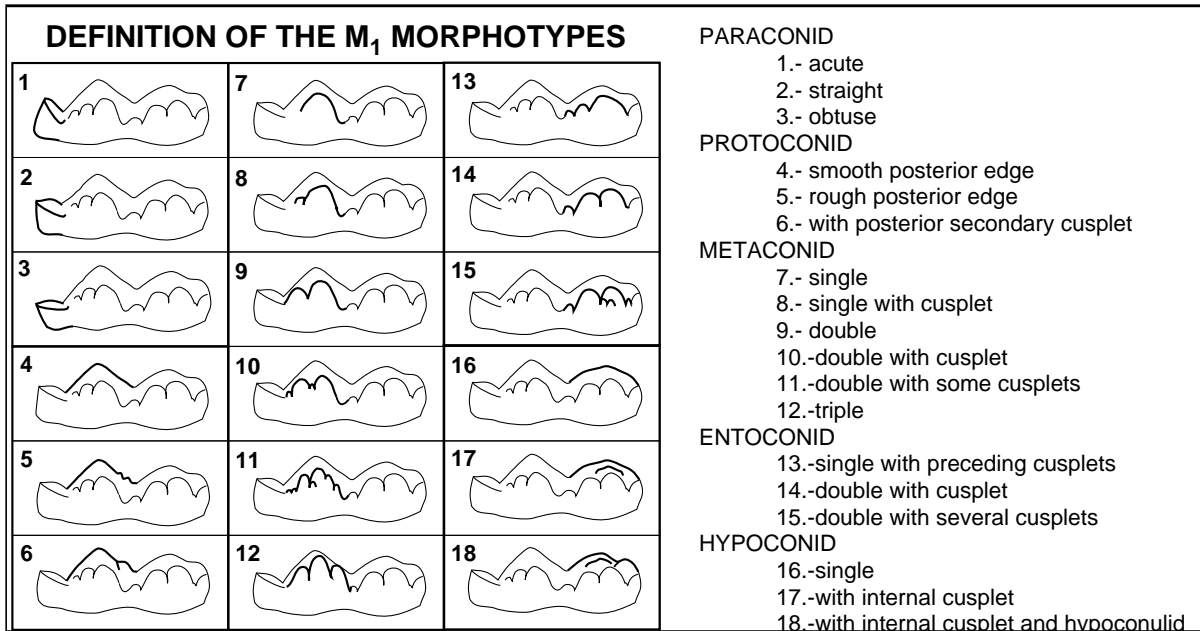


Figure 4.- Definition of the morphotypes of the Lower Carnassial.  
 Figure 4. - Définition des morphotypes de la première molaire inférieure.

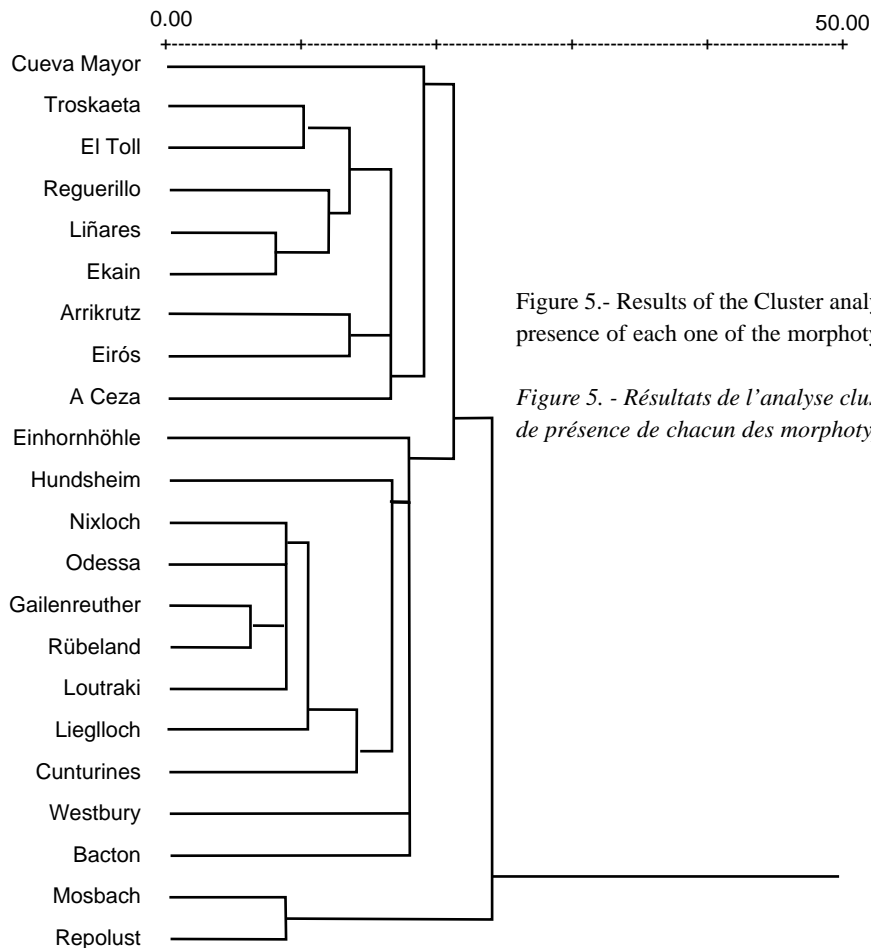


Figure 5.- Results of the Cluster analysis based on the percentage of presence of each one of the morphotypes.

