

COMPARATIVE DENTAL MICROWEAR ANALYSIS OF CAVE BEARS *URSUS SPELAEUS* ROSENMÜLLER, 1794 AND BROWN BEARS *URSUS ARCTOS* LINNAEUS, 1758

Ana C. PINTO LLONA¹

ABSTRACT: Dental Microwear Analyses (DMA) studies diet-related microscopic dental wear features, offering an additional and fresh insight into the diet of extinct animals. Most DMA studies have been carried on primates and hominines, as well as on herbivores. Very few approach carnivores and none to our knowledge studies bears. One of the chief drawbacks of DMA studies is that different authors choose different teeth, tooth areas, and methods rendering comparison across works difficult. Here we describe the methodology that we have devised for the analyses of dental microwear features in brown bears *Ursus arctos* and cave bears *U. spelaeus*, which could be applied to any species of bear. The diet of extant European brown bears is well known, and the comparison of their dental wear with that one seen on cave bears allows for some inferences. Although the collection of bear teeth analyzed here was small, we are hoping that the same methods may be adopted by other scientists researching on bear DMA.

Key words: Pleistocene, *Ursus spelaeus*, *Ursus arctos*, dental microwear, diet, molars, SEM.

INTRODUCTION

The diet of the extinct cave bear *Ursus spelaeus* is still greatly unknown, although we do have some clues: the morphological features of their chewing apparatus (for review see PINTO LLONA *et al.*, 2005; pages 87-121, 597-600 and SACCO & VAN VALKENBURGH, 2004) suggest both, non-predatory behaviour, and important adaptations to a tough vegetarian diet.

Comparative analyses of gross-wear features on the teeth of extant European brown bears *Ursus arctos* whose diet is known, with those on cave bear teeth, shows that tubers were in fact absent from their diet (PINTO & ANDREWS, 2001) and therefore tubers are not responsible for the extreme wear seen in cave bear teeth.

Taphonomic analyses of carnivore produced modifications on cave bear bones at several cave bear sites has shown that they actively scavenged on the carcasses of their con-specifics, both adult and infant, at all sites analysed, and also that they did so by following a very homogeneous and identifiable pattern that is peculiar to cave bears. This pattern is very distinct from the one produced by other large carnivores (PINTO & ANDREWS, 2004; PINTO LLONA *et al.*, 2005) including brown bears.

However, results obtained on the stable isotopic yield of cave bear bones are interpreted as indicators of a diet even more vegetarian than that of contemporary herbivore taxa (BOCHERENS *et al.*, 1994). It is possible that the cannibalistic scavenging carried out by cave bears constituted a minor part of an otherwise chiefly vegetarian diet, thus leaving no identifiable isotopic signature in their bones. On the other hand the metabolism of bears during hibernation and its effect on their isotopic signature is, to this day, poorly understood. It is thought that it involves significant mobilization of Nitrogen as discussed elsewhere (PINTO & ANDREWS, 2004; PINTO LLONA *et al. op. cit.*) and thus the metabolism of hibernation could be responsible of the apparent anomaly in that chemical signature.

A new line of evidence, complementary to the ones above, can offer fresh insights on the cave bear diet. Dental Microwear Analyses (DMA) is based on the assumption that different foodstuffs produce different and identifiable patterns of wear (WALKER *et al.*, 1978). DMA studies the varying percentages, length and width of *pits* and *scratches* on tooth enamel surfaces and their relative proportions.

¹ Instituto de Historia, Dept. de Prehistoria CSIC, c/Duque Medinaceli 8, 28014 Madrid, Spain. acpinto@ih.csic.es

