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Dental Microwear and Diet: as Indicators of Geographic and Cultural Contexts in Human Evolution

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Abstract

Use-wear analysis is a method in archeology and paleoanthropology that identifies the functions of tools and teeth by closely examining the characteristics of their surface damage. Thus, microscopic tooth buccal wear helps to improve our knowledge of Prehistoric man's way of life with regard to changing environments, resource usage, and technological practices. Aspects of buccal microwear analyzed in this study are restricted to the micro striae of the cheek teeth, which vary in number, length and orientation, evidencing major dietary patterns over long periods. Our information about human dietary history comes from the identification of different aspects of tooth micro striae observed in a variety of populations ranging from the almost carnivorous to the largely vegetarian ones, even though the majority of humans depend on plant foods to some extent.

The comparative examination of these surfaces on a large quantity of human remains, from the European Pleistocene to modern hunter-gatherers and urban people today, show variability that can be explained eco-geographically as well as culturally, allowing the reconstruction of a grid or an atlas of major eating patterns reflecting different dietary traditions worldwide. The data hereby presented here are the result of this approach which has been applied since 1976 to highlight these traces left by abrasive particles in the diet (La Préhistoire Française, edit. CNRS). As sources, we have used published papers that employed this methodology. The density of enamel buccal scratches gives an account of dietary changes in societies, while horizontal to vertical striae proportions indicate a large dietary spectrum in Anatomically Modern Humans. Whereas the orientation of the striae patterns in specific sites point to aquatic foods consumed by our waterside Stone Age ancestors.

Figure 4. Indices (NH/NT and NV/NT) plot highlighting the AMH from the Upper Paleolithic position. Sample is segmented by arbitrary chronological periods and the difference between individuals younger and older from 15 Ka (older= dark polygon). All AMH from the UP are round points while squares represent the position of the modern hunter-gatherers analyzed by Lalueza et al. (1996) (see Figures 2 and 3 for references). Names of the UP individuals can be found in Figure 3.

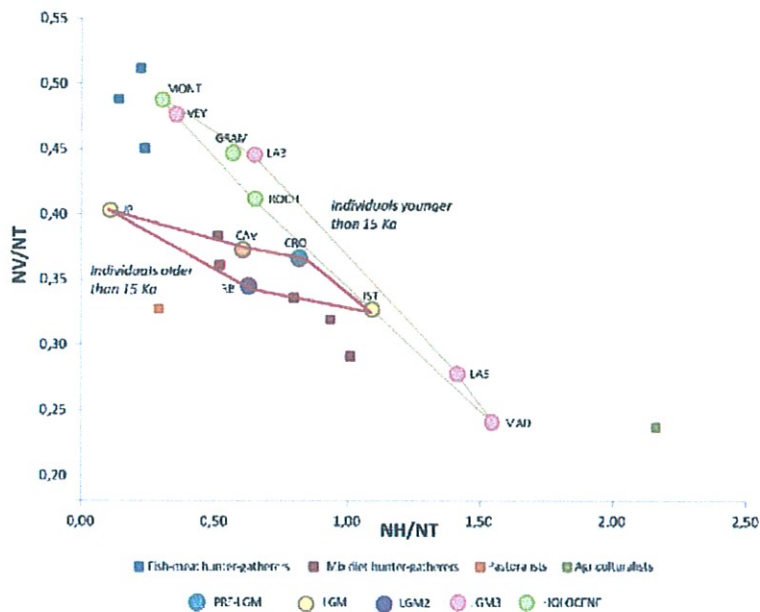


Figure 2. Index values of the populations analyzed by Lalueza et al. (1996) with the Paleolithic groups considered (circle=UP AMH; triangles=NEA). Similarity between European AMH and NEA is evident, being close to Tasmanian and Australian individuals while Near East Neandertals is the most distinct fossil group.



Table 2. Variables Showing Significant Differences between Middle Ages Populations and Hunter-Gatherers.

VARIABLE	F	P
NH	6.781	0.031
SH	6.352	0.036
NV	6.031	0.04
NMD	16.894	0.003
NT	13.381	0.006

	Mean right		23,33	150,49	62,74	78,33	152,18	85,1155	29	126,45	65,04	23,67	121,07	63,11	154,333	142,65	77,71	0,15	0,51	0,30
	Mean (N=5)	Puech <i>et al</i> <i>submitted</i>	19.00	160.57	71.41	78.00	160.01	87.18	27.00	121.60	70.01	15.00	127.74	60.95	144.00	148.95	90.48	0.13	0.54	0.24
Chalcolithic	16														299.68	55.63				
	16	Romero & De Juan 2007													110.06	93.33				
	12														120.42	90.84				
Islamic	36													91.61	68.77					
Modern																				
	Baume de Montchus 1965-8		25.33	159.92	93.02	90.33	150.59	103.19	45.00	129.20	94.33	43.33	105.26	77.28	204.00	140.05	102.84	0.18	0.49	0.09
	Isturitz 3 ~26- 20ka		34.33	170.81	110.69	77.33	179.13	128.28	57.67	174.42	131.16	49.33	144.79	95.85	218.67	167.21	123.13	1.02	0.32	0.17
	Gramat	Pinilla <i>et al</i> , in <i>press</i>	33.36	167.37	95.79	104.91	169.87	123.55	71.73	147.53	111.45	28.91	133.70	82.05	238.91	158.17	116.18	0.46	0.45	0.14
	Rochereil		63.00	125.48	64.37	110.00	138.61	89.00	73.00	121.89	71.06	20.00	89.03	43.07	266.00	127.18	76.84	0.57	0.41	0.24
	Lachaud 5		61.00	132.21	89.68	86.33	125.99	99.87	81.00	134.33	108.38	53.00	127.93	101.06	281.33	130.47	105.71	1.38	0.27	0.23
	Lachaud 3		50.00	162.70	115.14	121.50	146.94	103.89	57.50	109.84	78.24	38.00	125.14	98.35	267.00	135.84	99.01	0.54	0.45	0.20
	Cromagnon ~27,7ka																	0.73	0.36	0.26
	La Madeleine																	1.50	0.23	0.35
	Round-du-Bary	Pérez-Pérez <i>et al</i> 2003																0.52	0.34	0.18
	Veyrier-sous- Salève 1																	0.23	0.48	0.11
AMH	Cavillon ~28,8ka	Pinilla <i>et al</i> , in <i>press</i>	55.33	148.09	112.37	115.67	133.01	87.09	74.67	120.86	75.81	81.00	110.40	75.23	326.67	124.83	87.77	0.51	0.37	0.16
	Jeune Prince ~23,4ka		24.71	153.82	83.02	75.71	155.38	99.09	45.57	135.12	80.79	34.57	128.79	67.00	180.57	144.05	89.99	0.14	0.41	0.40
	MEAN (N=12)																	0.67	0.36	0.21

Teaford MF “What do we know and not know about diet and enamel structure?”
In: Ungar PS (ed) *Evolution of the Human Diet: The Known, the Unknown and the Unknowable* Oxford University Press, New York 2007 pp. 56-76

Trinkaus E & Hilton CE (1996) Neandertal pedal proximal phalanges: diaphyseal loading patterns *J Hum Evol* **30**: 399-425

Trinkaus E (1986) The Neandertals and modern human origins *Annual Review of Anthropology* **15**: 193-218

Trinkaus E “The Upper Paleolithic Transition” in: Trinkaus E (Ed) *The Emergence of Modern Humans. Biocultural adaptations in the later Pleistocene* Cambridge University press 1989 pp. 42-66

Ulijaszek SJ (2002) Human eating behavior in an evolutionary ecological context *Proc Nutr Soc* **61**:517-526

Wrangham R.(2013) The evolution of human nutrition *Current Biology*, **23**: R354-R355

Wood B (2013) Gritting their teeth *Nature* **493**: 486-487

Puech PF & Puech S “L’usure des dents de Banyoles” in: Maroto J (Ed) *La mandíbula de Banyoles en el context dels fòssils humans del Pleistocè Sèrie monogràfica* vol. 13, p. 105-115. Centre d’investigacions arqueològiques, Girona 1993

Puech PF, Puech B & Pinilla B (à paraître) Micro usure des dents et alimentation au Moyen-âge. *Société d’Histoire et d’Archéologie de Senlis, Comptes-rendus et mémoires*, Senlis.