Figure 5. - Résultats de l'analyse cluster basée sur les pourcentages de présence de chacun des morphotypes.

with a predominance of morphotypes 9 (double) and 10 (double with one cusplet) for the Upper Pleistocene sites and even more simple ones for the Middle Pleistocene populations.

Concerning the entoconid, the Iberian populations present high percentages of morphotype 15 (double with several cusplets), whilst the Central European sites from Upper Pleistocene show less splitted entoconids (morph. 14, double with one cusplet, is predominant). The morphotype 13 (single cusp preceded by two cusplets descending in size), considered as a typical feature of *Ursus deningeri* (Schütt, 1968; Bishop, 1982; Torres Pérez-Hidalgo, 1988a; Argant, 1991;1995), is present in high percents in the ancient populations, basically in Mosbach, Repolust, Bacton and Westbury, although in the dendrogram its importance seems to be masked by the other morphological features.

Finally, the hypoconid shows a quite homogeneous trend. The morphotype 18 (with inner cusp and hypoconulid) is the most abundant in all the sites. Only some of the old populations from Central Europe and isolated cases in the other group show a minor incidence of hypoconids reinforced by an inner cusp but lacking hypoconulid (morph. 17).

The sites from the East (Loutraki and Odessa) are similar in all the features to those from the Upper Pleistocene of Central Europe, as is reflected in the cladogram. The British ones, in spite of the differences found between them, are also grouped together into the Central European group. Finally, the separation between all the sites considered and the bears from Repolust and Mosbach seems to be caused by the exclusive presence in the later of single metaconids with preceding cusplets (morph. 13), the typical “deningeri” morphology that however is not predominant in other Middle Pleistocene populations.

### METRIC ANALYSIS

For the metric study, some measurements related to the size of the teeth and the convergence of the cusps were taken (fig 6): 1, total length (TL); 2, trigonid length (TrdL); 3, trigonid breadth (TrdB); 4, talonid breadth (TadB); 5, distance protoconid-paraconid (Pr-Pa); 6, distance protoconid-metaconid (Pr-Me); and 7, distance hypoconid-entoconid (Hy-En).

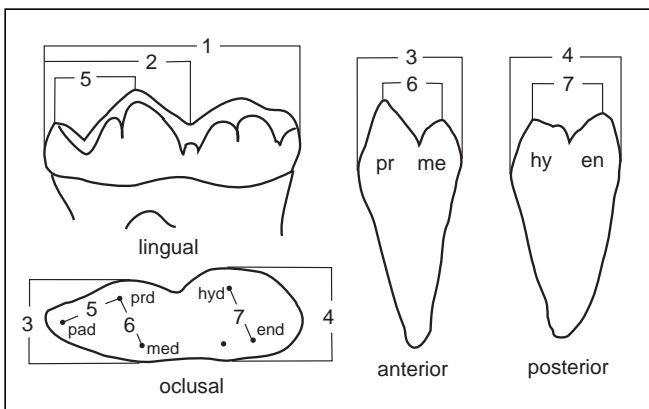


Figure 6.- Measurements of the Lower carnassial for the metric study.

Figure 6. - Mesures de la première molaire inférieure pour l'étude métrique.

Besides these measurements, three index of convergence were calculated, for the paraconid (PadCI), the trigonid cusps (TrdCI) and the talonid ones (TadCI):

$$\text{PadCI} = \frac{\text{Pr-PA} * 100}{\text{TrDL}}$$

$$\text{TrdCI} = \frac{\text{Pr-Me} * 100}{\text{TrdB}}$$

$$\text{TadCI} = \frac{\text{Hy-En} * 100}{\text{TadB}}$$

With this we try to compare the degree of convergence of the cusps with the purpose of observing whether the old populations display greater convergence than the modern ones, as it is to hope. Metric data are presented in Table III, and a selection of them in Figure 7.

Figure 7a shows the maximum measurements of the lower carnassial: average of total length plotted against the average of the maximum breadth (that of the talonid) from each site. Concerning the absolute length, the range is from 25.5 to 31.7 mm. Taking into account the age, the range of the Middle Pleistocene sites is from 25.5 to 29.2 mm; whilst Upper Pleistocene populations present a range of

29.8 to 31.7 mm, except two ones that reach to smaller sizes. One is Troskaeta, where the small subspecies *U. spelaeus parvilatipedis* TORRES 1991 was described (Torres Pérez-Hidalgo *et al.*, 1991), with no radiometric age. The second is Cunturines, a high alpine dwarf form recently considered, because of some morphologic and metric features, as a tardive subspecies of *Ursus deningeri* (Rabeder & Nagel, 2001).