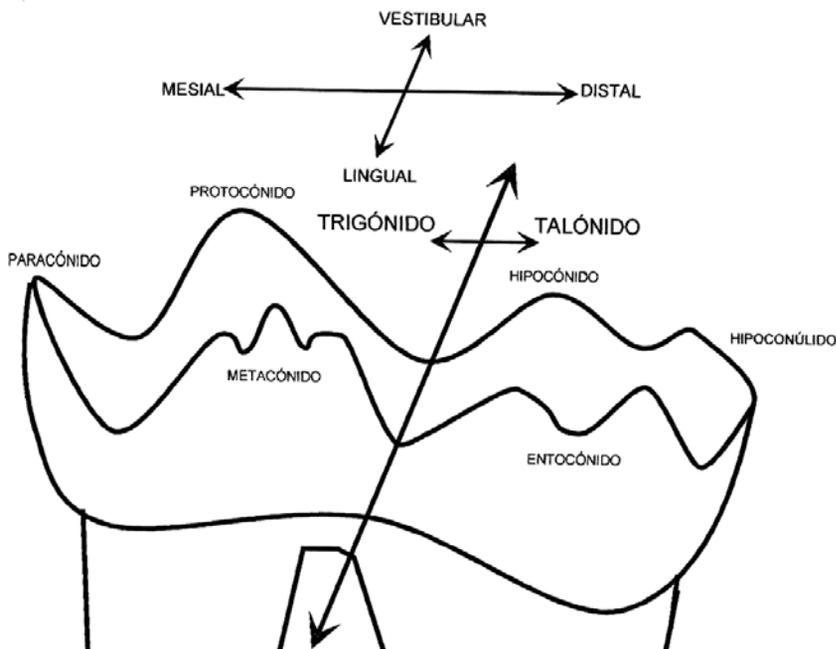
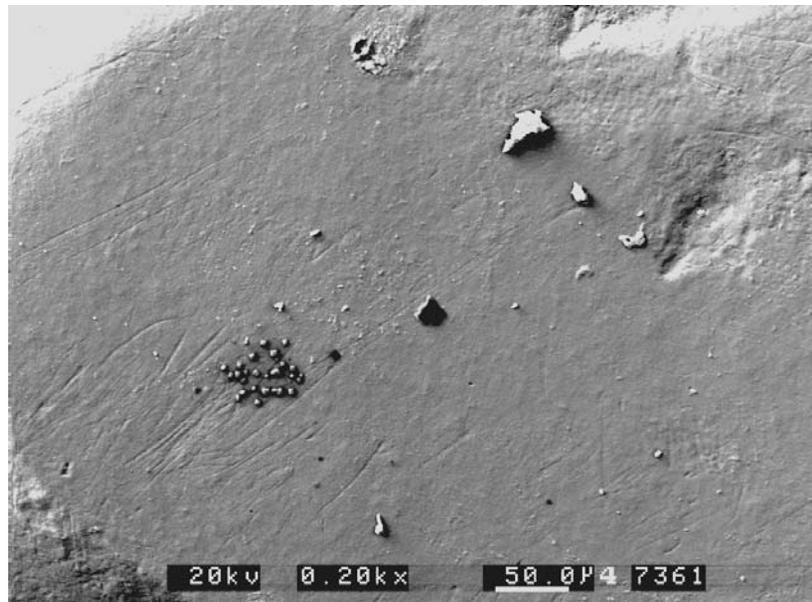


Figure 1. Right M_1 of *Ursus*. Mesially, the three cusps of the trigonid: protoconid, paraconid and metaconid. Distally, the three cusps of the tabloid: hypoconid, hypoconulid and entoconid.

Figure 2. Micrograph of the protoconid distal facet of a cave bear from Troskaeta. During hibernation bears do not eat, drink, urinate or defecate. In the shut mouth of the bear, dental microwear marks disappear during the hibernation, leaving featureless surfaces where sometimes the prisms of enamel can be distinguished as if after acid treatment. The facet above appears flat but for a few structures visible, probably plant silica phytoliths of a last mouthful of grass just after leaving hibernation and als just before dying, and the scratches produced by them.



DMA had not been carried out before on bears, and only a few works approach it on other carnivores; amongst these are the works by VAN VALKENBURGH *et al.* (1990) on the carnassial facet of several carnivores, TAYLOR & HANNAM (1987) on the buccal surface of the upper carnassial P4 of several species of African viverrids, STRAIT (1993) comparing microwear on several primates and quiroptera and others.

Here we present our approach to the bear DMA. We

choose to perform it on the low 1st molar, on a sample of cave bears and also of both fossil and extant brown bears, because of the evolutionary stability of this tooth.

