

Age-related variability in buccal dental-microwear in Middle and Upper Pleistocene human populations

Beatriz Pinilla Pérez ¹, Alejandro Romero ²,
Alejandro Pérez-Pérez ^{1*}

¹Secc. Antropología, Dept. Animal Biology, Biology Faculty, University of Barcelona, Avda, Diagonal 645, 08027 Barcelona, Spain; *E-mail: martinez.perez-perez@ub.edu

²Dept. of Biotechnology, Science Faculty, University of Alicante 99, 03080 Alicante, Spain

ABSTRACT Infants are thought to present a different buccal microwear pattern than adults and these, therefore, are generally analyzed separately. However, El-Zaatari & Hublin [2009] showed that occlusal texture in Neandertal and modern human juvenile populations did not differ from their elders. The microwear patterns of a sample of 193 teeth, corresponding to 61 individuals of *Homo heidelbergensis*, *H. neanderthalensis* and anatomically modern humans (AMH), were analyzed revealing that AMH infants up to 14 years old differ from older individuals in having fewer scratch densities, whereas the Neandertals have a much more variable microwear pattern. Age-at-death and dental age since emergence showed similar though somewhat diverging results, especially in the infant and subadult samples. Differences observed between the Neandertals and modern humans could be reflecting differential wearing patterns or distinct enamel structure and resistance to hard food items consumption. Interpopulation differences in striation densities were not apparent in either subadult or adult individuals, only adult Neandertals (26-45 yrs. old) showed fewer striations than the younger age groups. The AMH sample revealed a gradual cumulative pattern of striation density with age, suggestive of a non-abrupt change in diet.

KEY WORDS: microwear, age, teeth, Neandertals, humans

Dental microwear analysis has been applied both to occlusal surfaces [Ungar *et al.* 1999, King *et al.* 1999], including confocal roughness/texture analysis [Scott *et al.* 2005, El-Zaatari & Hublin 2009, Merceron *et al.* 2010], and buccal surfaces [Pérez-Pérez *et al.* 1994, Romero & De Juan 2007,

Pinilla *et al.* 2009, Galbany *et al.* 2009]. Buccal dental microwear analyses on the post-canine dentition have provided valuable information about feeding behavior on both extant primates [Galbany *et al.* 2009] and extinct hominid species [Pérez-Pérez *et al.* 2003, Estebananz *et al.* 2009]. Unlike

occlusal surfaces, on which both pits and scratches can be observed, buccal enamel surfaces only show scratches, since tooth-to-tooth contact is lacking. In addition, dentine exposure does not affect microwear feature preservation on buccal enamel surfaces. Enamel *post-mortem* damage affects microwear patterns on both occlusal and buccal enamel surfaces [King *et al.* 1999]. However, *ante-mortem* microwear features on buccal surfaces, caused by food-to-enamel contact, can be easily distinguished [Pérez-Pérez *et al.* 2003], whereas on occlusal surfaces microwear can be produced also by tooth-to-tooth contact, and thus the biomechanics of chewing may affect occlusal microwear patterns. Finally, occlusal microwear patterns seem to be indicative of short-term food consumption, commonly known as “the last supper effect” [Teaford & Oyen 1989], since occlusal microwear is affected by a fast turnover [Teaford & Tylenda 1991]. Thus, seasonality in food consumption also needs to be taken into consideration [Merceron *et al.* 2010]. On the other hand, buccal microwear patterns have been suggested to depend on long-term dietary practices and, thus, might be less sensitive to short or seasonal changes in food consumption [Romero *et al.* 2009]. Therefore, for interpopulation comparisons among groups with distinct dietary-related habits, the inter-group variability of the buccal microwear pattern is expected to be greater than intra-group variability [Pérez-Pérez *et al.* 1994], with the exception, perhaps, of highly stratified populations with significant intra-group dietary differences, such as those observed between males and females of an Islamic population from Spain [Romero & De Juan 2007].

Buccal microwear research has focused mainly on interpopulation differences and studies on intra-individual and intra-group

variability are scarce. Intragroup differences in buccal microwear patterns have been detected in the Spanish medieval site of La Olmeda (12th-18th century AD, Palencia) by Pérez-Pérez *et al.* [1994], showing that buccal microwear patterns can be used to trace both age- and sex-related differences in diet. Age-related analyses have shown that the buccal microwear pattern tends to stabilize at around 13-15 years of age. Romero & De Juan [2007] have also shown that microwear densities tend to increase with age in early prehistoric (Chalcolithic and Bronze Age periods), Islamic (900-1200 AD) and contemporary populations, with ages ranging from 17-25 to 25-35 years old, though differences appeared to be significant only for the Islamic group. However, El-Zaatari & Hublin [2009] found no age-related differences in enamel roughness on either Neanderthals or modern humans (AMH), and so age groups were subsequently analyzed together [Gamza 2010]. However, data on age-related variability in microwear patterns is still lacking, especially for buccal microwear patterns of Middle and Upper Pleistocene human populations, which limits the use and interpretation of microwear patterns. Age-at-death in ancient human populations tends to be low and fossil samples frequently include subadult individuals. Therefore, the aim of this paper was to test if buccal microwear patterns (striation density and average length) of patterns of three Middle and Upper Pleistocene populations (*Homo heidelbergensis*, *Homo neanderthalensis*, and *Homo sapiens*) are dependent on age (both the individual's age at death and dental age since emergence). If no age related patterns were present, subadult and adult individuals could be grouped in order to increase sample sizes for intergroup comparisons. If it were shown that microwear

patterns are age-dependant this limitation to comparisons of buccal microwear patterns needs to be taken into account.