Richards MP, Pettitt PB, Trinkaus E, Smith FH, Paunovic M & Karavanic I (2000) Neanderthal diet at Vindija and Neanderthal predation: The evidence from stable isotopes *Proc Natl Acad Sci USA* **97**: 7663-7666

Richards MP, Pettitt PB, Stiner MC & Trinkaus E (2001) Stable isotope evidence for increasing dietary breadth in the European mid-Upper Paleolithic. *Proc Natl Acad Sci USA* **98**: 6528-6532

Romero A & De Juan J (2007) Intra- and Interpopulation Human tooth surface microwear analysis: Inferences about diet and formation processes *Anthropologie* **45**(1): 61-70

Romero A, Galbany J, De Juan J & Pérez-Pérez A (2012) Short and long-term *in vivo* human buccal dental-microwear turnover. *Am J Phys Anthropol* **148**(3):467-472

Roselló E & Morales A (2006) Ictiofaunas musterienses en la península ibérica: ¿evidencias de pesca neandertal? *Munibe* **57**(1): 1283-195

Scott RG & Turner II CG (1988) Dental Anthropology *Ann Review of Anthropol* **17**: 99-126.

Steele TE (2010) A unique hominin menu dated to 1.95 million years ago *Proc Natl Acad Sci USA* **107**(24): 10771-10772

Stewart JR (2004) Neanderthal-Modern human competition? A comparison between the mammals associated with Middle and Upper Palaeolithic industries in Europe during OIS 3 *Int J Osteoarchaeol* **14**: 178-189

Stiner MC, Munro ND, Surovell TA, Tchernov E & Bar-Yosef O (1999) Paleolithic population growth pulses evidenced by small animal exploitation *Science* **283**: 190-194

Stiner MC, Munro ND & Surovell TA (2000) The tortoise and the Hare: Small-game use, the broad spectrum revolution, and Paleolithic demography *Curr Anthropol* **41**: 34-74

Stiner MC (2001) Thirty years on the “Broad spectrum revolution” and Palaeolithic demography *Proc Natl Acad Sci USA* **98**: 6993-6996

Lozano M, Bermúdez de Castro JM, Carbonell E & Arsuaga JL (2008) Non-masticatory uses of anterior teeth of Sima de los Huesos individuals (Sierra de Atapuerca, Spain) *J Hum Evol* **55**(4): 713-728

Mahoney P (2006) Brief Communication: Intertooth and Interfacet dental microwear variation in an Archaeological sample of Modern Humans from the Jordan valley *Am J Phys Anthropol* **129**: 39-44.

Marean C W (2011) "Coastal South Africa and the co-evolution of the modern human lineage and the coastal adaptation" in: Bicho N., Haws J. A., and Davis L. G. (Ed) *Trekking the Shore: Changing Coastlines and the Antiquity of Coastal Settlement*, New York: Springer, chap. 18 pp.421-440.

Martínez LM, Galbany J & Pérez-Pérez A (2004) Paleodemography and dental microwear of *Homo habilis* from East Africa *Anthropologie* **42**(1): 53-58

Molnar S (1972) Tooth wear and culture: a survey of tooth functions among some prehistoric populations *Curr Anthropol* **13**: 511-526

Morin E (2008) Evidence for declines in human population densities during the early Upper Paleolithic in western Europe *PNAS* **105**(1): 48-53

Pérez-Pérez A *Evolucion de la dieta en Cataluna y Baleares desde el paleolitico hasta la edad Media a partir de restos esqueléticos* PhD 1990

Pérez-Pérez A, Lalueza C & Turbon D (1994) Intra individual and Intra group Variability of Buccal Tooth Striation Pattern *American Journal of Physical Anthropology* **94**:175-187

Pérez-Pérez A, Espurz V, Bermúdez de Castro JM, de Lumley MA & Turbón D (2003) Non-occlusal dental microwear variability in a sample of Middle and Late Pleistocene human populations from Europe and the Near East *J Hum Evol* **44**: 497-513

Peters C (1982) Electron-optical microscope study of incipient dental microdamage from experimental seed and bone crushing *Am J Phys Anthropol* **57**: 283-301

Pettitt PB, Richards MP, Maggi R & Formicola V (2003) The Gravettian burial known as the Prince (Il Principe): new evidence for his age and diet *Antiquity* **77**(295): 15-19

Pinilla B, Romero A & Pérez-Pérez A (2011) Age-related variability in buccal dental microwear in Middle and Upper Pleistocene human populations *Anthropological Review* **74**: 25-37.

El-Zaatari, S., Grine, F.E., Ungar, P.S., & Hublin, J.J. (2011) Ecogeographic Variation in Neandertal Dietary Habits: Evidence from Occlusal Molar Microwear Texture Analysis *J Hum Evol* **61**(4): 411-424

Enghoff, L.B. (1991) Mesolithic Eel-fishing at Bjørnsholm, Denmark, Spiced with Exotic Species *Journal of Danish Archaeology* **10**: 105-118

Estebaranz, F., Martínez, L.M., Galbany, J., Turbón, D. & Pérez-Pérez, A. (2009) Testing Hypotheses of Dietary Reconstruction from Buccal Dental Microwear in *Australopithecus afarensis*. *J Hum Evol* **57**: 739-750

Estebaranz F, Galbany J, Martínez LM, Turbón D & Pérez-Pérez A (2012) Buccal dental microwear analyses support greater specialization in consumption of hard foodstuffs for *Australopithecus anamensis*. *J Anthropol Sci* **90**: 163-185

Fiorenza L, Benazzi S, Tausch J, Kullmer O, Bromage TG & Schrenk F (2011a) Molar macrowear reveals Neanderthal eco-geographic dietary variation *PLoS ONE* **6**(3): e14769

Galbany J & Pérez-Pérez A (2004) Buccal enamel microwear variability in Cercopithecoidea primates as a reflection of dietary habits in forested and open savanna environments *Anthropologie* **42** (1): 13-19

Galbany J, Martínez LM, López-Amor HM, Espurz V, Romero A, De Juan J & Pérez-Pérez A (2005) Error Rates in Buccal-Dental Microwear Quantification Using Scanning Electron Microscopy *Scanning* **27**: 23-29

Galbany J, Estebaranz F, Martínez LM & Pérez-Pérez A (2009) Buccal dental microwear variability in extant African Hominoidea primates: taxonomy versus ecology *Primates* **50**(3): 221-230

Galbany J, Altmann J, Pérez-Pérez A & Alberts SC (2011) Age and individual foraging behavior predict tooth wear in Amboseli baboons. *Am J Phys Anthropol* **144**(1): 51-59

Gamza TR (2010) Short communication: Intra-Individual Microwear variation: deciduous versus permanent dentition *Dent Anthropol* **23**(2): 66-68

Gordon KD (1982) A study of microwear on chimpanzee molars: implications for dental microwear analysis *Am J Phys Anthropol* **59**: 195-215

Gordon KD (1984) The assessment of jaw movement direction from dental microwear *Am J Phys Anthropol* **63**(1): 77-84

6. References

Alrousan, M. & Pérez-Pérez, A. (2008) Non-Occlusal Microwear of the Last Hunter-Gatherer from Near East and Europe. In: Nogués AJ & Pinilla S (Eds) *Genes, ambiente y enfermedades en las poblaciones humanas* University of Zaragoza Press, pp. 45-59

Alroussan, M. (2009) *The Mesolithic-Neolithic Transition in the Near East, Biological Implications of the Shift in Subsistency Strategies Through the Analysis of Dental Morphology and Dietary Habits of Human Populations in the Mediterranean Area 12,000-5,000 B.P.* PhD

Antunes, M.T., Cunha, A.S., Schwartz, J. & Tattersall, I. (2000) The Latest Neanderthals Evidence from Portugal. In: Antunes MT (Ed) *Últimos Neandertais em Portugal: evidencia, odontológica e outra* Academia das Ciências de Lisboa, Lisboa, pp. 269-303

Bacon F *The works of Francis Bacon, Baron of Verulam, Viscount St. Alban_ and Lord High Chancellor of England* A. Millar, London, vol. n°1 1765: 501

Balter, V. & Simon, L. (2006) Diet and Behavior of the Saint-Césaire Neanderthal Inferred from Biogeochemical Data Inversion *J Hum Evol* 51(4): 329-338

Bar-Yosef, O. (2004) Eat What is There: Hunting and Gathering in the World of Neanderthals and their Neighbors *Int J Osteoarchaeol* 14: 333-342

Bax, J.S. & Ungar, P.S. (1999) Incisor Labial Surface Wear Striations in Modern Humans and their Implications for Handedness in Middle and Late Pleistocene Hominids *Int J Osteoarch* 9: 189-198

Belfer-Cohen, A. & Hovers, H. (2010) Modernity and Enhanced Working Modernity in the Levant *Current Anthropology* 51(S1): 167-175.