MATERIALS AND METHODS

Although initially we revised large collections of low M1 from several cave bear collections, the usable sample was limited by three factors: (1) Teeth showing any taphonomic post-depositional alteration were excluded from

Table 1
Facet denomination according to BUTLER (1952) and, between brackets, KAY (1977). From HUNTER & FORTELIUS (1994).

FACET	UPPER MOLAR	LOWER MOLAR
1(2)	Distal Metacone	Mesial protoconid
2(1)	Mesial Paracone	Distal protoconid
3(5)	Mesial Protocone	Distal metaconid
4(7n)	Distal Hypocone	Lingual metaconid
5(10n)	Buccal Hypocone	Lingual protoconid
6(3)	Distal Paracone	Mesial hypoconid
7(4)	Mesial Metacone	Distal hypoconid
8(8)	Mesial Hypocone	Distal entoconid
9(6)	Distal Protocone	Mesial entoconid
10(9)	Buccal Protocone	Lingual hypoconid

the sample following KING *et al.*, (1999). Furthermore, this type of analyses is carried out on enamel, thus (2) our sample was limited to teeth conserving it on the occlusal surfaces, presumably those of relatively young adults. Additionally, (3) some specimens belonged to animals that died during or soon after hibernation: according to our observations (PINTO *et al.*, 2005), dental microwear features are erased by long hibernation periods, during which time bears do not eat nor drink at all for several months each year. The obliteration of all dental microwear features, as well as the noticeable exposure of the enamel prisms in these specimens suggests that the acidity in the mouth of the bears is greater during hibernation (fig. 2).

Having discounted the specimens that for one or other of the above reasons were unsuitable for this type of analyses, the sample finally employed included six extant brown bear low M1 plus four Holocene ones, both from the Cantabrian mountains of Asturias, and seven cave bear specimens, from Troskaeta cave in the Basque country. All of these locations are in northern Spain.

Since our objective was to compare dental wear in brown and cave bears, a set of facets had to be chosen that homogeneously appear in both species of bears. On the selected specimens we therefore recorded exhaustively the presence or absence of discrete wear facets in each of the cusps -paraconid, metaconid, protoconid, entoconid, hypoconid and hypoconulid (fig. 1).

One interesting observation derived from this approach was that none of the cave bears in the sample has a carnassial facet -that is, the wear facet that forms by the shearing occlusion of the upper P4 (lingually) and the lower M1 (bucally) in carnivores. In contrast, all fossil brown bear low M1 specimens have it, while only 60% of extant brown bears from the northern Iberian Peninsula, whose diet has a very important vegetarian component (PINTO *et al.*, 2001; 2005) showed a carnassial facet, cor-

responding with assessed predatory behaviour in each of these types of bears (COUTURIER, 1954).

Occlusal facets and facet denomination have been the object of several studies (for a review see HUNTER & FORTELIUS, 1994). Following the advice of these authors, we adapted facet denomination from extant literature by BUTLER (1952) and KAY (1977). Tab. 1 shows these denominations, and fig. 3 is our adaptation of it to the bear low M1.

Once assessed the homogeneity of their presence on both brown and cave bear teeth, we choose to carry out the analyses in two facets, that is one Trigonid facet and one Talonid facet, since those are thought to have different functions during mastication. The facets employed throughout the analyses were the distal facet of the protoconid Facet 2(1), and the lingual facet of the hypoconid Facet 10(9) (fig. 3).

High precision Coltene™ moulds or peelings were taken from the occlusal surfaces and reinforced with dental putty. The resulting moulds were then positivized by using slow curing Araldit™. These Araldit™ replicas were then gold or platinum coated and Scanning Electron Microscope micrographs were taken of the chosen facets. The settings employed for the SEM throughout the study were x 200 magnification, 35 mm working distance, and 20 Kv potency -since the resin casts would fuse with higher potency.

The pictures thus obtained were then digitised and analysed by using Microwear 2.2 software developed by Dr. Ungar (UNGAR *et al.*, 1991; UNGAR, 1995a; UNGAR, 1995b) and available to the author. For the bears we used a *pit to scratch* ratio of 1:4, that is, marks whose width is more than ¼ of the length are classified as pits. The software records individual features and classifies them according to our settings, in so doing performing some basic statistics.