As for the talonid breadth, the range varies from 12.3 to 15.2 mm. The Middle Pleistocene bears range from 12.3 to 14.2 mm. Repolust presents a very broad talonid in comparison with the other Middle Pleistocene populations. Modern populations range from 14.0 to 15.2 mm. Again, Troskaeta and Cunturines reach the smallest talonid breadths.

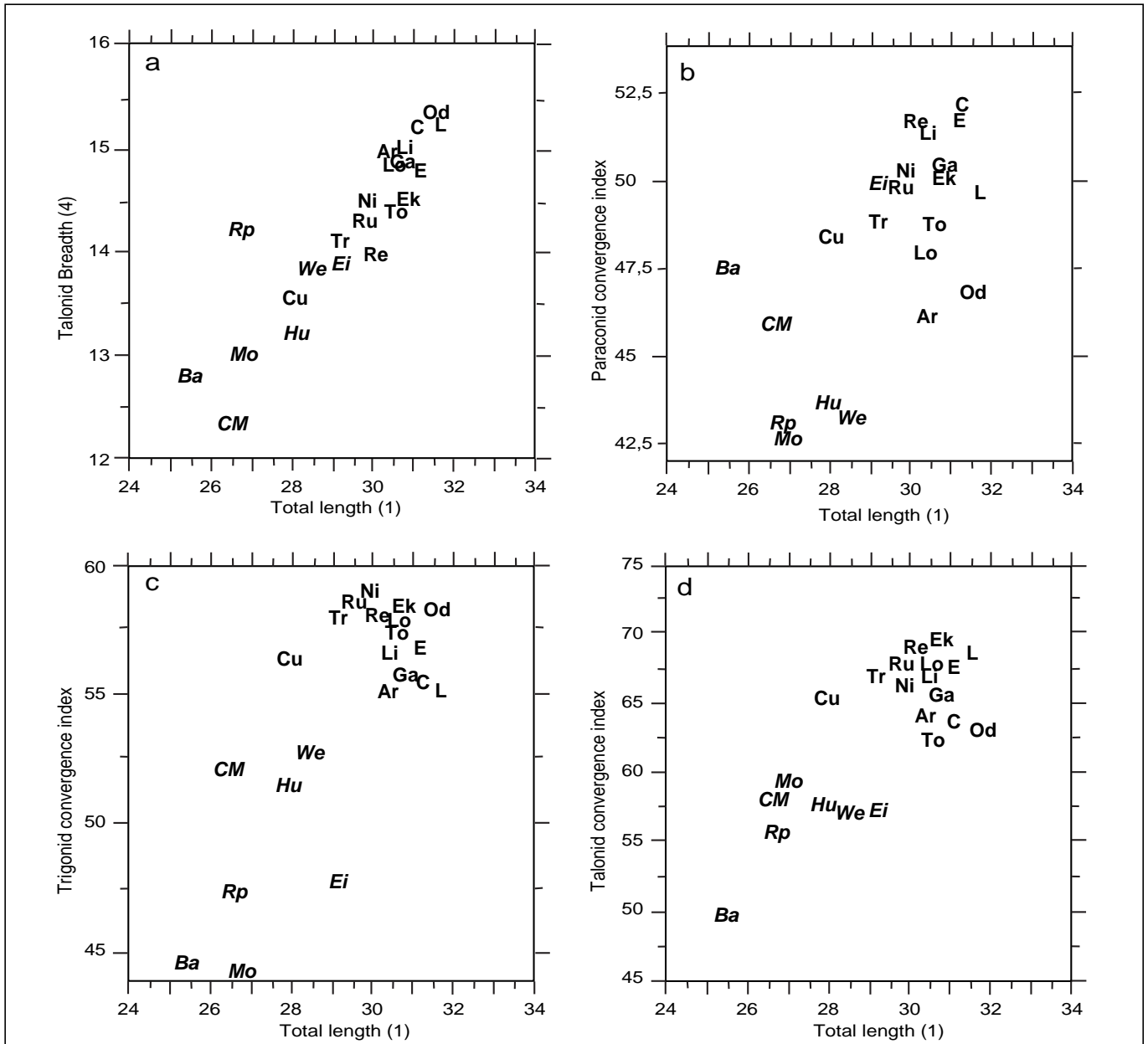


Figure 7.- Total length of the carnassial plotted against the Talonid breadth (a) and Convergence Index of the Paraconid (b), Trigonid (c) and Talonid (d).

Figure 7.- Longueur totale de la première molaire inférieure par rapport à la contre largeur du talonide (a) et indice de convergence du paraconide (b), du trigonide (c) et du talonide (d).

The average values of the absolute length of the carnassial are plotted against the averages of Paraconid Convergence Index (7b), Trigonid convergence Index (7c) and Talonid Convergence Index (7d) of each site.

It can be observed clearly that, in general, the convergence of the cusps is more marked in the oldest populations than in the recent ones. This phenomenon, however, is not parallel in the three index considered.