Bermúdez de Castro, J.M., Bromage, T.G., & Fernández-Jalvo, Y (1988) Buccal Striations on Fossil Human Anterior Teeth: Evidence of Handedness in the Middle and early Upper Pleistocene *J Hum Evol* 17: 403-412

Binford, L.R. (1984) *Faunal Remains from Klasies River Mouth* New York Academic Press

Binford, L.R. (1985) Human Ancestors: Changing Views of their Behaviour *J Anthropol Archaeol* 4: 292-327

Binford, L.R. (1989) The Emergence of Modern Humans: Biocultural Adaptations in the Later Pleistocene. In: Trinkaus E (Ed) *The Emergence of Modern Humans* Cambridge Univ Press, New York, pp. 18-41

lower NH/NT value, might be indicative of an increase in aquatic food consumption, namely fish, by the proto-Neolithic European groups. The exploitation of aquatic resources might have extended back in time to the Middle Paleolithic (Marean, 2011) and human features could have evolved because our ancestors waded in watery environments in very different times. Though, it may not have been until harpoons became widely used, in the Late Upper Paleolithic, that fish became the common food source in some places (Strauss, 1995, 2003, 2005, 2010; Richards et al., 2000; Drucker & Gambier, 2005; Morin, 2008), with consumption increasing still after 12 ka and culminating 8 ka ago with the “aquatic revolution” (Enghoff, 1991; Coles, 1992).

It is interesting to highlight the specific ‘*aquatic landscapes*’ shared by the fossils Le Jeune Prince, Cavillon, Veyrier-sous-Salève 1963, and Lachaud 3. The first two are significant because of their geographic locations, on the seashore in Liguria, and also because of the cultural context: Gravettian. The microwear pattern of both these individuals is very similar in density and length for each of the four orientations (Pinilla et al., in press) that corresponds to the same type of foods characterized by the importance of maritime relative to terrestrial game evidenced in Le Prince by isotopic analysis (Pettitt et al., 2003). While Cavillon probably did ingest important quantities of lacustrine food (i.e. mollusks, arthropods and tide pool snails) that produced the high density of striae. This interpretation would appear to make sense considering their locations (Figures 3 and 4) and if we also consider the length of striae in its different orientations these would seem to indicate the coarse quality of food like that consumed in the medieval (Figure 5). Additional observations relate to the proximity of Veyrier-sous-Salève 1963 and Lachaud 3 to Gramat, Rochereil and Baume de Montclus in similar river/lake habitats with the same mode of food preparation, in spite of having an older age and thus assumed to be from a different cultural level. The former two subjects may have consumed important quantities of fish as attested by their microwear values which place them with fish eating modern hunter-gatherers or “fisher-foragers”. In the case of Veyrier-sous-Salève 1963, this hypothesis is even more probable since at that time the Geneva basin was transformed into swamps and lakes as the ices gradually melted (Dellenbach, 1935, Page 183). Aquatic fauna began to invade the marshes, as evidenced by the remains of frogs, suggesting that these too were part of the human diet. Harpoons were also found in the neighborhood (Bullinger, 2002).

4. Conclusion

The recognition of motifs in dental microwear striation, the dominant feature of the buccal enamel posterior dentition surfaces, provides an indication of dietary patterns in food consumption. Through direct data based on the mechanistic details of the mastication of foods from the fossils themselves.

With the use of buccal tooth striae analysis, major and distinct dietary patterns have emerged. If an identified connection is established between particular diets and food practices, and a specific microwear pattern which is consistent throughout a

studies on these populations may prove to be of special interest considering the Spanish Middle Ages traditions and anthropological findings on variations in religious dietary habits. The differences observed in the Chalcolithic have been explained in depth by Romero and De Juan (2007) and are in accordance with the anticipated results and the archaeological evidence.

3.2. *An Atlas of Dietary Habits.* Abrasivity can be useful for identifying the main types of subsistence but it is difficult to assess whether it is related to diet or preparation techniques. According to Pinella (2012) those variable are more related to cultural practices and extrinsic elements ingested with the food. Puech (1976) and Lalueza et al. (1996) found that vertical and horizontal scratches were useful in discriminating diets. Discussions focused on specialized types of societies with ethnographic and archaeological descriptions by anthropologists, where basic subsistence was defined. The conclusion was that it was mainly carnivorous human groups who presented a higher proportion of vertical scratches, together with a lower percentage of horizontal ones. The reverse was the case in the mainly vegetarian individuals, while populations with mixed diets (e.g., Bushmen, Australians, etc.) presented mean values for both indices. The inclusion of La Olmeda and Adélaïde in the sample showed that both were close to one another but are plotted at the top of the vertical values with a low horizontal striae index. It seems difficult to imagine that groups from the Middle Ages consumed less vegetables and more meat than Eskimos, and therefore, since vertical scratches are also characteristic of hunter-gatherers from prehistory, these may also have resulted from the coarseness of food since large food particles and fibre stimulate chewing activity. The pastoralists and agriculturalists included in the Lalueza et al. (1996) study would seem to have fitted in these indices, but more probably because of the nature of the groups. Further analyses, including those of populations investigated by the same researcher, will reveal whether indices are useful in the case of all human groups or only in nomadic-seminomadic populations. Therefore, we have limited our analyses to data from Lalueza et al. (1996) and from Paleolithic individuals.

Fossil remains from the Paleolithic (AMH and NEA) show similar microwear patterns (AMH NH/NT=0.67; NV/NT=0.36; NEA from Europe NH/NT=0.69; NV/NT=0.30). The most similar hunter-gatherers groups are those from Tasmania (NH/NT=0.55; NV/NT=0.38) and Australia (NH/NT=0.56; NV/NT=0.36), which are traditionally described as being mixed diet groups with significant amounts of vegetables in their diet. Interestingly, European fossils (both AMH and Neandertals) are close to one another being the most distinct Near East individuals, especially for the proportion of horizontal scratches (NH/NT= 0.25; NV/NT=0.39) (Figure 2). The values obtained indicate a mixed diet in the fossil groups, but a more carnivorous one in the Near East individuals. This result is in accordance with that obtained in 1996 by Lalueza et al., and in 2012 by Pinilla.