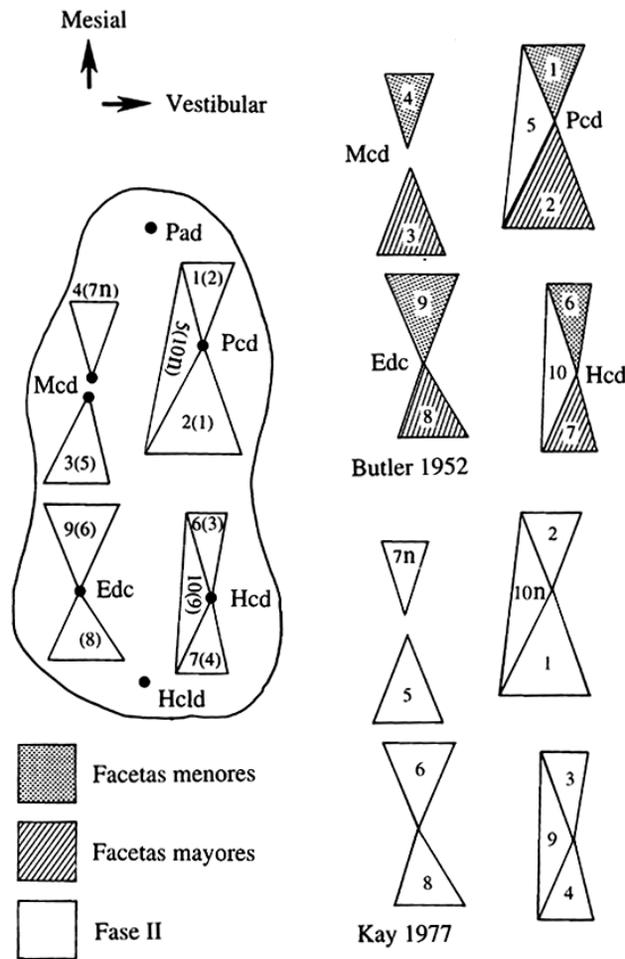


Figure 3. Occlusal view of a bear right low M1, showing facet location and denomination according to the frameworks by BUTLER (1952) and KAY (1977).

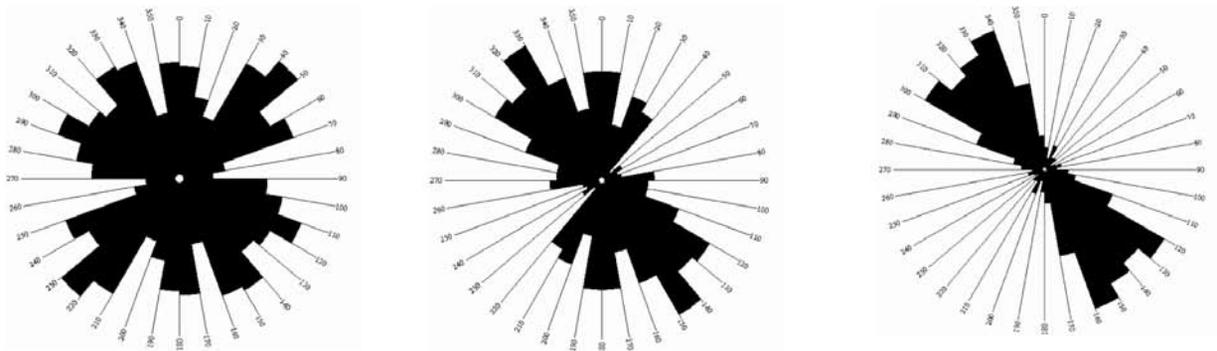


Figure 4. Orientation of dental microwear features in Facet 2(1). Left, extant brown bear, middle Holocene fossil brown bear, right cave bear. If puncture-crushing of hard objects is responsible for the diverging orientation of wear marks, it could be suggested that cave bears do not practice it. Orientation diverges most between the two bears of allegedly most similar diets, chiefly vegetarian.