As for the convergence of the paraconid (Fig. 7b), several levels of convergence can be distinguished: maximum, with most of the Middle Pleistocene populations; medium, with Bacton, Atapuerca, and two recent ones (Arrikruz and Odessa); and a minimum degree of convergence in the rest of the Upper Pleistocene populations. The grouping in this last level, however, is loose. Surprisingly, the oldest population, Bacton, does not present highly convergent paraconids. It seems that the higher or lower degree of convergence of this cusp is not well defined, and could reflect the variability in their morphology.

The Figure 7c shows the distribution of the populations according to the convergence of the trigonid cusps. Here the pattern is more logical, with three levels: the oldest populations show very convergent cusps; a central group is formed by some other Middle Pleistocene sites, and finally the modern populations share a low degree of convergence.

The same pattern is clearly seen in the Figure 7d, concerning the convergence of the talonid cusps. The three levels are well separated; decreasing in degree of convergence, Bacton is first, then all Middle Pleistocene populations and finally the group of the modern ones.

## DISCUSSION

The morphologic analysis suggests that, after a wide diffusion of the species across Europe at early time, the populations were isolated, by diverse geographic barriers or simply the distance. The fact that the oldest populations are grouped next to more recent ones from the same geographical area, that is to say, next in the space but not in the time, reflects the fact that the expansion of the cave bear happened

at a very early time, and that later did not exist great migratory movements that returned to put in contact remote populations. This fact caused probably a parallel evolution and the consequent appearance of geographic types more or less defined.

The increasing size of the lower carnassial along the cave bear lineage is clear. However, the metric differences observed along the lineage don't show any discontinuity except the above mentioned of Repolust. With our data, we cannot give a good explanation for this phenomenon, that probably has a parallelism in other cheek teeth and should be investigated with more detail.

Taking into account the definition of chronospecies only clear morphological differences between two groups from a single lineage are concluding to establish different species. The stratigraphic position of the bone remains gives not enough evidence to make a separation.

Our results allow us to reject a well defined separation of both species. All the Middle Pleistocene populations here considered (including those subspecies described such as *U. spelaeus* var. *hercynica* from Einhornhöhle (Rode, 1935), *U. deningeri savini* from Bacton (Kurtén, 1969a), *U. deningeri hundsheimensis* (Zapfe, 1946), *Ursus deningeri* n. ssp. from Cunturines (Rabeder & Nagel, 2001) show a higher affinity to their geographically closer modern relatives than among them. Also, the grouping does not reflect the differences observed in some Upper Pleistocene sites by several authors that named different subspecies such as *U. spelaeus parvilatipedis* from Troskaeta (Torres Pérez-Hidalgo *et al.*, 1991), or *U. spelaeus odessanus* from Odessa (Von Nordmann, 1858). Thus, the morphological differences between the lower carnassial of both species are not well defined.

Concerning the convergence of the cusps, it is possible to affirm that the Middle Pleistocene populations present more convergent cusps than the Upper Pleistocene ones (with the exception of the paraconid). The Convergence indexes here considered could be good indicators of the degree of evolution attained by a population. However we do not think they could be used to differentiate both species, since the sample is scarce and much more populations of intermediate age should be included in order to see if the difference is well defined or not.



## CONCLUSIONS

The Cave Bear had a wide geographic distribution, not specially conditioned by the biotope. Although basically herbivore, it could withstand seasonal cold with no need to make great migratory movements thanks to its capacity to enter in dormancy.

It is a polymorphic and polytypic species, which is increased by the abundance of findings in the European karstic systems. According to our results, the lower carnassial of the cave bear has undergone an increase in the size and the occlusal surface throughout the Pleistocene. Nevertheless, noticeable differences of chronological origin are not observed in their morphology, but their geographic realm has more importance to establish the similarities and differences between sites. The passage of more primitive forms (*U. deningeri*) to the more modern (*U. spelaeus*) took place gradually and independently in different areas, and therefore it cannot be established chronologically for all Europe in a generalized way.

According to the morphology of the lower carnassial it is not possible, in our opinion, to affirm that *U. deningeri* and *U. spelaeus* are different species. This is not a new idea; in fact, it is found in many papers concerning the phylogeny of cave bears, such as Ehrenberg (1928), Erdbrink (1953), Kurtén (1976) and Mazza & Rustioni (1994). In our opinion, only more detailed studies on other cheek teeth and postcranial skeleton are necessary to establish a reliable difference between both species, in case they exist.

## ACKNOWLEDGEMENTS

The authors would like to thank: Juan Ramón Vidal Romani (A Coruña), Jesús Altuna & Koro Mariezkurrena (San Sebastián), Julio Gómez Alba & Jaume Gallemí (Barcelona), Gernot Rabeder (Wien), Andy Currant (London), Mikael Fortelius (Helsinki), Evangelia Tsoukala (Thessaloniki) and Karl-Heinz Fischer (Berlin) for the facilities given for the study of the collections used in this paper, and more specially to E. Tsoukala for the unpublished metric data from Loutraki. We also thank T. Torres Pérez-Hidalgo and A. Argant for their constructive review of an earlier version of the manuscript. This paper is a contribution to the Research Project XUGA PGIDT 00 PXI16201PR.