Materials and methods

Sample studied

The hominin fossil specimens studied came from the cast collection housed at the University of Barcelona. The total analyzed sample included 836 teeth corresponding to 174 individuals from Middle to Upper Pleistocene sites, mostly from Europe, and belonging to three distinct hominin species: *Homo heidelbergensis* (N=15, including Kabwe), *Homo neanderthalensis* (N=77, including Tabun 2), and anatomically modern humans (AMH) (N=75, including Skhûl, Border Cave and Cave of Hearths). Negative moulds of the teeth were made using *President MicroSystems*TM (Coltène®, Regular Body) polyvinyl-siloxane and *Ferroc*® polyurethane resin (parts A and B) was used to obtain the positive casts. All casts were sputter-coated with a 400 Å gold layer. Age determinations of the fossil specimens studied were obtained from the literature. Since not all fossil specimens initially considered showed both well-preserved buccal microwear and age-at-death determinations, the final available sample used to test for age-related differences in buccal microwear patterns included only 193 out of the 836 analyzed teeth (23.1%), corresponding to 61 out of the 174 initially studied individuals (35.1%). This final sample (Table 1) did not include teeth that were damaged *post-mortem*, and the anterior dentition was not included because the buccal microwear in these teeth can be affected by cultural rather than dietary-related striations [Lozano *et al.* 2008]. As not all teeth erupt at the same age within

a given individual, enamel surfaces could have different functional life spans since emergence (microwear patterns can only be formed during the period that the tooth is exposed to abrasive food items) and, thus, microwear densities could be more strongly correlated with age since emergence than with the individuals' age at death. Therefore, tooth age since emergence was computed following Skinner [1997] and teeth were analyzed as independent cases to determine the relationship between age and buccal microwear densities.

Methods

The age-since-emergence of each tooth was computed by subtracting the individual's age-at-emergence from the age-at-death (obtained from the literature). It was beyond the scope of this analysis to speculate on the differences in timing of dental development and emergence between Neandertals and modern humans [Wolpoff 1979, Ramírez-Rozzi & Bermúdez de Castro 2004, Macchiarelli *et al.* 2006, Reid and Dean 2006, Guatelli & Reid 2008, Olejniczak *et al.* 2008, Bayle *et al.* 2009], not to mention *H. heidelbergensis*. Although most studies on dental eruption are based on emergence standards of modern humans [Ubelaker 1978, Williams 2006], a Neanderthal emergence standard [Granat & Heim [2003] was used for both the Neanderthal and *H. heidelbergensis* samples. All the statistical analyses were performed twice, using the two procedures. Age intervals were then established according to previous studies of buccal microwear variability [Pérez-Pérez *et al.* 1994, Romero & De Juan 2007], from which 4 age categories were derived: A1 (0 to 5 years old), A2 (6 to 13 years old), A3 (14 to 25 years old) and A4 (25 to 45 years old).

Table 1. Individuals analyzed in this study for which buccal microwear was preserved and age-at-death established in the literature.

| Site | Specimen | Teeth | Age (yrs.) | Reference | Density |
|---------------|------------------------|---|------------|---|---------|
| ARAGO | A16, A21, A36 (Ind. 1) | LP ³ , M ¹ , M ² ; RP ³ , M ² , M ³ | 20-25 | [Pérez-Pérez <i>et al.</i> 2003] | 274 |
| | A13 (Ind. 3) | RP ₃ -M ₃ | 16 | [Wolpoff 1999:530] | 315 |
| | A40, A68 (Ind. 5) | RM ₁ -M ₂ | 25-30 | [Tautavel Museum] | 183 |
| | A6 (Ind. 6) | RM ₂ | 18-20 | [Tautavel Museum] | 256 |
| | A54 (Ind. 7) | RM ¹ | 18-20 | [Tautavel Museum] | 386 |
| | A69 (Ind. 8) | RM ₂ | 15-18 | [Tautavel Museum] | 197 |
| | A7, A25 (Ind. 9) | RP ³ , RM ₁ | 10 | [Tautavel Museum] | 251 |
| MAUER | MA | RP ₃ -M ₃ ; LM ₁ -M ₃ | 18-25 | [Kraatz 1992] | 231 |
| PONTNEWYDD | PN4 | Rm ² -M ¹ | 8 | [Green 1984] | 365 |
| STEINHEIM | ST | RP ⁴ -M ³ | 25 | [Street <i>et al.</i> 2006] | 141 |
| BANYOLES | BA-1 | LM ₃ , RM ₃ | 40 | [De Lumley 1973] | 189 |
| GIBRALTAR | GB2 | Lm ₁ -m ₂ ; Rm ¹ -m ² | 5 | [Tilhler 1982, Williams 2006] | 264 |
| GROTTA BREUIL | GB-2 | LM ₁ | 30 | [Manzi & Passarello 1995] | 262 |
| | GT-2 | RM ₃ | 35-40 | [Mallegni 1991, 40; Williams 2006] | 300 |
| GUATTARI | GT-3 | LM ₁ -M ₂ ; RM ₁ -M ₃ | 18-20 | [Mallegni 1991] | 284 |
| KULNA | KU-1 A17 092 | RP ² -M ¹ | 14 | [Jelinek 1966] | 259 |
| LA QUINA | H-5 | LP ₃ -M ₃ ; RP ₄ -M ₃ ; LP ³ , M ¹ ; RM ¹ , M ² | < 30 | [Trinkaus 1980, 20; Williams 2006] | 333 |
| LE MOUSTIER | LM-1 | LP ₄ -M ₂ ; RP ₄ -M ₂ | 15.5-16 | [Thompson & Bilsborough 1997] | 134 |
| MALARNAUD | MA | RM ₁ | 11.2 | [Granat & Heim 2003] | 105 |
| MONT-GAUDIER | MG4 | LM ₁ | 12-14 | [Duport & Vandermeersh 1976] | 179 |
| MONTMAURIN | MM1 | LM ₁ -M ₃ ; RM ₁ -M ₃ | 15.5 | [Granat & Heim 2003] | 277 |
| OCHOZ | OC-1 | LP ₃ -M ₃ ; RP ₃ -M ₂ | 25 | [Williams 2006] | 175 |
| SAINT CESAIRE | SC1 | LP ₃ , RM ₁ -M ₂ ; LP ⁴ , M ² ; RP ⁴ , M ¹ | 36 | [Wolpoff 1999: 689] | 197 |
| SUBALYUK | S-1 | RM ₁ -M ₃ | 25-35 | [Pap <i>et al.</i> 1996, 25; Williams 2006] | 113 |
| TABUN | TB-1 | LP ₄ -M ₂ ; RP ₃ , M ₁ , M ₂ ; LP ⁴ , M ² ; RP ³ , P ⁴ | 30-35 | [McCown & Keith 1939] | 114 |
| VINDIJA | VI-11.39 (206) | RM ₁ | 15 | [Wolpoff <i>et al.</i> 1981] | 389 |
| | VI-11.40a (226) | LM ₁ | 19 | [Wolpoff <i>et al.</i> 1981] | 229 |
| ZAFARRAYA | Z-16 | RP ₃ | 12 | [Barroso <i>et al.</i> 2006] | 262 |