Individual values for the fossil remains show great variability. This result is in agreement with previous studies and has been tentatively explained by researchers as an eco-geographic variation pointing to the importance of local-climatic adaptations of the Paleolithic humans to their environment (Burke, 2000, 2004; Pérez-Pérez et al., 2003; Bar-Yosef, 2004; El-Zaatari et al., 2011; Fiorenza et al., 2011). A feature that makes hominins unique from the perspective of nutritional adaptations is food processing.

to the intra-individual variations (Pérez-Pérez et al., 1994; Alrouzan, 2009). However, this assertion has been rarely tested. Most microwear papers use only one tooth, and, whenever possible, the same in all subjects in order to avoid this problem (e.g., M₂; see: Galbany et al., 2009). Although this is the case with large numbers of samples of extant populations, however when considering fossil remains, especially from the Paleolithic era, where samples are scarce, this limitation is forgotten and whichever tooth available is considered under the assumption that no differences will be found. Yet, as I mentioned before, differences might exist. In some cases, differences between teeth existed without knowing whether to attribute them to characteristics of the sample (Estebanz et al., 2009) or intra-population differences (Alrouzan, 2009). We encourage researchers to analyze all the teeth available, and to thoroughly examine the microwear pattern internally (in occlusal microwear, differences have been found in tooth series M1-M2-M3 as well as in the different occlusal facets: Gordon, 1982; Teaford & Tylenda, 1991; Teaford & Runestad, 1992; Mahoney, 2006). These differences are no handicap, if the procedure is always standardized. In the sample included in this paper, Adélaïde presents 5 well-preserved postcanine teeth (62.5% of the mandibular teeth involved), three from the right side (P3LR, and M1LR, M2LR) and two from the left (P4LL, M2LL). All teeth were analyzed and the results show that they present a similar pattern, with the density of vertical scratches dominating other orientations, and the longest scratches being horizontal on all teeth. The buccal microwear patterns, driven by cheek cycling movements to process food during chewing, showed no important differences (not even a tendency) independent of whether premolar or molar teeth were observed (Table 1). Moreover, no significant differences ($P = <0,005$) were found as a result of laterality, even though only mandibular teeth can be used in this way, given that no differences in motion can be performed by maxilla-mandible. For analytical purposes, this preliminary analysis indicates, therefore, that the examination of one tooth per individual is adequate to avoid over-representation although, if the sample allows it, the median of the well-preserved teeth helps to avoid problems related to intra-individual variation. Moreover, by excluding individuals with severe dental pathologies (Lalueza & Berkovitz, 1992), no laterality is found.

2.4. *Intra-population differences.* Even though some authors have argued that there are no significant differences between infant and adult microwear patterns (Gamza, 2012), the analyses performed on the buccal area (Pérez-Pérez et al., 1994; Pinilla et al., 2011) prevents the use of infants. However, the inclusion of the La Olmeda youngsters did not distort the results given that these subjects had all permanent teeth (P3-M2), and were useful for the analyses ($P = <0,005$). Nevertheless, we encourage researchers to perform age-related analyses prior to making any assumptions as there could be differences related to food itself or to food consistency that might alter abrasivity values.

2.5. *Statistics.* Normality was analyzed for each using the K-S test (Kolmogorov-Smirnov) and the results indicate that all the microwear variables follow normal

2. Materials and Methods

2.1. *Materials.* Analysis was performed on already published data on individuals from different cultures with different chronologies, subsistence and mobility patterns. Given that all the microwear data had been published previously it was therefore generally available (Table 1). The populations include mean values for: 1) 36 (18-35 years old) subjects, **actually living in Spain at Alicante** (Romero & De Juan, 2007); 2) 77 subjects (65 adults over 20 years old and 12 youngsters around 16 years old) from La Olmeda, near Palencia in Spain, from IX to XII century (Pérez-Pérez et al., 1994); 3) 1 subject, to whom we assigned the name of Adelaide (Puech et al., **in print**), from the Middle Ages, from the sarcophagus of the collegiate church of Saint-Frambourg in Senlis Oise (France); 4) 12 Islamic subjects from the Middle Ages, from La Losilla (IX-XII century) in Valencia (Spain) (Romero & De Juan, 2007); 5) 16 subjects from the Chalcolithic period from Villena (Valencia, Spain) (Romero & De Juan, 2007); 6) 16 subjects from the Bronze Age site of the Cabezo Redondo (1800 to 1500 BC.) (Romero & De Juan, 2007); 7) 153 modern hunter-gatherer and agricultural subjects with solid contrasts in dietary habits to serve as baseline data, collected during the XIXth century, with precise information on their diets and ways of life, from the British Natural History Museum comprising: 20 Eskimo Inuits eating mainly fish and very few vegetables (Canada); 20 Fueguians subsisting on fish (Tierra del Fuego), 17 Indians, again predominantly fish eaters, from Vancouver (Canada); 5 Lapps, pastoralists with a high consumption of meat, fish and cereal (North Europe); 15 Bushmen with a mixed diet from the Kalahari (South Africa); 18 Australians with a mixed diet from a mesothermal environment; 11 Tasmanians; 18 Andaman Islanders; 9 Veddahs (Sri Lanka); 20 Hindu agriculturalists from Orissa and Buthan (Lalueza et al., 1996); 8) 12 Upper Paleolithic subjects restricted geographically to France, these being: Cromagnon 4, La Madeleine, Round du Bary and Veyrier-sous-Salève 1963 (Perez-Perez et al., 2003), Baume de Montclus, Isturitz 3, Gramat, Rochereil, Lachaud 3, Lachaud 5, Cavillon and Le Jeune Prince (Pinilla *et al.* **in print**); and 9) 8 Neanderthals from the two following geographical areas, from Western Europe: Banyoles, La Chaise Suard, La Chaise abri Bourgeois, St. Césaire and La Quina V; and from the Near East: Amud 1; Tabun 1 and Tabun 2 (Perez-Perez et al., 2003).

All available data has been obtained using the same methodology to enable comparisons. However, two important limitations should be noted. Firstly, data were obtained by different researchers and therefore **inter-observer error may have given rise to quantitative errors. The analysis of this methodological error has been quantified around 6%, considered to be assumable** (see: Galbany et al., 2005). Secondly, not all researchers included data from **all the 15 microwear variables, this limitation affected comparisons.**

2.2. *Methods.* All data were obtained by faculty at the Animal Biology Department, University of Barcelona, who followed exactly the same methodology. No original material was used. Only high resolution casts were observed. Moulds were obtained from museums and institutes (see references for the sources of material). In all cases, a standard procedure was applied at every stage: cleaning the teeth, obtaining the **positive** replica of the surface at a microscopic level (for a detailed description of the procedure, see: Galbany & Pérez-Pérez, 2004; Galbany et al., 2005, 2009). In all cases,

KEY WORDS: *dental microwear, enamel striae, diets, types of food, hunter–gatherer, pastoralist, agriculturalist, culture, ethnographic atlas, aquatic landscapes, comparative method*

1. Introduction

Studies on different biological populations have reported that there are various typologies of tooth wear, and that these reflect the prevalent diets or subsistence strategies (Campbell, 1939). During the last decades, a quantitative method has been developed to record the representatative movements of food between the cheek and the back teeth by the dental buccal wear striae on tooth enamel, demonstrating its utility in revealing dietary preferences (Puech, 1976; Puech, 1981; Pérez-Pérez et al., 1994; Lalueza et al., 1996; Pérez-Pérez et al., 2003; Galbany et al., 2005; Galbany et al., 2009, 2011; Martínez et al., 2004; Estebanz et al., 2009, 2012). Striae are produced by abrasive mechanisms linked to patterns of chewing, food qualities, grit, dirt and processing techniques (Puech & Prone, 1979; Peters, 1982; Puech, 1983; Piperno, 1988; Scott & Turner, 1988:110; Piperno & Ciochon, 1990; Lalueza & Pérez-Pérez, 1994; Teaford & Lytle, 1996; Mahoney, 2006; Alrousan & Pérez-Pérez, 2008). However, the multi-origins of striae should prevent researchers from categorical assessments, at least when culture plays a significant role in dietary habits (either in the procurement or the treatment of food). Moreover, the categorization of behavior is fundamentally difficult since most subjects do not demonstrate a single behavior but usually several different ones, to varying degrees. They do not eat isolated nutrients, but rather meals consisting of a variety of foods with complex combinations, thus the evaluation of a determined diet has little meaning if not to analyze the adaptations in the modes of selection and preparation of foods.

It seems fairly obvious that the exploitation of resources depended on a large number of factors including efficiency, availability, preferences, etc. especially in hunter-gatherer populations. However, some authors have argued that during the Paleolithic period some groups might have been really specialized, consuming only a particular type of food (either vegetables or meat) independent of climatic variations, the geographical distribution of the groups, and chronology (see for example: Bocherens et al., 2005). Evidence emerging during the last decade, from buccal microwear and other methods, points to a higher variation in the Paleolithic people's diet with an important eco-geographic component (Pérez-Pérez et al., 2003; El-Zaatari et al., 2011; Fiorenza et al., 2011, etc.). Regarding the economic variability in the groups, it is becoming more widely accepted that some populations, probably only in certain environments, might have consumed important quantities of fish and seafood (Antunes, 2000; Balter & Simon, 2006; Roselló & Morales, 2006; Stringer et al., 2008; Hardy & Moncel, 2011). One of the first descriptions relates to the broad food choices of the proto-Neanderthal man located in a fluvial lake of Banyoles (with a disputed date by Grün et al., 2006), that was tentatively extended to fish, from comparisons in the particularly severe wear which was very similar to that of more modern humans from

Lake Mungo, who lived 40 kyr ago on the lakeshore, adapting to a deteriorating climate in dry conditions, with a staple year-round diet of fish (Puech, P.-F. & Puech, S., 1993; Bowler, 2003). Fish were the primary mode of subsistence for the Mungo man, who has left evidence that he ate sand perch and cod and also freshwater mollusks. In the bushes nearby, he hunted mammals and found eggs (Jones, 1973).