## REFERENCES

- ALTUNA, J. 1972. Fauna de mamíferos de los yacimientos prehistóricos de Guipúzcoa. *Munibe*, **24**: 1-461.
- ARGANT, A. 1991. Carnivores quaternaires de Bourgogne. *Documents des Laboratoires de Géologie Lyon*, **115**: 1-301.
- ARGANT, A. 1995. Un essai de biochronologie à partir de l'évolution dentaire de l'ours des cavernes. Datation du site de La Balme à Collomb (Entremont-le-Vieux, Savoie, France). *Quaternaire*, **6**: 139-149.
- ARGANT, A. 2001. Cave Bear ancestors. *Cadernos do Laboratorio Xeolóxico de Laxe*, **26**: 341-348.
- AUGUSTE, P. 1992. Etude archéozoologique des grands mammifères du site Pleistocène Moyen de Biache-Saint-Vaast (Pas-de-Calais, France): apports biostratigraphiques et paléoenvironnementaux. *L'Antropologie*, **9**: 49-70.
- BISCHOFF, J. L.; FITZPATRICK, J.; FALGUÈRES, C.; BAHAIN, J. & BULLEN, T. 1997. Geology and preliminary dating of the Sima de los Huesos chamber, Cueva Mayor de Atapuerca, Burgos. *Journal of Human Evolution*, **33**: 129-154.
- BISHOP, M.J. 1982. The mammal fauna of the Early Middle Pleistocene cavern infill site of Westbury-Sub-Mendip, Somerset. *Special Papers in Palaeontology*, **28**: 1-108.
- BOCHERENS, H.; BILLIOU, D.; PATOU-MATHIS, M.; BONJEAN, D.; OTTE, M. & MARIOTTI, A. 1997. Paleobiological implications of the isotopic signatures (13C, 15N) of fossil mammal collagen in Scladina Cave (Sclayn, Belgium). *Quaternary Research*, **48**: 370-380.
- BOCHERENS, H., FIZET, M. & MARIOTTI, A. 1994. Diet, physiology and ecology of fossil mammals as inferred from stable carbon and nitrogen isotope biogeochemistry: implications for Pleistocene bears. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **107**: 213-225.
- DONNER, J.J. & KURTÉN, B. 1958. The floral and faunal succession of "Cueva del Toll", Spain. *Eiszeitalter und Gegenwart*, **9**: 72-81.
- EHRENBERG, K. 1928. *Ursus deningeri* und *Ursus spelaeus*. *Akademie der Wissenschaft in Wien. Akademik Anzeiger*, **10**: 1-4.
- ERDBRINK D.P. 1953. *A review of fossil and recent bears of the Old World with remarks on their phylogeny based upon their dentition*. Amsterdam: Jan de Lange Ed. 597 pp.
- FERNÁNDEZ MOSQUERA, D. 1998. Isotopic biogeochemistry (d13C, d15N) of cave bear, *Ursus spelaeus*, from Cova Eirós site, Lugo. *Cadernos do Laboratorio Xeolóxico de Laxe*, **23**: 237-249.
- FERNANDEZ MOSQUERA, D.; VILA TABOADA, M. & GRANDAL d'ANGLADE, A. 2001. Stable isotopes data (delta C13, delta N15) from the cave bear (*Ursus spelaeus*): a new approach to its palaeoenvironment and dormancy. *Proceedings of the Royal Society of London B*, **268** (1472): 1159-1164.
- FICCARELLI, G. 1979. Osservazione sull'evoluzione del genere *Ursus*. *Bulletino della Società Paleontologica Italiana*, **18** (2): 166-172.
- GRANDAL D'ANGLADE, A. 1993a. *El Oso de las Cavernas en Galicia: el yacimiento de Cova Eirós*. Nova Terra, 8. A Coruña: Laboratorio Xeolóxico de Laxe. 246 pp.