Homo heidelbergensis

Homo neanderthalensis

| | | | | | |
|------------------------|---|---|---|---|---------------------------------|
| ABRIC PATAUD | API | $LM_1-M_2, RP_3, M_1-M_2, RM_1$ | 14-15 | [Billy 1975] | 222 |
| ALMONDA | AMD Cisterna 3 AMD Cisterna1 | Rm_1 RM_1 | 2 8 | [Trinkaus pers. com.] [Trinkaus pers. com.] | 297 240 |
| BARMA GRANDE | BG- 3 BG- 4 | LM_1-M_2 LP^4-M^2 | 12-13 14-15 | [Fornicola 1989] [Fornicola 1989] | 210 358 |
| BRASSEPOUY | BR-96/884 | LM_2 | 10 | [Gambier <i>et al.</i> 2004] | 195 |
| CALDEIRAO | CA11 CA2 | Rm_2 Lm_2 | 2-6 10-12 | [Trinkaus <i>et al.</i> 2001] [Trinkaus <i>et al.</i> 2001] | 194 209 |
| CAVE OF HEARTHS | CH005 | RP_3, M_1-M_2 | 12 | [Tobias 1971] | 274 |
| COMBE CAPELLE | CC-2 | $LM_1-M_2, RM_1, LP^4-M^1, M^3$ | 40-50 | [Hoffmann & Wegner 2002] | 364 |
| DOLNI VESTONICE | DV-13 DV-14 DV-15 DV-31 DV-37 | $LM_2, RP_4, M_2-M_3, LP^3, M^2, RP^4, M^2$ RP_3-M_2, LP^3 $LP_3-P_4, RP_3-P_4, LP^3-M^1, RP^3-M^2$ RM_3 LM_2 | 21-25 13-15 21-25 21-25 16-20 | [Trinkaus & Svoboda 2006: 34] [Trinkaus & Svoboda 2006: 35] [Trinkaus & Svoboda 2006: 37] [Trinkaus & Svoboda 2006: 40] [Trinkaus & Svoboda 2006: 41] | 228 225 218 318 299 |
| FARINCOURT | Farincourt 1960-7 | LP_3-P_4, LP^3, M^2 RP_4 | 36-45 11 | [Trinkaus & Jelinek 1997] [Skinner 1997] | 271 234 |
| LACHAUD | Lachaud 1980-6 Lachaud 1980-8-1 Lachaud 5 | LM_2 LM_2 RM_1 | 18.6 15.8 11-12 | [Skinner 1997] [Skinner 1997] [Skinner 1997] | 247 187 124 |
| LE MOURIN | Le Mourin2 | RM_1 | 11-12 | [Bouvier, 1971] | 124 |
| LES ROIS | Les Rois A 1958-148-1 Les Rois B 1965-148-2 | RM_1 LP^4 | 10-11 11 | [Mouton & Joffroy, 1958] [Mouton & Joffroy, 1958] | 260 302 |
| MLADEC | Mladec 1 Mladec 2 Mladec 8 | RM^2 LM_1-M_3, RM^1 LM^1, M^2 | 16-17 17 35 | [Wolpoff <i>et al.</i> 2006] [Wolpoff <i>et al.</i> 2006] [Frayer <i>et al.</i> 2006] | 364 284 331 |
| PAVLOV | Pavlov 1 Pavlov 2 Pavlov 28 | LP^3, RM^2 LM^1, RP^3, P^4, M^2 LM_3 | 36-45 26-35 18-35 | [Trinkaus & Svoboda, 2006: 42] [Trinkaus & Svoboda, 2006: 42] [Trinkaus & Svoboda, 2006: 44] | 306 377 293 |
| PŘEDMOSTI | A17088 | LM_1-M_3, RM_2 | 25-30 | [Velemínska & Bruzek, 2008] | 323 |
| SKHUL | Skhul 5 | RM_1, M_3 | 30-40 | [Johanson & Blake, 1996] | 138 |
| SOLUTRE | Solutre 1956-49 | Lm_2 | 5 | [Skinner, 1997] | 190 |
| ST. GERMAIN LA RIVIÈRE | St. Germain La Rivière B3 | Rm_2 | 7 | [Skinner, 1997] | 203 |
| ST. GERMAIN LA RIVIÈRE | St. Germain La Rivière B5-7 | Lm_2 | 5 | [Skinner, 1997] | 165 |