A lot of attention has focused on the so called “Middle-to-Upper Paleolithic transition” suggesting that human diet may have changed significantly in relation to technology, which allowed the more regular and efficient capture of animals (Binford, 1984, 1985, 1989, 1992, etc.), with the inclusion of some hitherto unused foods by previous human populations (see: Trinkaus, 1986, 1989; Stiner, 2001, 2002; Trinkaus & Hilton, 1996; Stiner et al., 1999, 2000; Stiner & Munro, 2002; Kaplan et al., 2000; Richards et al., 2001; Uliljaszek, 2002; Stewart, 2004; Kuhn & Stiner, 2006; Stiner & Kuhn, 2009). However, we should not forget that the underlying transmission and retention of feeding behavior is essentially dependent on cultural mechanisms (rites, myths and social identities, see Bacon, 1765; Belfer-Cohen & Hovers, 2001).

The fossil remains of once-living organisms provide hard evidence of human evolution, involving different groups of species and populations, since the time that our ancestors essentially lived in trees feeding on edible leaves and fruits. We argue that many aspects of these fossil remains provide a natural archive of prehistoric hominid food consumption in terms of dietary patterns which were dependent upon: climate, collecting and hunting proficiency, food-processing technology, and available foods. Thus, here we aim to extract information on how organisms responded to different food sources from tooth wear analysis, which provides direct evidence from the use of teeth. Yet tooth wear is difficult to interpret, there being no straightforward explanation, given the multiple causes of observable manifestations. A great amount of the wear is related to diet, but abrasion is more complex as it includes abrasive particles which can be traced either to cooking food directly on a fire or to drying it in the open air, both permitting grains of sand and dust to be incorporated in the food, producing particular aspects that are compatible with the functional use of the teeth by our closest extinct human relatives (Puech, 1979, 1981).

The primary purpose of this study is to explore diversity in the human diet since a fundamental principle of human health and nutrition assumes that a varied diet increases overall health. Hence, those hominid populations that chose to diversify their subsistence base may have had a selective advantage. Archaeologists are now pushing the concept of a broad-spectrum diet adaptation back in time to the Oldowan stone artifact culture, and direct evidence of the slaughter of terrestrial and aquatic animals has been dated to 1.95 Ma. (Steele, 2010).

To test the broadening of diet as a model of nutritional ecology, with the adoption of the buccal dental microwear method, we have documented the characteristics of wear in a variety of environmental, temporal, and cultural contexts which provide fragmentary glimpses into what were complex and evolving patterns of subsistence, settlements, and mobility over the last **hundred thousand** years. The tooth microwear of Middle Paleolithic and Upper Paleolithic hunter-gatherers has been compared to that of modern individuals with known diets from different environments and economies in order to discern eating patterns reflecting different dietary traditions.

only cheek teeth (premolar and molar) were considered in this analyses since the striae produced by abrasives show the path traveled by the food bolus compressed by the cheeks and because the anterior teeth are highly affected by paramasticatory activities (Brace, 1967: 814; Molnar et al., 1972; Puech, 1979; Larsen, 1985; Bermúdez de Castro et al., 1988; Lalueza, 1992; Lalueza & Frayer, 1997; Bax & Ungar, 1999; Lozano, 2001; Lozano et al., 2004, 2008). Scratches formed on the sides of the back teeth by the food bolus, which is moved backwards and forwards in circular movements by the cheeks in the chewing process, are directly related to abrasive particles along with ingested food (Romero et al., 2012). A crucial step in the microwear analyses is the elimination of all teeth that present post-mortem or non-dietary related buccal surfaces. Only microwear images in which striae are clear and delimited are analyzed in buccal microwear studies (see: King et al., 1999; Pérez-Pérez et al., 2003; Martínez & Pérez-Pérez, 2004; Teaford, 2007). The striae characteristics are observed using low magnification scanning electron microscope photographs of the dental impression surfaces. The standardization of the process allowed the present comparisons since all images were obtained at a 100X magnification (Puech & Pant, 1980; Pérez-Pérez, 1990; Pérez-Pérez et al., 1994). The micrograph, of a 0.56 mm² area, was software treated (i.e., Photoshop) to reduce tilt and uniform grayscale. The final stage involves the semiautomatic measurement of the striae (the software used is: Sigma Scan SPSSTM) and the recording of density and length in four orientations: horizontal (H), vertical (V), back oblique to 45° (mesio-distal direction, MD), and forward oblique 45° (distal to mesial direction, DM). Moreover, standard deviation of lengths (S) is also recorded for all orientations, and the summary variables (total density, total length, and total standard deviation of length) are obtained (this entire procedure is standardized and we recommend the previously cited papers for a description). In 1996, Lalueza et al. considered that the proportion of horizontal vs. vertical scratches on the buccal surface could well explain primary dietary differences and, since then, these variables are also considered: NH/NT, NV/NT and NH/NV. Therefore, 18 variables are considered in the analyses (it should be noted, however, that not all these variables were available in the papers used and therefore the quantity of these variables depends on the authors. See Table 1).

The overall characteristics depend on the types of food consumed and the methods used in their preparation such as cooking (Puech, 1978; Puech & Pant, 1980; Pérez-Pérez, 1990; Pérez-Pérez et al., 2003). Thus, the interpretation of patterns gives rise to fundamental questions regarding factors that are both intrinsic (i.e., the durability of the tooth tissue and the abrasivity of food: Puech, 1983; Piperno, 1988; Lalueza & Pérez-Pérez, 1994) and extrinsic (i.e., processing techniques and dust etc.: Puech & Pant, 1980; Peters, 1982; Teaford & Lytle, 1996; Alrousan & Pérez-Pérez, 2008), and the analysis of the process calls for experimental methods (Puech, 1979; Puech & Prone, 1979; Puech et al., 1981; Wood, 2013).

2.3. *Intra-individual variability.* It is often assumed that all teeth from the same individual will present the same characteristics since the food intake and the techniques related to ingestion procedures are the same, making internal variability always inferior

distributions. Therefore, parametric tests were applied. This analysis was performed for each data subset and in all cases data followed normal distributions. For statistical purposes, SPSS 18 was used. Statistical analyses included One-way ANOVA and MANOVA (signification at 0.005). As sample size is small, to avoid a possible skew of data, re-sampling using 1000 permutations was applied, and the results given in this paper are always those obtained after bootstrapping. The Levene test for equality of the variances of the sample was also used. Only the length of horizontal scratches (XT) was found to be significant ($P=0.020$), therefore this variable was not included in the ANOVA. Most microwear analyses include PCA (Principal Component Analyses) and LDA (Linear Discriminant Analyses). However, variables providing information about diets are more complex to examine, being more useful when the objective is to differentiate groups. Furthermore, they require the same set of variables in all individuals (which in this study was not always found). Finally, explaining dietary differences using abrasivity (NT and XT) and indices (NH/NT and NV/NT) allows the use of straightforward statistical analyses.