- GRANDAL D'ANGLADE A. 1993b. Sexual dimorphism and inter-population variability in the lower carnassial of the cave bear, *Ursus spelaeus* Ros.-Hein. *Cadernos do Laboratorio Xeolóxico de Laxe*, **18**: 231-239.
- GRANDAL D'ANGLADE, A. 1993c. Estudio morfológico de los molariformes de Oso de las Cavernas (*Ursus spelaeus* ROSENMÜLLER-HEINROTH) de varias poblaciones europeas. *Cadernos do Laboratorio Xeolóxico de Laxe*, **18**: 241-256.
- GRANDAL D'ANGLADE, A. & VIDAL ROMANÍ, J.R. 1997. A populational study on the cave bear (*Ursus spelaeus* ROS.-HEIN.) from Cova Eirós (Triacastela, Galicia, Spain). *Geobios*, **30** (5): 723-731.
- GRANDAL D'ANGLADE A. & LÓPEZ GONZÁLEZ, F. 1998. A population study on the Cave Bears (*Ursus spelaeus* Rosenmüller-Heinroth) from Galician caves, NW of Iberian Peninsula. *Cadernos do Laboratorio Xeolóxico de Laxe*, **23**: 215-224.
- HÄNNI, C.; LAUDET, V.; STÉHELIN, D. & TABERLET, P. 1994. Tracking the origins of the cave bear (*Ursus spelaeus*) by mitochondrial DNA sequencing. *Proceedings of the National Academy of Sciences USA*, **91**: 12336-12340.
- KURTEN, B. 1968. *Pleistocene Mammals of Europe*. London: Weindenfeld & Nicholson. 317 pp.
- KURTÉN B. 1969a. Die Carnivoren- Reste aus den Kiesen von Süßenborn bei Weimar. *Paläontologische Abhandlungen A (Paläozoologie)*, **III** (3/4): 735-756.
- KURTÉN B. 1969b. A radiocarbon date for the cave bear remains (*Ursus spelaeus*) from Odessa. *Commentationes Biologicae*, **31** (6): 1-3.
- KURTÉN, B. 1976. *The Cave Bear Story. Life and Death of a Vanished Animal*. New York: Columbia University Press. 163 pp.
- LIDÉN, K. & ANGERBJÖRN, A. 1999. Dietary change and stable isotopes: a model of growth and dormancy in cave bears. *Proceedings of the Royal Society of London B*, **266**: 1779-1783.
- LOREILLE, O.; ORLANDO, L.; PATOU-MATHIS, M.; PHILIPPE, M.; TABERLET, M. & HÄNNI, C. 2001. Ancient DNA analysis reveals divergence of the cave bear, *Ursus spelaeus*, and brown bear, *Ursus arctos*, lineages. *Current Biology*, **11** (3): 200-203.
- MAZZA, P. & RUSTIONI, M. 1994. On the phylogeny of Eurasian bears. *Palaeontographica Abteilung A*, **230** (1-3): 1-38.
- MOTTL, M. 1947. Die Repolsthöhle, eine Protoaurignacienstation bei Peggau in der Steiermark. *Verhandlungen der geologischen Bundesanstalt*, **1947**: 200-205.
- NELSON, D.E., ANGERBJÖRN, A., Lidén, K. & TURK, I. 1998. Stable isotopes and the metabolism of the european cave bear. *Oecologia*, **116**: 177-181.
- RABEDER, G. 1983. Neues vom Höhlenbären: zur Morphogenetik der Backenzähne. *Die Höhle*, **2** (34): 67-85.
- RABEDER, G. 1997. Ursiden-Chronologie der österreichischen Höhlenfaunen. *Geologische Blatt NO-Bayern*, **47** (1-4): 225-238.
- RABEDER, G. 1999. Die Evolution des Höhlenbärengebisses. *Mitteilungen der Kommission für Quartärforschung der Österreichischen Akademie der Wissenschaften*, **11**: 1-102.
- RABEDER, G. & TSOUKALA, E. 1990. Morphodynamic analysis of some cave bear teeth from Petralona cave (Chalkidiki, North Greece). *Beiträge zur Paläontologie von Österreich*, **16**: 103-109.
- RABEDER G. & NAGEL, D. 2001. Phylogenetic problems of the Alpine Cave-Bears. *Cadernos do Laboratorio Xeolóxico de Laxe*, **26**: 359-364.
- REINHARD, E., TORRES, T. & O'NEIL, J. 1996. 18O/16O ratios of cave bear tooth enamel: a record of climate variability during the Pleistocene. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **126**: 45-59.
- RODE, K. 1935. Untersuchungen über das Gebiss der Bären. *Monographie Geologie Paläontologie*, **7**: 1-162.
- SIMPSON, G.G. 1961. *Principles of Animal Taxonomy*. New York: Columbia University Press. 247 pp.
- SCHÜTT, G. 1968. Die cromerzeitlichen Bären aus der Einhornhöhle bei Scharzfeld. *Mitteilungen aus dem Geologischen Institut der Technischen Hochschule Hannover*, Heft 7: 1-121.
- THENIUS, E. 1959. Ursidenphylogese und Biostratigraphie. *Zeitschrift für Saugetierkunde*, **24**: 78-84.
- TORRES PÉREZ-HIDALGO, T. 1984. El oso de las cavernas (*Ursus spelaeus* Ros.) de los niveles X e IX de Ekain. Pp. 297-316. In: J. ALTUNA y J. M. MERINO (eds.), *El yacimiento prehistórico de la cueva de Ekain (Deba, Guipuzcoa)* San Sebastián. Sociedad de Estudios Vascos.
- TORRES PÉREZ-HIDALGO, T. 1988a. Evolución de la carnívora inferior en los géneros *Ursavus* y *Ursus* (Carnívora, Mammalia). *Paleontología y Evolución*, **22**: 41-50.
- TORRES PÉREZ-HIDALGO, T. 1988b. *Osos (Mammalia, Carnívora, Ursidae) del Pleistoceno de la Península Ibérica*. Madrid. Publicaciones Especiales del Boletín Geológico y Minero. 316 pp.
- TORRES PÉREZ-HIDALGO, T. 1992. The european descendents of *Ursus etruscus* CUVIER (Mammalia, Carnívora, Ursidae). *Boletín Geológico y Minero*, **99** (6): 886-940.
- TORRES PÉREZ-HIDALGO, T., COBO RAYÁN, R. & SALAZAR RINCÓN, A. 1991. La población de oso de las cavernas (*Ursus spelaeus parvilatipedis* n. ssp.) de Troskaeta'ko koba (Ataún, Guipúzcoa). *Munibe*, **43**: 3-85.
- VILA TABOADA, M., FERNÁNDEZ MOSQUERA, D., LÓPEZ GONZÁLEZ, F., GRANDAL D'ANGLADE, A. & VIDAL ROMANÍ, J.R. 1999. Paleoecological implications inferred from stable isotopic signatures (d13C, d15N) in bone collagen of *Ursus spelaeus* ROS.-HEIN. *Cadernos do Laboratorio Xeolóxico de Laxe*, **24**: 73-87.
- VON NORDMANN, A. 1858. Palaeontologie Suedrusslands, I. *Ursus spelaeus (Odessanus)*. *Finnischen Societät der Wissenschaften*, **XII**:1-110.
- WEINSTOCK, J. 2001. Age structure and sex ratio of Cave Bears in the Zoolithenhöhle, Southern Germany. *Cadernos do Laboratorio Xeolóxico de Laxe*, **26**: 289-299.
- ZAPFE, H. 1946. Die Altpleistozänen Bären von Hundsheim in Niederösterreich. *Jahrbuch der geologischen Bundesanstalt*, **3/4**: 95-164.