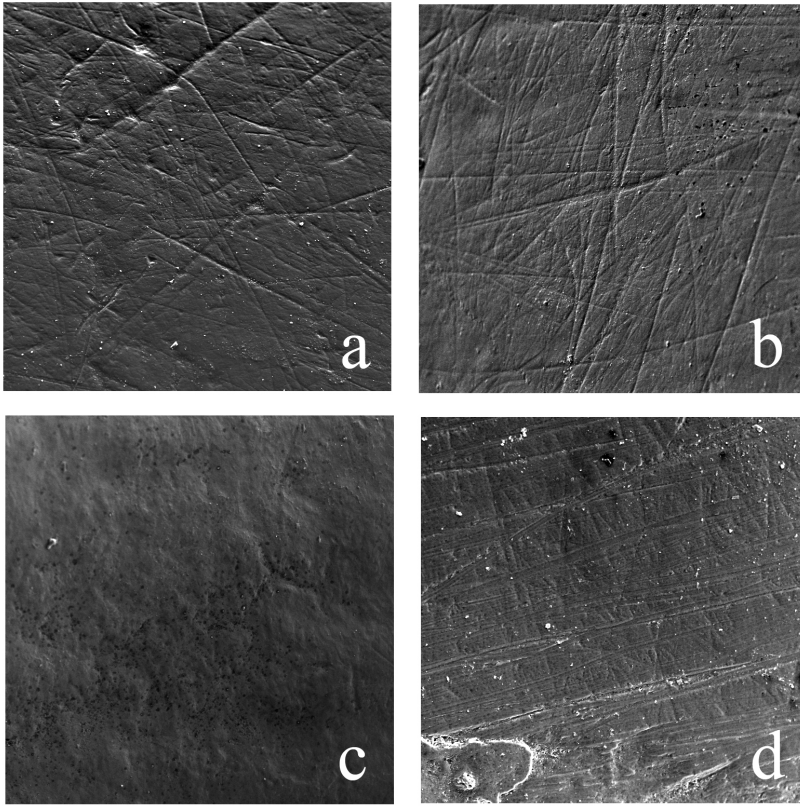


Fig. 1. Buccal microwear surfaces: a) Neandertal well preserved enamel surface of specimen VI-11.39 206 from Vindija (Croatia), RM₁; b) Neandertal well-preserved enamel surface of La Quina V (France), RM₁; c) Unemerged tooth from Engis (Belgium), RM₁ (lacking enamel microwear features); d) Modern human enamel of a *post-mortem* damaged enamel from Dolni Vestonice (Czech Republic), specimen III, LP⁴.

Scanning electron micrographs were taken using Leica 360 (*Parc Científic de Barcelona*) and Hitachi S3000N (SSTT *Universidad de Alicante*) scanning electron microscopes (SEM), following standardized microwear procedures [Pérez-Pérez *et al.* 2003, Galbany *et al.* 2009]. SEM images (Fig. 1), taken at 100X magnification and processed in Adobe Photoshop CS-5, were cropped to exactly cover 0.56 mm² square enamel patch and grey levels were automatically adjusted to increase image contrast. Scratch density and length (in μm)

were measured with *Sigma Scan 5.0* (SPSS Inc.). A total of 15 variables were derived, including the density (NT), average length (XT) and standard deviation of the length (ST) of all observed striations by orientation categories: horizontal (H), vertical (V), mesio-distal (MD) and disto-mesial (DM)), as well as for all the scratches (T) (see Pérez-Pérez *et al.* [2003] and Galbany *et al.* [2009] for a detailed description of variable definitions). All images were analyzed by the same researcher (BP) in order to prevent interobserver errors [Galbany *et al.* 2005].

All statistical analyses were performed with SPSS 15 for Windows™. Kolmogorov-Smirnov tests were used to check for the Normality of the analyzed variables and one-way ANOVA and MANOVA tests were used to check for significant differences ($P < 0.05$) among age groups. Principal Component (PCA) and Discriminant analyses (LDA) were used to describe group similarities in buccal microwear patterns.

Results

If dental emergence ages were taken into account, no significant differences in total striation density were observed in either the *H. heidelbergensis* ($N=31$, $F=0.723$, $P=0.494$) or the modern humans ($N=90$, $F=1.772$, $P=0.159$) samples. For the *H. heidelbergensis* sample age groups A2 ($N=4$), A3 ($N=27$) and A4 ($N=1$) were represented, while for the AMH sample all four age groups were represented (A1, $N=4$; A2, $N=13$; A3, $N=48$; A4, $N=25$), as was also the case for the Neandertal sample (A1, $N=4$; A2, $N=3$; A3, $N=48$; A4, $N=25$). However, significant age-related differences were observed only in the Neandertal sample ($N=80$, $F=7.470$, $P=0.000$). The *post-hoc* test within the ANOVA showed that differences in striation densities were exclusively due to differences between A3 and A4 ($P=0.000$), with the A3 (14-25 years old) group showing significantly higher striation densities than A4 (>25 years old). Interestingly, the subadult groups (A1 and A2) did not show significant differences in striation density compared to the adult ones (A3 and A4) in any of the groups compared.

If a combined factor of population group (*H. heidelbergensis*, *H. neanderthalensis* and *H. sapiens*) and age-at-death was used to test for differences in striation density, an overall significant ANOVA value was

obtained ($N=201$, $F=3.518$, $P=0.000$), indicating that in addition to the already detected age difference between A3 and A4 for the Neandertals, interpopulation differences were also detected. In fact, the *post-hoc* tests showed that the only significant differences in striation density observed were between groups A3 ($NT=289.98$) and A4 ($NT=188.32$) for the Neandertals ($P=0.000$), already discussed above, and between the Neandertal A4 group and the AMH A3 ($NT=269.88$, $P=0.009$) and A4 ($NT=293.80$, $P=0.001$) groups. Thus, the Neandertal A4 (26-45 years old, $N=25$) group showed a distinct but characteristically small striation density (Fig. 2).

Finally, if the median number of striations of all available teeth per individual was selected as representative of the striation density of each studied specimen, as a microwear methodological standardization [Pérez-Pérez *et al.* 2003 Galbany *et al.* 2009, Pinilla *et al.* 2009, Estebaranz *et al.* 2009], ages-at-death group comparisons of the 59 studied individuals showed no significant differences between the groups. In summary, the Neanderthals and *H. heidelbergensis* samples did not show significant age related differences in striation densities, which may support the hypothesis that the Neanderthals infants, and for the same reason also those of *H. heidelbergensis*, could have had a wider dietary range, overlapping that of older individuals, than modern humans (AMH), as suggested by El-Zaatari & Hublin [2009]. A consistent increase in scratch density from infancy to adulthood can be observed for the modern human sample (Fig. 2). Striation densities tend to increase, or at least stabilize, in older groups, with younger individuals having fewer scratches – a pattern not seen in either *H. heidelbergensis* or Neandertals. The *H. heidelbergensis* sample was not represented by individuals younger than 6 years