3. Results and Discussion

3.1. *Paleolithic and historic dietary changes.* The first analysis included only those groups for which the original 15 variables were available. This limited the sample to the Middle Ages populations of La Olmeda (Pérez-Pérez et al., 1994) and Adélaïde (Puech et al., in print) and 8 Upper Paleolithic modern humans: Baume de Montclus, Isturitz 3, Farincourt, Gramat, Rochereil, Lachaud 3, Lachaud 5, Cavillon, and Le Jeune Prince (Pinilla et al., in print). The main difference between hunter-gatherer groups and those of the Middle Ages can be found in the higher density of scratches, and therefore a more abrasive diet was evaluated in prehistoric groups (NT $P=0.006$), 80% of the density variables being significantly different (Table 2). The difference between these two groups is clear; Paleolithic individuals surpass in all cases 170 striae, while those from the Middle Ages do not surpass 150 striae (Figure 1). The possibility that this key difference was related to abrasivity, induced us to include data from historic and protohistoric groups (extant modern humans, Islamic, Chalcolithic and Bronze Age) for which density and length of striae are available (Romero & De Juan, 2007). The analysis of the summary variables of the density and length of the scratches confirms the difference observed between the Paleolithic and the other populations, but the scenario is more complex (Figure 1). Extant modern humans, Islamic, Chalcolithic and Bronze Age groups differed from hunter-gatherers from the Upper Paleolithic and the Middle Ages in that the length of the scratches were shorter ($F=54.743$ $P=0.000$); with regards to the density of scratches, results showed that the Upper Paleolithic and the Chalcolithic groups showed higher densities, while groups from the bronze age, Islamic, Middle Ages and extant humans showed significantly lower densities ($F=39.646$ $P=0.000$). Especially interesting was the comparison between the Islamic vs the Christian populations from the Middle Ages. There were significant differences, evident in the length of the scratches. The lack of individual values together with those of the 15 variables did not allow any further conclusions to be made but the growing number of

Stone tools and damaged bones, millions of years old, tell us that early man cracked and split bones to extract marrow. The difference in the action of teeth between crushing and grinding when processing meat being determined by the type of meat selected. This activity, affecting food consistency, indicates that man was conscious of having direct control over his own sources of food. *Man the Hunter*, while on the look out for possible new foods, soon discovered that seeds and grain can best be eaten when milled. It should be noted that the enamel surface of *Australopithecus* and *Homo habilis* teeth (1,8 to 3 million years ago) present microwear attributed to amorphous silica present in *Cyperaceae* (sedges) and *Gramineae* (Puech, 1986). Food processing accounts for the mastication of diverse diets by the unpracticed teeth of hominins (Wrangham, 2013).

The plotting of individuals in the indices figure shows, apart from the vast variability observed, ranges of dispersion in the two populations greatly overlapping, which might be indicative of similar diets in Neandertals and modern humans (Pinilla, 2012). Nevertheless, different tendencies can be observed when comparing both groups: 1) the variation observed in AMH is greater than that observed in Neandertals (AMH NH/NT S=0.42; NV/NT S=0.10; NEA NH/NT S=0.27; NV/NT S=0.09); 2) R^2 values differ showing Neandertals to have the lowest value ($R^2= 0.14$), AMH the mean value ($R^2= 0.31$) and modern hunter-gatherers the highest value ($R^2= 0.79$) which is related to the intra-group variability observed. Nevertheless the main source of variability within Neandertals are the different geographical areas. If we consider only European Neandertals, even though they vary chronologically, the dispersion is minimal (NH/NT S=0.19; NV/NT S=0.04). There are no clear differences between OIS 3 and OIS 4 individuals, so no obvious chronological, climatic or geographic distribution can be assessed (please note that Pérez-Pérez et al., 2003, found a tendency whereby individuals from OIS 4 (a cold isotopic stage) showed higher densities and individuals from OIS 5 and 3 (warmer isotopic periods) lower densities; but this distinction is not seen in the indices with this sample (Figure 3). While diet might have been more or less stable in those groups, differences might have been related to abrasivity (related either to changes in food consistency and/or food processing techniques) which are not visible in the indices.

3.3. *Some fishing sites*. However, the variation observed in the AMH can be explained chronologically (Figure 4) with Early Upper Paleolithic subjects (including the pre-LGM Cromagnon, the LGM Cavillon, Jeune Prince and Isturitz, and the early post LGM Round du Bary) showing a pattern more similar to that of Neandertals, with lower values for both variables and less variability than can be witnessed in individuals from the Late Upper Paleolithic (including the late LGM Veyrier-sous-Salève 1963, La Madeleine, Lachaud 3 and Lachaud 5, and the Holocene/proto-Holocene individuals of Gramat, Rochereil, and Baume de Montclus). Samples have been segmented in two chronological periods; younger and older from 15,000 years. It corresponds to the retreat of the ice sheets after the Last Glacial Maximum and to the earliest evidence of pottery which provided new ways for processing and consuming foods (Craig et al. 2013). The AMH sample plotted at the top of the vertical scratches portion, showing a

number of dispersed populations, this pattern may be considered a core attribute of a civilization (the term used in the way Bacon referred it to “culture”, 1765). As a result, dental enamel buccal microwear pattern analysis emerges as a complementary tool when examining archaeological assemblages in determining human food consumption.

To summarize, we found that: 1) the density of scratches is significant, providing an account of changes in societies over time and indicating the series of stages from hunting and gathering to present day societies; 2) the horizontal to vertical striae proportion, helps to determine the predominant dietary pattern forming the basis of cultural identity, and allows the creation of a food atlas which reveals a broad dietary spectrum in AMH which must have played a vital role in the demographic expansion that occurred after the last Ice Age; and 3) in specific sites the microwear striae orientation pattern points to aquatic foods being consumed by our Stone Age ancestors.

While a number of practitioners are now using the same approach, not enough work has yet been done to explore all the possibilities of this method. Adjustments for striae variables in multivariate analyses are necessary to remove the confounding effects of the interaction of other dietary components. In terms of accuracy, the evolution in the study of tooth microwear is spectacular, offering clusters of identified food groups and additional features could expand the scope and utility of buccal microwear analysis. We think that more striae data will improve the identification of major dietary clusters whose atlas can be used to locate fossils. Different magnifications of the microwear of the buccal surface could further help to clarify the striae distribution by adding new evidence about the striae length of the buccal face of the cheek teeth corresponding to particular types of food. Different measurement systems are essential to ascertain the characteristics of the food consumed in order to study the nutritional adaptations of Paleolithic man in applied physical anthropology. The aim of this method is to characterize feeding behaviors conditioned by the major dynamic forces of geography, technical progress and culture, an exercise which has been informative up until now since it has confirmed the hypothesis made by Raymond Dart (1961, 1969) that “fishing may well have preceded agriculture as a civilized factor in human history”. The coastal, riverside and lacustrine settlements might be related to excellent positions facilitating specialized fishing practices.

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- Binford, L. (1992) Subsistence: A Key to the Past. In: Jones S, Martin R & Pilbeam D (Eds) *Cambridge Encyclopedia of Human Evolution* Cambridge University Press, pp. 365-368
- Bocherens, H., Drucker, D.G., Billiou, D., Patou-Mathis, M. & Vandermeersch, B. (2005) Isotopic Evidence for Diet and Subsistence Pattern of the Saint-Césaire I Neanderthal: Review and Use of a Multi-Source Mixing Model *J Hum Evol* **49**: 71-87
- Bowler, J.M., Harvey Johnston, H., Olley, J.M., Prescott, J.R., Roberts, R.G., Shawcross, W., Nigel, A., & Spooner, N.A. (2003) New Ages for Human Occupation and Climatic Change at Lake Mungo, Australia *Nature* **421**: 837-840.
- Brace, C.L. (1967) Environment, Tooth Form, and Size in the Pleistocene *J Dent Res* **46(S)**: 809-816
- Bullinger, J. (2002) Les Stations de Veyrier. In: Curdy P & Praz JC (eds) *Premiers hommes dans les Alpes de 50000 à 5 000 avant Jésus-Christ* (Musées cantonaux du Valais). Lausanne: Payot, pp. 135-39
- Burke, A. (2000) Preface: Hunting in the Middle Paleolithic. *Int J Osteoarch* **10**: 281-285
- Burke, A. (2004) The Ecology of Neanderthals: Preface *Int J Osteoarch* **14**: 155-161
- Campbell, T.D. (1939) Food, Food Values and Food Habits of the Australian Aborigines in Relation to their Dental Conditions *Australian Dental Journal* **43**: 1-15.
- Coles, B. (Ed) (1992) *The Wetland Revolution in Prehistory*. Exeter: The Prehistoric Society.
- Craig, O.E., Saul, H., Lucquin, A., Nishida, Y., Taché, K., Clarke, L., Thompson, A., Alftoft, D.T., Uchiyama, J., Ajimoto, M., Gibbs, K., Isaksson, S., Heron, C.P., Jordan, P. (2013) Earliest Evidence for the Use of Pottery. *Nature* **496**: 351-354
- Dart, R.A. (1961) The Recency of Man's Aquatic Past. *The New Scientist* 1668-1670
- Dellenbach, M.E. (1935) La Conquête du Massif Alpin et de Ses Abords par les Populations Préhistoriques *Revue de géographie alpine* **23(2)**:147-416
- Drucker, D.G. & Gambier, D.H. (2005) Determination of the Dietary Habits of a Magdalenian Woman from Saint-Germain-la-Rivière in Southwestern France Using Stable Isotopes *J Hum Evol* **49**: 19-35