SITE	Age	Reference	n	deposited in
<b>IBERIAN PENINSULA</b>				
Eirós	24 Ky BP	Grandal & Vidal 1997	35	Laboratorio Xeolóxico de Laxe-Spain
A Ceza	35 Ky BP	Grandal & López 1998	11	
Liñares	35 Ky BP	Grandal & López 1998	10	
Troskaeta	Upper Pleistocene	Torres et al. 1991	9	Sociedad de Ciencias Aranzadi-Spain
Ekain	Upper Pleistocene	Torres 1984	23	
El Toll	Upper Pleistocene	Donner & Kurtén 1958	8	
Arrikruz	Upper Pleistocene	Torres 1988b	16	
<b>BRITISH ISLANDS</b>				
Westbury	Middle Pleistocene	Bishop 1982	7	Natural History Museum. London
Bacton	Lower Pleistocene	Kurtén 1969a, Bishop 1982	6	
<b>CENTRAL EUROPE</b>				
Rubeland	Upper Pleistocene	Fischer 1995	15	Institut für Paläontologie. Humboldt Universität Berlin
Gailenreuther	Upper Pleistocene	Weinstock 2001	21	
Einhornhöhle	Middle Pleistocene	Rode 1935, Schütt 1968	8	
Mosbach	Middle Pleistocene	Zapfe 1946, Kahlke 1961	2	
Repolust	Middle Pleistocene	Mottl 1947, Temmel 1996	3	Institut für Paläontologie der Universität Wien
Hundsheim	Middle Pleistocene	Zapfe 1946, Kurtén 1969a	8	
Nixloch	18 Ky BP	Rabeder 1997	20	
Lieglloch	28 Ky BP	Fernández et al. 2001	14	
Cunturines	42-47 Ky BP	Rabeder & Nagel, 2001	30	
<b>EAST</b>				
Loutraki	30-35 Ky BP	Tsoukala & Rabeder, pers. com.	40	University of Thessaloniki
Odessa	26,9 Ky BP	Kurtén, 1969b	30	University of Helsinki

Table I.- Some data of the studied sites.