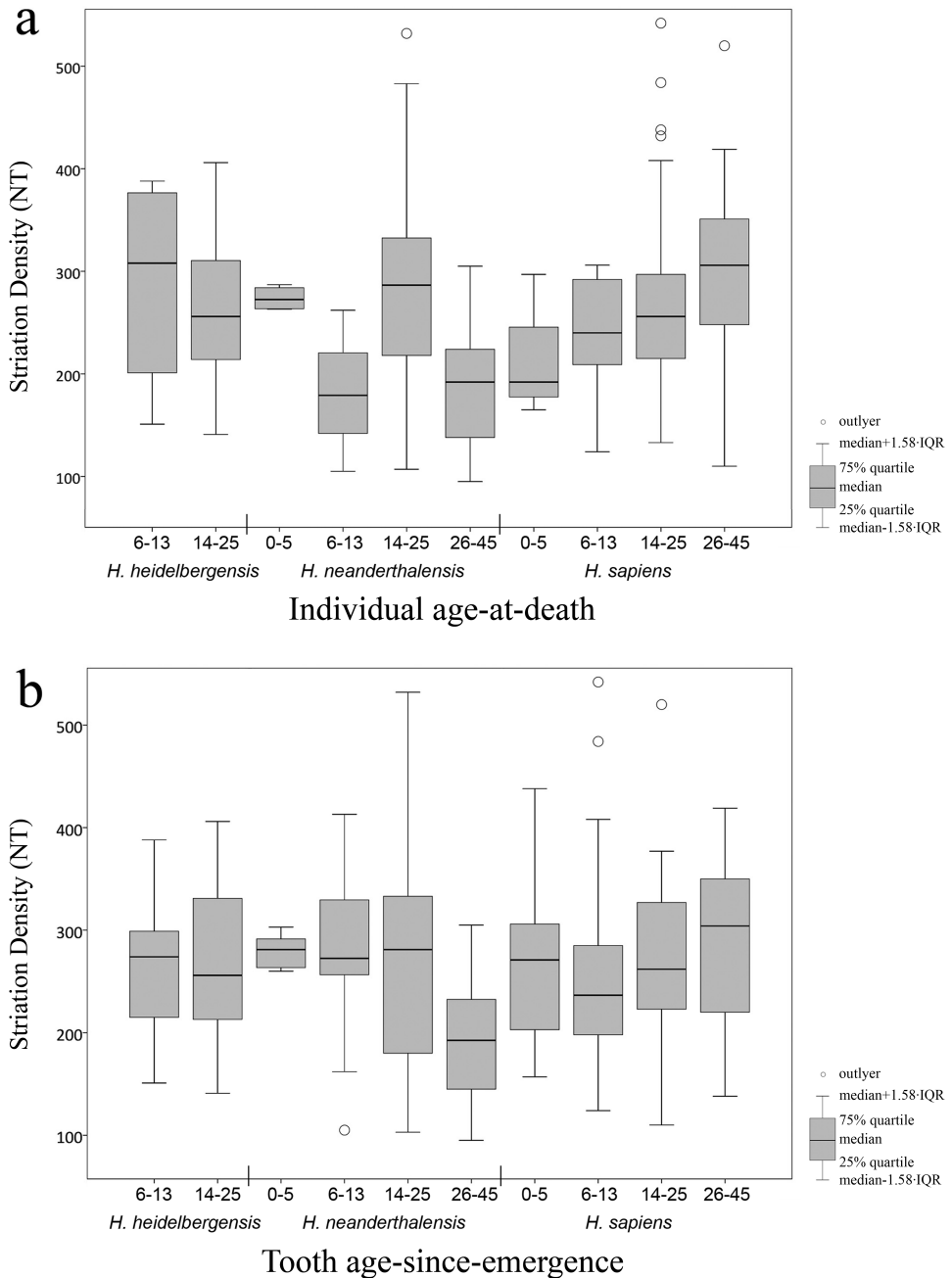


Fig. 2. Box plots showing the variability of striation density (NT) for the 3 populations considered (*H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens*) by age groups (0-5, 6-13, 14-25, 26-45 years old): a) striation densities by individual age-at-death, b) striation density by dental age-since-emergence; inter-quartile range (IQR) = 75% quartile - 25% quartile.

old or by individuals older than 25 years, and thus a detailed age analysis could not be made. The Neanderthal sample was well represented and individuals older than 25 years had fewer scratches than the younger groups. This decrease in striation density with age needs to be carefully considered since the available samples for each age group are still small. However, in the AMH group a steady increase of striation density with age-at-death was observed (not so clear-cut if dental age since emergence was considered), which clearly differentiates AMH infants (with less scratches) from elder individuals – a pattern not observed in *H. heidelbergensis* or Neandertals. The consistent increase in striation density in AMH from 6 to 45 years of age is consistent with the described cumulative nature of the striation pattern, in which striations are added one on top of the other until the more recent ones ‘erase’ the older ones as the enamel turnover maintains the stability of the microwear pattern.

Discussion

Intrapopulation comparisons of striation densities were necessarily limited, since not all teeth were preserved in all individuals and not all age groups were represented in all populations. However, this research provides relevant information about buccal microwear formation rates by age groups in ancient human populations. The buccal microwear pattern is a characteristic trait of a population that depends on its dietary habits, food processing techniques, and feeding behavior [Pérez-Pérez *et al.* 1994, Romero & De Juan 2007]. Age-related variability might be linked to changes in food consistency in infants and elders as Pérez-Pérez *et al.* [1994] pointed out. Moreover, concerning children, dietary changes at the end of weaning are likely to have relevant consequences

in microwear densities. Neandertal infants from 2 to 5 years showed larger striation densities than those from 6 to 13, which could be indicative that weaning occurred at an early age in this group, with young infants having a significantly abrasive diet compared to subadults; an alternative explanation would be that enamel of deciduous teeth is less resistant to abrasion than that of the permanent dentition. Only in the AMH sample does the microwear density increase from infants to subadults, which could reflect a progressive increase in harder foods consumption, perhaps after weaning, as has already been shown by Pérez-Pérez *et al.* [1994]. However, this may have been due to shorter life expectancies within the nomadic prehistoric hunter-gatherers studied here than in a sedentary medieval population.