- Grün R, Maroto J, Eggin S, Stringer C, Robertson S, Taylor L, Mortimer G & McCulloch M (2006) ESR and U-series analyses of enamel and dentine fragments of the Banyoles mandible *J Hum Evol* **50**: 347-358
- Hardy BL & Moncel MH (2011) Neanderthal Use of Fish, Mammals, Birds, Starchy Plants and Wood 125-250,000 Years Ago *PLoS ONE* **6**(8): e23768
- Jones R (1973) Emerging picture of Pleistocene Australians *Nature* **246**:278–281
- Kaplan H, Hill K, Lancaster J & Hurtado AM (2000) A theory of human life history evolution: diet, intelligence, and longevity *Evol Anthropol* **9**: 156-185
- King T, Andrews P & Boz B (1999) Effect of taphonomic processes on dental microwear *Am J Phys Anthropol* **108** (3): 359-373
- Kuhn SL & Stiner M C (2006) Whar's a mother to do? The division of labor among Neanderthals and Modern Humans in Eurasia *Curr Anthropol* **47**(6): 953-980
- Lalueza C (1992) Information obtained from the microscopic examination of cultural striations in human dentition *Int J Osteoarchaeol* **2**: 155-169
- Lalueza C & Berkovitz B (1992) Differences in Striations Pattern in Individuals with Unilateral Buccal Pathologies *International Journal of Anthropology* **7**: 27-39
- Lalueza C & Pérez-Pérez A (1994) Dietary information through the examination of plant phytoliths on the enamel surface of human dentition *J Arch Sci* **21**: 29-34
- Lalueza C, Pérez-Pérez A & Turbón D (1996) Dietary inferences through buccal microwear analysis of Middle and Upper Pleistocene human fossils *Am J Phys Anthropol* **100**: 367-387
- Lalueza C & Frayer DW (1997) Non-dietary marks in the anterior dentition of the Krapina Neanderthals *Int J Osteoarchaeol* **7**: 133-149
- Larsen CS (1985) Dental modifications and tool use in the Western Great Basin *Am J Phys Anthropol* **67**: 393-402
- Lozano M (2001) Estrias culturales en la superficie vestibular de la dentición anterior de los individuos de la Sima de los Huesos (Sierra de Atapuerca, Burgos) *Rev Esp Antrop Biol* **22**: 39-50
- Lozano M, Bermúdez de Castro JM, Martín-Torres M & Sarmiento S (2004) Cutmarks on fossil human anterior teeth of the Sima de los Huesos site (Atapuerca, Spain) *J Archaeol Sci* **31**: 1127-1135

Pinilla B *Dieta y adaptacionesw ecológicas de las poblaciones humanas del Pleistoceno Medio y Superior*, Barcelona (PhD, University of Barcelona) 2012

Pinilla B, Perez-Perez A, Puech B & Puech PF (in press) "Usure dentaire et mode masticatoire de la Dame de Cavillon" in: de Lumley H (ed) *Monographie de la grotte du Cavillon*, tome 3: Etude anatomique du squelette de la Dame du Cavillon, Institut de Paléontologie Humaine, Paris, pp. 838-862

Piperno D *Phytolith analysis: an archaeological and geological perspective* Academic Press, San Diego 1988

Piperno D & Ciochon R (1990) Scratching the surface of evolution *New Scientist* (10 Nov), 47-49

Puech PF (1976) "Recherche sur le mode d'alimentation des hommes du Paléolithique par l'étude microscopique des couronnes dentaires" in: de Lumley H (ed) *La Préhistoire Française*. CNRS, Paris, pp. 708-709

Puech PF (1978) L'alimentation de l'homme préhistorique. *La Recherche* **94**: 1029-1031

Puech PF (1979) The diet of early man: evidence from abrasion of teeth and tools *Current Anthropology* **20**(S): 90-92.

Puech PF & Prone A (1979) Reproduction expérimentale des processus d'usure dentaire par abrasion : implications paléoécologiques chez l'Homme fossile *Comptes rendus*, série D, **289**:895-898

Puech PF & Pant R (1980) Un modèle d'étude de l'alimentation des hommes fossiles *Bull Mém Soc Anthropol Paris* **7**(13): 61-64

Puech PF (1981) Tooth Wear in La Ferrassie Man *Current Anthropology* **22**: 424-430

Puech PF, Prone A & Albertini H (1981) Reproduction expérimentale des processus d'altération de la surface dentaire par friction non abrasive et non adhésive: application à l'alimentation de l'Homme fossile *C R Acad Sci Paris Ser II*, **293**: 729-734

Puech PF (1983) Acidic-food choice in H.habilis at Olduvai *Current Anthropology* **25**: 349-350.

Puech PF (1986) Tooth microwear in Homo habilis at Olduvai, In "Teeth Revisited: Proceedings of the VIIth International Symposium on Dental Morphology" Russell D.E., Santoro J.-P., Sigogneau-Russell D., Eds, Mém. Mus. Natn. Hist. Nat. Paris, série C, **53** :399-414.

Stiner MC & Munro ND (2002) Approaches to prehistoric diet breadth, demography, and prey ranking systems in time and space, in: Hockett B (Ed) *Advances in Paleolithic zooarchaeology J Archaeol Method Theory* **9**: 181-214

Stiner MC (2002) Carnivory, coevolution, and the geographic spread of the genus *Homo* *J Arch Res* **10**: 1-63

Stiner MC & Kuhn SL "Paleolithic diet and the division of labor in Mediterranean Eurasia" in: Hublin JJ & Richards MP (Eds) *The Evolution of Hominin Diets: Integrating Approaches to the Study of Palaeolithic Subsistence*. Springer Science + Business Media B. V. 2009 pp. 157-169

Strauss LG (1995) The Upper Paleolithic of Europe: an overview *Evol Anthropol* **4**: 4-16

Strauss LG "The Aurignacian"? Some thoughts" in: Zilhão J & d'Errico F (Eds) *The Chronology of the Aurignacian and of the Transitional Technocomplexes: Dating, Stratigraphies, Cultural Implications* Proceedings of Symposium 6.1 of the XIVth Congress of the UISPP (University of Liège, Belgium, September 2-8, 2001) *Trabalhos de Arqueologia* **33**, 2003 pp. 11-17

Strauss LG (2005) A mosaic of change: the Middle-Upper Paleolithic transition as viewed from New Mexico and Iberia *Quat Int* **137**: 47-67

Strauss LG "Faunal exploitation by the last Neandertals and by early Upper Paleolithic humans on the Iberian Peninsula: Continuity and/or change?" in: *Variability in human hunting behavior during Oxygen Isotope Stages (OIS) 4/3 : implications for understanding modern human origins* 11th International Conference of ICAZ (International Council for Archaeozoology), Paris 23-28 August 2010 (Abstract)

Stringer CB, Finlayson JC, Bartond RNE, Fernández-Jalvo Y, Cáceres I, Sabin RC, Rhodes EJ, Currant AP, Rodríguez-Vidal J, Giles-Pacheco F & Riquelme-Cantal JA (2008) Neanderthal exploitation of marine mammals in Gibraltar *Proc Natl Acad Sci USA* **105** (38): 14319-14324

Teaford MF & Tylenda CA (1991) A new approach to the study of tooth wear *J Dent Res* **70**: 204-207

Teaford MF & Runestad JA (1992) Dental Microwear and diet in Venezuelan primates *Am J Phys Anthropol* **94**: 339-363

Teaford MF & Lytle J (1996) Brief Communication: Diet-Induced Changes in Rates of Human Tooth Microwear: A Case study Involving Stone-Ground Maize *Am J Phys Anthropol* **100**: 143-147

TABLES

Table 1. Sample analyzed, including the population and/or individual considered, number of Individuals (N; where the whole population is considered), article used as reference, and microwear values. Note that not all individuals/groups have all microwear variables. Depending on the data contained in the article. The subject Adélaïde has 5 postcanine well-preserved buccal surfaces. All teeth have been kept to analyze intra-individual variability and possible effects of laterality.