Table I.- *Quelques données des sites étudiés.*

	SITE	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Iberian Peninsular	Eirós	6	91	3	3	34	63	0	38	41	15	06	0	0	6	94	0	0	100
	A Ceza	0	100	0	15	10	75	0	5	50	0	50	0	0	30	70	0	0	100
	Liñares	0	100	0	18	9	73	0	0	60	0	0	40	0	40	60	0	10	90
	Troskaeta	17	83	0	50	25	25	3	10	42	3	23	19	7	10	83	0	3	97
	Ekain	0	100	0	14	7	79	1	9	38	9	1	42	0	51	51	0	0	100
	El Toll	5	95	0	64	0	36	4	27	48	0	17	4	7	7	86	3	9	88
	Arrikruz	0	100	0	6	0	94	0	36	36	6	6	16	0	14	86	0	14	86
	Reguerillo	0	100	0	48	0	52	0	10	41	9	5	34	0	30	70	0	0	100
Atapuerca	0	100	0	64	0	36	3	10	3	60	24	0	7	7	86	10	0	90	
British	Westbury	12	88	0	0	37	63	0	12	50	38	0	0	63	37	0	0	0	100
	Bacton	0	100	0	0	0	100	0	17	17	68	0	0	66	44	0	0	17	83
Central Europe	Rübeland	14	86	0	0	40	60	0	7	40	40	13	0	0	100	0	7	7	86
	Gailenreuther	10	90	0	0	33	66	0	10	24	47	14	5	0	100	0	0	0	100
	Einhornhöhle	25	75	0	0	25	75	0	25	75	0	0	0	25	75	0	0	25	75
	Mosbach	50	50	0	0	25	75	0	50	50	0	0	0	100	0	0	0	25	75
	Repolust	67	33	0	0	33	67	0	67	33	0	0	0	100	0	0	0	33	67
	Hundsheim	25	75	0	0	25	75	0	50	0	25	25	0	25	75	0	0	0	100
	Nixloch	0	100	0	0	15	85	0	9	43	39	9	0	5	95	0	0	5	95
	Lieglloch	27	66	7	0	53	47	0	7	33	60	0	0	7	93	0	0	7	93
Cunturines	50	45	5	0	45	55	0	4	48	48	0	0	27	58	15	0	0	100	
EAST	Loutraki	0	100	0	0	47	53	0	0	24	70	6	0	0	100	0	6	0	94
	Odessa	0	100	0	12	12	76	0	0	20	65	15	0	0	100	0	0	0	100

Table II.- Percentages of appearance of the defined morphotypes of the Lower carnassial in the studied sites. All data are original except Atapuerca and Reguerillo (Torres Pérez-Hidalgo *et al.*, 1991).

Table II.- *Pourcentages de la présence des morphotypes définis de la première molaire inférieure dans les sites étudiés. Toutes les données sont des auteurs sauf Atapuerca et Reguerillo (Torres Pérez-Hidalgo et al., 1991).*

	SITE	TL	TrdL	TrdB	TadB	Pr-Pa	Pr-Me	Hy-En	PadCI	TrdCI	TadCI
Iberian Peninsular	Eirós	31.2	18.2	12.7	14.8	9.8	7.2	10.0	51.8	56.7	67.6
	A Ceza	31.2	19.0	13.0	15.2	9.9	7.2	9.6	52.0	55.5	63.6
	Liñares Sur	31.7	19.0	12.8	15.2	9.4	7.0	10.4	49.5	54.9	68.3
	Troskaeta	29.2	18.0	11.9	14.1	8.8	6.8	9.4	48.9	57.9	66.8
	Ekain	30.8	19.0	12.3	14.5	9.6	7.2	10.1	50.2	58.3	69.6
	El Toll	30.6	18.7	12.1	14.4	9.1	6.9	8.9	48.7	57.3	62.3
	Arrikruz	30.4	19.1	12.3	14.9	8.8	6.6	9.4	46.1	55.0	64.0
	Reguerillo	30.1	18.2	11.6	14.0	9.4	6.7	9.4	51.6	58.0	69.0
	Atapuerca	26.6	17.0	10.4	12.3	7.8	5.4	7.8	45.9	52.0	58.0
Brit. Isl.	Bacton	25.5	15.8	10.2	12.8	7.5	4.5	6.4	47.5	44.7	49.9
	Westbury	28.5	17.2	10.8	13.8	7.4	5.7	7.9	43.2	52.7	57.1
Centr. Europe	Rübeland	29.8	18.3	11.6	14.3	9.1	6.8	9.7	49.9	58.5	67.9
	Gailenreuther	30.8	19.3	12.4	14.9	9.7	6.9	9.7	50.3	55.7	65.4
	Einhornhöhle	29.2	18.1	11.4	13.9	9.1	5.5	7.9	50.0	47.8	57.2
	Mosbach	26.7	17.4	10.0	13.0	8.3	4.4	8.3	42.6	44.3	59.9
	Repolust	26.6	18.2	11.3	14.2	7.9	5.3	8.4	43.1	47.1	55.5
	Hundsheim	28.0	17.6	10.9	13.2	7.7	5.6	7.6	43.6	51.4	57.5
	Nixloch	29.9	18.4	11.9	14.5	9.3	7.0	9.6	50.3	58.7	66.0
	Lieglloch	30.5	18.6	12.5	14.9	9.6	7.1	10.0	51.5	56.5	67.0
	Cunturines	28.0	17.2	11.5	13.5	8.3	6.5	8.8	48.4	56.1	65.0
East	Loutraki	30.6	18.7	11.8	15.0	8.9	6.8	9.8	47.5	57.5	65.4
	Odessa	31.6	19.5	12.5	15.3	9.2	7.3	9.7	46.8	58.2	63.4

Table III.- Metrical data of the Lower carnassial from in the studied sites. All data are original except Atapuerca and Reguerillo (Torres Pérez-Hidalgo, 1988b).

Table III.- Données métriques de la première molaire inférieure des sites étudiés. Toutes les données sont des auteurs sauf Atapuerca et Reguerillo (Torres Pérez-Hidalgo, 1988b).