Although Pérez-Pérez *et al.* [1994] suggested that the buccal striation pattern might be dependent on both the individual’s age-at-death and tooth age-since-emergence, as expected if the pattern is a dynamic, cumulative process during the individual’s life, the results found here fail to show such clear cumulative microwear formation process in the archaic humans, and only in modern humans did the age-at-death analysis of striation density show a clear cumulative pattern. In the ancient groups, once erupted, a tooth seems to quickly attain its functional microwear pattern. However, enamel structure, biomechanical and functional factors are likely to be responsible for a larger fraction of the variability observed. A more detailed investigation, with larger samples, is still needed to understand the pattern formation of the buccal microwear and how differences in age of emergence may affect the microwear in more recent populations. Macrowear and dentine exposure results [Skinner 1997] have suggested that Neandertal infants might have had more abrasive

diets than modern human infants. Striation densities of infants were shown to be larger in Neandertals than in humans only if age-at-death, instead of dental age since emergence, was used (Fig. 2). If these lower striation densities in AMH is confirmed, cultural differences in modern humans, such as stone boiling practices and soup consumption in the Upper Paleolithic humans [Haddingham 1979, Pfeiffer 1986], or still later in the Late Upper Paleolithic [Nakazawa *et al.* 2009], might explain the results obtained.

Conclusions

The buccal microwear striation pattern is a characteristic trait of a population reflecting long-term dietary shifts. Results from this study indicate that infants have a consistently high-density microwear pattern, similar to that of the adult individuals in all three populations studied: *Homo heidelbergensis*, *Homo neanderthalensis* and *Homo sapiens* (anatomically modern humans). The shift towards adult dietary behavior appears to have taken place at around 13 years of age. From this age onwards, age did not seem to affect the microwear pattern observed in the archaic humans, whereas in modern humans a cumulative pattern with age was observed. Therefore, the individual age-at-death should be taken into account when analyzing buccal microwear, especially in children. When analyzing the same ages, infant feeding behavior appears to have been different among the species, especially in AMH, whose infants seem to have less abrasive dietary habits compared to their predecessors. However, these results need to be considered along with changes in geography [Pinilla *et al.* 2009], chronology and climate [Pérez-Pérez *et al.* 2003, Pinilla *et al.* 2009], all of which might have played an important role in food availability and consumption in Paleolithic hominins.

Notes

Acknowledgements This research was funded by a predoctoral fellowship (BP, AP2006-01274) and a research grant (APP-CGL2007-60802/BTE), both of the *Ministerio de Ciencia e Innovación* of the Spanish Government. The microwear images were taken at the *Serveis Científicotècnics* (UB-PCB) of the Universitat de Barcelona and at the scanning microscopy unit (SSTT-UA) at Universitat de Alicante. We also would like to acknowledge the anonymous reviewer for his/her helpful suggestions in improving the manuscript, as well as the language advisor – D.J. Chorn, and the Managing Editor of *Anthropological Review* – K.A. Kaszycka, for their assistance. A draft version of this paper was presented at the 17th Congress of the European Anthropological Association in August 2010.

References

- BARROSO C., H. DE LUMLEY, 2006, *La grotte du Boquete de Zafarraya. Málaga. Andalousie*, Junta de Andalucía, Seville
- BAYLE P., J. BRAGA, A. MAZURIER, R. MACCHIARELLI, 2009, *Dental developmental pattern of the Neanderthal child from Roc de Marsal: A high-resolution 3D analysis*, *J. Hum. Evol.*, **56**, 66–75
- BILLY G., 1975, *Etude anthropologique des restes humains de l'Abri Pataud*, [in:] *Excavation of the Abri Pataud (I)*, *Bull. Am. Sch. Preh. Res.*, **30**, 200–61
- BOUVIER J.M., 1971, *Les mandibules humaines du Magdalénien français*, PhD thesis, Université de Paris VII (2 vol), Paris
- DE LUMLEY M.A., 1973, *Anténeanderthaliens et Néanderthaliens du Basin Méditerranéen Occidental Européen* Éditions du Laboratoire de Paléontologie Humaine et de Préhistoire, Études Quaternaires Mém. **2**, Marseille
- DEAN M.C., 2006, *Tooth microstructure tracks the pace of human life-history evolution*, *Proc. Royal Soc. Britain*, **273**, 2799–808
- DUPORT L., B. VANDERMEERSCH, 1976, *La mandibule moustérienne de Montgaudier (Montbron, Charente)*, *C. R. Acad. Sci. Paris*, **283**, 1161–64
- EL-ZAATARI S., J.J. HUBLIN, 2009, *Occlusal microwear texture analysis of Middle and Upper Paleolithic juveniles*, *Am. J. Phys. Anthropol.*, **S48**, 123