RESULTS

Having measured and classified dental microwear features in these extant brown bears, Holocene fossil brown bears and Troskaeta cave bears, we effected the following observations:

Cave bears have more marks in both facets than either extant or fossil brown bears: average number of marks in Facet 2(1) in extant brown bears is 80.1, in fossil brown bears is 99.3 and in cave bears is 163.7; average number of marks in facet 10(9) in extant brown bears is 87.4, in fossil brown bears is 131.3 and in cave bears is 153.4.

Both types of brown bears tend to have a greater proportion of *scratches* relative to *pits* than cave bears: Facet 2(1) average number of pits and scratches in extant brown bears is 22.6% and 77.4% respectively; in fossil brown bears is 6.3% and 93%, and in cave bears is 33.4% and 66.6% respectively. As for Facet 10(9), extant brown bears 26.5% and 73.5%, fossil brown bears 18.7% and 81.3% and cave bears 49.5% and 50.1%.

Regarding scratch size, cave bears have the shortest and widest scratches in Facet 2(1) (extant brown bears $63.72 \mu \times 2.69 \mu$, fossil brown bears $72.27 \mu \times 2.99 \mu$ and cave bears $48.23 \mu \times 3.73 \mu$) and pit size is similar in both fossil brown and cave bears (extant brown bears $31.05 \mu \times 18.66 \mu$, fossil brown bears $23.92 \mu \times 12.53 \mu$, cave bears $23.13 \mu \times 11.18 \mu$). As for Facet 10(9), scratch sizes are more homogeneous amongst the three types of bears (extant brown $56.96 \mu \times 2.92 \mu$, fossil brown $62.83 \mu \times 2.79 \mu$, cave bears $57.83 \mu \times 4.24 \mu$), while pit sizes are smaller for cave bears (extant brown $23.7 \mu \times 12.86 \mu$, fossil brown $21.56 \mu \times 12.06 \mu$, cave bears $20.31 \mu \times 10.56 \mu$).

SUMMARY AND DISCUSSION

We present here a standardized method for the Dental Microwear Analyses of the 1st low Molar of the bear, devised with the aim of shedding complementary light on the dietary habits of the extinct cave bear by comparing its dental wear with that of modern bears of known diet. The number of specimens available to this study was limited because of the excessive wear leading to enamel loss on occlusal surfaces and by the obliteration of dental wear features presumably during hibernation. A small collection of low M1, of modern and Holocene fossil brown bears, as well as cave bears from Troskaeta, were analyzed. On these we choose to analyze the distal facet of the protoconid in the Trigonid and the lingual facet of the hypoconid in the Talonid. Cave bears showed to have significantly more marks than brown bears in both facets.

In the three types of bear, pits are more numerous

on facet 10(9) than in facet 2(1), pointing to the superior grinding function of the Talonid. In brown bears, scratches in facet 2(1) are longer than those in 10(9). Numerous long narrow scratches are sometimes related with grazing behaviours; we know that brown bears do graze. Conversely, cave bears have the longer and wider scratches in facet 10(9) suggesting a different feeding behaviour than that of brown bears at least relating to grazing. On the other hand pits are on average larger on facet 2(1) than in the Talonid facet, in the three groups of bears considered.

Cave bears show a marked preference in the orientation of the marks, that is more erratic for brown bears, and this must be related to the dynamics of chewing as well as to the foodstuffs ingested.

VAL VALKENBURGH *et al.* (1990), when assessing bone chewing behaviours in carnivores, showed that dental microwear marks in hyaenas have a combination of relatively long marks and a larger proportion of pits than scratches. Felids, that eat less bone, had narrow scratches with few pits. TAYLOR & HANNAM (1987) concluded that faunivore animals tend to have greater mark density than fruit or leaf eaters, although such differences did not prove statistically consistent.

Of the three bear types considered, cave bears *U. spelaeus* have the highest proportion of pits relative to scratches in both facets, and also the greater mark density. A large concentration of scratches is thought to be associated with the ingestion of grass because of the opal phytoliths contained in it. Brown bears are known grass eaters and had larger percentages of scratches on both facets.