<u>Population</u>	<u>N</u>	<u>Reference</u>	<u>NH</u>	<u>XH</u>	<u>SH</u>	<u>NV</u>	<u>XV</u>	<u>SV</u>	<u>NMD</u>	<u>XMD</u>	<u>SMD</u>	<u>NDM</u>	<u>XDM</u>	<u>SDM</u>	<u>NT</u>	<u>XT</u>	<u>ST</u>	<u>NH/NT</u>	<u>NV/NT</u>	<u>NH/NV</u>
<i>Fuegian</i>	20																	0.24	0.51	0.13
<i>Inuit</i>	20																	0.25	0.45	0.11
<i>Vanconuv</i>	17																	0.17	0.49	0.08
<i>Lapps</i>	5																	0.33	0.46	0.15
<i>Andamane</i>	18	Lalueza et al 1996																0.89	0.33	0.30
<i>Veddahs</i>	9																	0.95	0.32	0.31
<i>Bushmen</i>	15																	1.04	0.29	0.31
<i>Tasmania</i>	11																	0.55	0.38	0.21
<i>Áust</i>	18																	0.56	0.36	0.20
<i>Hindus</i>	20																	2.17	0.24	0.51
<i>La Olmeda</i>	65	Pérez-Pérez et al 1994	5.50	97.40	53.00	46.50	171.20	127.50	12.90	124.10	87.70	18.20	126.90	91.60	83.10	151.20	127.00	0.07	0.56	0.12
	P4L left		19	161.31	93.51	73	159.51	106.63	32	121.60	68.58	13	127.74	60.95	137	147.89	94.21	0.14	0.53	0.26
	M2L left		10	233.72	136.73	88	160.01	87.18	13	143.30	70.01	10	122.74	49.94	121	161.23	90.48	0.08	0.73	0.11
<i>Adélaïde</i>	Mean left		14,5	197.51	115,11	80,5	159,76	96,90	22,5	132,45	69,29	11,5	125,24	55,45	129	154,56	92,34	0,11	0,63	0,19
	P3L right		29	141.35	56.41	78	126.88	62.86	34	95.58	38.01	15	97.68	30.93	156	119.94	56.74	0.19	0.50	0.37
	M1L right		24	160.57	71.41	82	160.16	85.62	27	119.50	78.46	30	135.53	94.42	163	148.95	85.06	0.15	0.50	0.29
	M2L right		17	149.53	60.41	75	169.50	106.87	26	164.27	78.66	26	130.00	63.98	144	159.07	91.33	0.12	0.52	0.23

NE4	Banyoles			1.00	0.31	0.31
	La Chaise Suard	Pérez-Pérez <i>et al</i> 2003		0.60	0.25	0.15
	La Chaise Bourgeois			0.72	0.35	0.26
	St. Césaire			0.64	0.32	0.21
	La Quina V			0.47	0.26	0.12
	<u>MEAN (N=5)</u>			<u>0.69</u>	<u>0.30</u>	<u>0.21</u>
	Amud 1	Pérez-Pérez <i>et al</i> 2003		0.19	0.54	0.11
	Tabun 1			0.30	0.37	0.11
	Tabun 2			0.25	0.26	0.06
	<u>MEAN (N=3)</u>			<u>0.25</u>	<u>0.39</u>	<u>0.09</u>
	<u>MEAN (N=8)</u>		<u>0.47</u>	<u>0.34</u>	<u>0.15</u>	

FIGURES

Figure 1. Density (NT) and Length (XT) of scratches on Upper Paleolithic modern humans from Baume de Montclus, Isturitz 3, Farincourt, Gramat, Rochereil, Lachaud 3, Lachaud 5, Cavillon and Le Jeune Prince (Pinilla et al., [in print](#)), Middle Ages individuals from La Olmeda (Pérez-Pérez et al., 1994) and Adélaïde (Puech et al., [in print](#)), extant humans, Islamic, Bronze Age and Chalcolithic (Romero & De Juan, 2007).

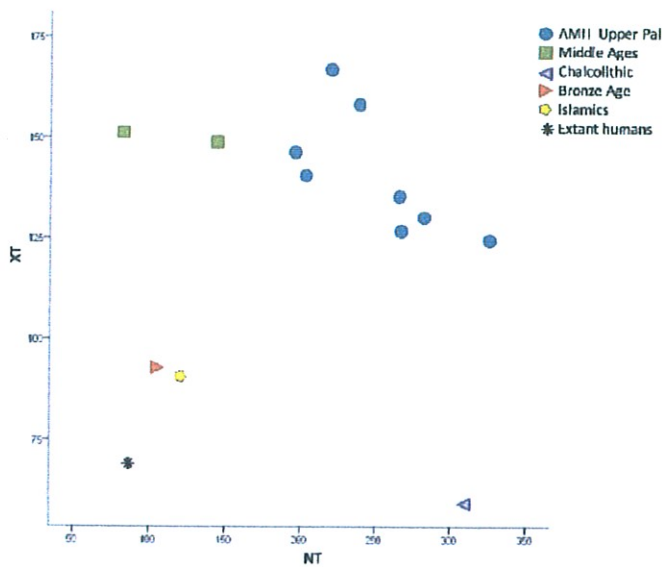


Figure 3. Individual values of the fossil remains in the indices plot. Individuals are described in the plot abbreviated. AMU=Amud; TB1= Tabun 1; TB2= Tabun 2; QUI=Quina 5; SUA=Lachaise Suard; BURG= La Chaise Burgois; BANY= Banyoles; CÉS= St. Césaire; JP= Jeune Prince; MAD= La Madeleine; LA3= Lachaud 3; LA5= Lachaud 5; IST=Isturitz; CRO= Cromagnon 4; RB= Round du Bary; CAV= Cavillon; ROCH= Rochereil; GRAM= Gramat; VEY= Veyrier-sous-Salève 1963; MONT= Baume de Montclus. Hunter-gatherers are represented by squares, keeping the color that represents main subsistence but lacking the population identification (blue= mainly meat dependent; red= mixed diets; orange=pastoralists; green= vegetarian agriculturalists). Population identification can be found in Figure 2.

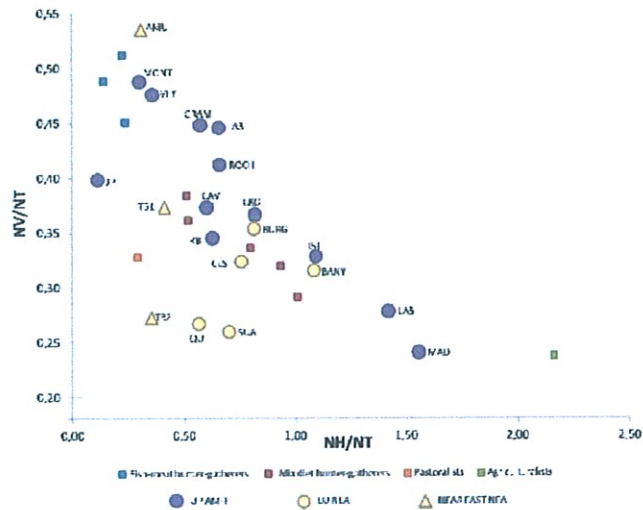


Figure n°5. Percentages of Jeune Prince and Cavillon striae for each orientation in length (X). In both individuals length of each orientation shows a close pattern in all orientations with minimal changes, indicating that the difference between the two individuals is only due to total-density but not to the pattern itself.