- ESTEBARANZ F., L.M. MARTÍNEZ, J. GALBANY, D. TURBÓN, A. PÉREZ-PÉREZ, 2009, *Testing hypotheses of dietary reconstruction from buccal dental microwear in Australopithecus afarensis*, *J. Hum. Evol.*, **57**, 739–50
- FORNICOLA V., 1989, *The upper Paleolithic burials of Barma Grande, Grimaldi, Italy* Hominidae, Proc. 2nd International Congress Human Paleontology, pp. 483–86
- FRAYER D.W., J. JELÍNEK, M. OLIVA, M.H. WOLPOFF, 2006, *Aurignacian male crania, jaws and teeth from the Mladec Caves, Moravia, Czech Republic*, [in:] *Early modern humans at the Moravian Gate. The Mladec caves and their remains*, M. Teschler-Nicola (ed.), Springer-Verlag, Austria, pp. 185–272
- GAMBIER D., B. MAUREILLE, R. WHITE, 2004, *Vestiges humains des niveaux de l'Aurignacien ancien du site de Brassempouy (Landes)*, *Bull. Mém. Soc. Anthropol. Paris*, **16**(1-2), 49–87
- GAMZA T.R., 2010, *Short communication: Intra-individual microwear variation: Deciduous versus permanent dentition*, *Dent. Anthropol.*, **23**(2), 66–68
- GREEN H.S., 1984, *Pontnewydd Cave, a Lower Palaeolithic Hominid Site in Wales: The First Report*, *Nat. Mus. Wales*, Cardiff
- GALBANY J., L.M. MARTÍNEZ, L.H. LÓPEZ-AMOR, V. ESPURZ, O. HIRALDO, ET AL., 2005, *Error rates in dental buccal microwear quantification using Scanning Electron Microscopy*, *Scanning*, **27**, 23–29
- GALBANY J., F. ESTEBARANZ, L.M. MARTÍNEZ, A. PÉREZ-PÉREZ, 2009, *Buccal dental microwear variability in extant African Hominoidea primates: Taxonomy versus ecology*, *Primates*, **50**, 221–30
- GRANAT J., J.L. HEIM, 2003, *Nouvelle méthode d'estimation de l'âge dentaire des Néandertaliens*, *L'Anthropologie*, **107**, 171–202
- GUATELLI-STEINBERG D., D.J. REID, 2008, *What molars contribute to an emerging understanding of lateral enamel formation in Neandertals vs. modern humans*, *J. Hum. Evol.*, **54**, 236–50
- HADINGHAM E., 1979, *Secrets of the Ice Age*, Walker and Co., New York
- HOFFMANN A., D. WEGNER, 2002, *The rediscovery of the Combe Capelle skull*, *J. Hum. Evol.*, **43**, 557–81
- JELÍNEK J., 1966, *Jaw and an intermediate type of Neanderthal Man from Czechoslovakia*, *Nature*, **212**, 701–2
- JOHANSON D., E. BLAKE, 1996, *From Lucy to Language*, Simon and Schuster, New York
- KING T., P. ANDREWS, B. BOZ, 1999, *Effect of taphonomic processes on dental microwear*, *Am. J. Phys. Anthropol.*, **108**, 359–73
- KRAATZ R., 1992, *Der Mensch von Mauer e Homo erectus heidelbergensis*, [in:] *Reiss-Museum der Stadt Mannheim*, G.A. Wagner, K.W. Beinhauer (eds.), Schichten von Mauer, pp. 22–35
- LOZANO M., J.M. BERMÚDEZ DE CASTRO, E. CARBONELL, J.L. ARSUAGA, 2008, *Non-masticatory uses of anterior teeth of Sima de los Huesos individuals (Sierra de Atapuerca, Spain)*, *J. Hum. Evol.*, **55**, 713–28
- MACCHIARELLI R., L. BONDIOLI, A. DEBÉNATH, A. MAZURIER, J.F. TOURNEPICHE, ET AL., 2006, *How Neanderthal molar teeth grew*, *Nature*, **444**, 748–51
- MALLEGNI F., 1991, *Guattari 2 and 3: The stomatognathic apparatus*, *Quaternaria Nova*, **1**, 25–36
- MANZI G., P. PASSARELLO, 1995, *At the archaic/modern boundary of the genus Homo: The Neandertals from Grotta Breuil*, *Curr. Anthropol.*, **36**, 335–66
- MCCOWN T.D., A. KEITH, 1939, *The Stone Age of Mount Carmel. The human remains from the Levallois-mousterian*, Oxford at the Clarendon Press, Oxford
- MERCERON G., G. ESCARGUEL, J.M. ANGIBAULT, H. TIXIER, 2010, *Can dental microwear textures record inter-individual dietary variations?*, *PLoS ONE*, **5**, e9542
- MOUTON P., R. JOFFROY, 1958, *Le Gisement Aurignacien des Rois a Mouthiers (Charente)* IX Supplément “Gallia”, C.R. Acad. Sci., Paris
- NAKAZAWA Y., L.G. STRAUSS, M.R. GÓZALEZ-MORALES, D. CUENCA SOLANA, J. CARO SAIZ, 2009, *On stone-boiling technology in the Upper Paleolithic: Behavioral implications from an Early Magdalenian hearth in El Mirón Cave, Cantabria, Spain* *J. Archaeol. Sci.*, **36**, 684–93
- OLEJNICZAK AJ, T.M. SMITH, R.N.M. FEENEY, R. MACCHIARELLI, A. MAZURIER, ET AL., 2008, *Dental tissue proportions and enamel thickness in Neanderthal and modern human molars*, *J. Hum. Evol.*, **55**, 12–23
- PAP I., A.M. TILLIER, B. ARENSBURG, S. WEINER, M. CHECH, 1995, *First scanning electron microscope analysis of dental calculus from European Neanderthals: Subalyuk, (Middle Paleolithic, Hungary). Preliminary report*, *Bull. Mém. Soc. d'Anthr. Paris*, **7**, 69–72