In view of the observations on dental wear in other carnivores, and of our observations here, we believe that our results are consistent with dietary behaviours that include a greater consumption of bone on the part of cave bears relative to brown bears, as has also been assessed by the taphonomic analyses of carnivore produced bone modification on cave and brown bear bone deposits.

Acknowledgements: This research has been made possible by grants awarded to the author by FICYT (Fundación Investigación Ciencia y Tecnología de Asturias) and by a joint agreement Fundación Oso de Asturias, DuPont and the Natural History Museum. Use of the Scanning Electron Microscope at the NHM was possible with support of the European Commission Large Scale Facilities, Training and Mobility for Researchers Programme. Thanks to Dr. J. Naves that provided access to teeth of extant brown bears, to Sociedad Ciencias Aranzadi that keeps the Troskaeta collection, to Dr. T. King for insights on replication and feedback, to Dr. P. Ungar for sharing his software, and to the SEM staff at the Natural History Museum.

REFERENCES

- 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.
- BUTLER, P. M., 1952. The milk-molars of Perissodactyla, with remarks on molar occlusion.- *Proceedings of the Zoological Society (London)*, **121**: 777-817.
- COUTURIER, M. A. J., 1954. *L'Ours Brun*.- Ed. MARCEL COUTURIER, Grenoble, France.
- HUNTER, J. P. & FORTELIUS, M., 1994. Comparative dental occlusal morphology, facet development and microwear in two sympatric species of *Listriodon* (Mammalia: Suidae) from the middle Miocene of Western Anatolia (Turkey).- *Journal of Vertebrate Paleontology*, **14**: 105-126.
- KAY, R. F., 1977. The evolution of molar occlusion in *Cercopithecoidea* and early catharrines.- *Am. J. Phys. Anthropol.*, **46**: 327-352.
- KING, T., ANDREWS, P. & BOZ, B., 1999. Effect of taphonomic processes on Dental Microwear.- *Am. J. Phys. Anthropol.*, **108**: 359-373.
- PINTO LLONA, A. C. & ANDREWS, P. J., 2001. Dental wear and grit ingestion in extant and extinct bears from N. Spain.- *Cadernos do Laboratorio de Xeoloxia de Laxe*, **26**: 423-429.
- PINTO, A. C. & ANDREWS, P. J., 2004. Scavenging behaviour patterns in cave bears *Ursus spelaeus*.- *Revue de Paléobiologie*, Genève, **24** (2): 845-853.
- PINTO LLONA, A. C., ANDREWS, P. J. & ETXEBARRIA, F., 2005. *Taphonomy and Palaeoecology of Bears from the Quaternary of Cantabrian Spain*. Ed. FOA, NHM (London) & Dupont Iberica. Grafinsa, Oviedo, 680 pgs.
- SACCO, T. & VAN VALKENBURGH, B., 2004. Ecological indicators of feeding behaviour in the bears (Carnivore, Ursidae).- *J. Zool., Lond.* **263**: 41-54.
- STRAIT, S. G., 1993. Molar Microwear in Extant Small-Bodied Faunivorous Mammals. An Analyses of Feature Density and Pit Frequency.- *American Journal of Physical Anthropology*, **92**: 63-79.
- TAYLOR, M. E. & HANNAM, A. G., 1987. Tooth microwear and diet in the African viverridae.- *Can. J. Zool.* **65**: 1696-1702.
- UNGAR, P. S., 1995a. A semiautomated image analyses procedure for the quantification of dental microwear II.- *Scanning*, **17**: 57-59.
- UNGAR, P. S., 1995b. Microwear Image Analysis Software. Version 2.2
- UNGAR, P. S., SIMONS, J. C. & COOPER, J. V., 1991. A semiautomated image analyses procedure for the quantification of dental microwear.- *Scanning* **13**: 31-36.
- VAN VALKENBURGH, B., TEAFORD, M. F. & WALKER, A., 1990. Molar microwear and diet in large carnivores: inferences concerning diet in the sabertooth cat *Smilodon fatalis*.- *J. Zool. Lond.*, **222**: 319-397
- WALKER, A., JOECK, H. N. & PEREZ, L., 1978. Microwear of mammalian teeth as an indicator of diet.- *Science*, **201**: 208-210.