- PÉREZ-PÉREZ A., C. LALUEZA, D. TURBÓN, 1994, *Intraindividual and intragroup variability of buccal tooth striation pattern*, *Am. J. Phys. Anthropol.*, **94**, 175–88
- PÉREZ-PÉREZ A., V. ESPURZ, J.M. BERMÚDEZ DE CASTRO, M.A. DE LUMLEY, D. TURBÓN, 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
- PFEIFFER J.E., 1986, *Cro-Magnon hunters were really us, working out strategies for survival*, *Smithsonian Magazine*, October, pp.74–85
- PINILLA B., J. GALBANY, F. ESTEBARANZ, L. MARTÍNEZ, ET AL., 2009, *La influencia del Clima en la dieta de H. neanderthalensis y H. sapiens: Microestriación Vestibular y Fluctuaciones Climáticas* [in:] *Genes, Ambiente y Enfermedades en Poblaciones Humanas*, J.L. Nieto, J.A. Obón, S. Baena (eds.), Universidad de Zaragoza, pp. 573–86
- RAMIREZ ROZZI F.V., J.M. BERMÚDEZ DE CASTRO, 2004, *Surprisingly rapid growth in Neanderthals*, *Nature*, **428**, 936–39
- REID D., C. DEAN, 2006, *Variation in modern human enamel formation times*, *J. Hum. Evol.* **50**, 329–46
- ROMERO A., J. DE JUAN, 2007, *Intra- and interpopulation human tooth surface microwear analysis: Inferences about diet and formation processes*, *Anthropologie*, **45**, 61–70
- ROMERO A., J. GALBANY, N. MARTÍNEZ-RUIZ, J. DE JUAN, 2009, *In vivo turnover rates in human buccal dental-microwear*, *Am. J. Phys. Anthropol.*, **S48**, 223
- SCOTT R.S., P.S. UNGAR, T.S. BERGSTROM, C.A. BROWN, F.E. GRINE, ET AL., 2005, *Dental microwear texture analysis reflects diets of living primates and fossil hominins*, *Nature* **436**, 693–95
- SKINNER M., 1997, *Dental wear in Immature Late Pleistocene European Hominines*, *J. Archaeol. Sci.*, **24**, 677–700
- STREET M., T. TERBERGER, J. ORSCHIET, 2006, *A critical review of the German Paleolithic hominid record*, *J. Hum. Evol.*, **51**, 551–79
- TEAFORD M.F., O.J. OYEN, 1989, *In vivo and in vitro turnover in dental microwear*, *Am. J. Phys. Anthropol.*, **80**, 447–60
- TEAFORD M.F., C.A. TYLEND, 1991, *A new approach to the study of tooth wear*, *J. Dent. Res.*, **70**, 204–7
- THOMPSON J., A. BILSBOROUGH, 1997, *The current state of the Le Moustier 1 skull*, *Acta Praehistorica et Archaeologia*, **29**, 17–38
- TILLIER A.M., 1982, *Les enfants neanderthaliens de Devil's Tower (Gibraltar)*, *Zeitschrift Morphol. Anthropol.*, **73**, 125–48
- TOBIAS P.V., 1971, *Human skeletal remains from the Cave of Hearths, Makapansgat, Northern Transvaal*, *Am. J. Phys. Anthropol.*, **34**, 335–68
- TRINKAUS E., 1980, *Sexual differences in Neanderthal limb bones*, *J. Hum. Evol.*, **9**, 377–97
- TRINKAUS E., J. JELÍNEK, 1997, *Human remains from the Moravian Gravettian: The Dolni Vestonice 3 postcrania*, *J. Hum. Evol.*, **33**, 33–82
- TRINKAUS E., S.E. BAILEY, J. ZILHAO, 2001, *Upper Paleolithic human remains from the Gruta do Caldeirão, Tomar, Portugal*, *Revista Portuguesa de Arqueologia*, **4**, 5–17
- TRINKAUS E., J. SVOBODA, 2006, *Early Modern Human Evolution in Central Europe. The People of Dolni Vestonice and Pavlov*, Oxford Univ. Press, Oxford
- UBELAKER D.H., 1978, *Excavating Human Skeletal Remains*, Aldine, Chicago
- UNGAR P.S., M.F. TEAFORD, F.E. GRINE, 1999, *A preliminary study of molar occlusal relief in Australopithecus africanus and Paranthropus robustus*, *Am. J. Phys. Anthropol.*, **S28**, 269
- VELEMINSKA J., J. BRUZEK, 2008, *Early Modern Humans from Predmosti nr. Prerov: A new reading of old documentation*, Prague Academia, Prague
- WILLIAMS F.L., 2006, *A comparison of the Krapina lower facial remains to an ontogenetic series of Neandertal fossils*, *Periodicum Biologorum*, **108**, 279–88
- WOLPOFF M.H., 1979, *The Krapina dental remains*, *Am. J. Phys. Anthropol.*, **50**, 67–113
- WOLPOFF M.H., F.H. SMITH, M. MALEZ, J. RADOVICIC, D. RUKAVINA, 1981, *Upper Pleistocene human remains from Vindija cave, Croatia, Yugoslavia*, *Am. J. Phys. Anthropol.*, **54**, 499–545
- WOLPOFF M.H., 1999, *Paleoanthropology*, McGraw-Hill, New York
- WOLPOFF M.H., D.W. FRAYER, J. JELÍNEK, 2006, *Aurignacian female crania and teeth from the Mladec caves, Moravia, Czech Republic*, [in:] *Early modern humans at the Moravian Gate: The Mladec caves and their remains*, M. Teschler-Nicola (ed.) Springer, Vienna, pp. 273–340

Streszczenie

Policzkowe mikrostartarcie zębów wykazuje charakterystyczne, trwałe i zależne od diety cechy. Na materiałach historycznych wykazano [Pérez-Pérez *et al.* 1994], że w analizie trzeba uwzględniać również wiek osobnika, szczególnie u dzieci, które mają zarówno zęby mleczne, jak i świeżo wyrżnięte zęby stałe. W populacjach górnoplejstocenijskich zbadano jednak tylko mikrostartarcie na zgryzowych powierzchniach zębów. Ostatnio El-Zaatari & Hublin [2009] stwierdzili brak związanych z wiekiem różnic w nierównościach szkliwa, i to zarówno w populacjach neandertalskich, jak i u człowieka anatomicznie nowoczesnego (AMH), wobec czego grupy reprezentowane zębami mlecznymi można analizować łącznie ze stałymi [Gamza 2010].

Dla populacji historycznych wykazano, że wzór mikrostartarcia stabilizuje się około 13 roku życia, niezależnie od zęba (m2, M1, M2). Nie próbowano jednak badać procesu tej stabilizacji u prehistorycznych łowców-zbieraczy. Celem tej pracy jest ustalenie, w jakim wieku wzór policzkowego mikrostartarcia stabilizuje się u środkowo- i górnoplejstocenijskich osobników i przetestowanie różnic między wzorem mikrostartarcia u dorosłych oraz u dzieci i osobników dorastających. Badana próba zawierała 836 wysokiej rozdzielczości odlewów zębowych, dostępnych na uniwersytecie w Barcelonie. Zęby należały do 174 osobników z trzech populacji: *Homo heidelbergensis*, *H. neanderthalensis* i *H. sapiens* (AMH). Zęby, na których nie zachowało się policzkowe mikrostartarcie lub od osobników o nieustalonym wieku wyeliminowano, podobnie jak wszystkie zęby przednie. Ostatecznie próba liczyła 193 zęby 59 osobników. Wiek zębowy od momentu wyrżnięcia obliczono za Skinnerem [1997]. Dla AMH wiek wyrzynania przyjmowano za Ubelakerem [1979] i Williamsem [2006], a dla *H. neanderthalensis* i *H. heidelbergensis* – za Gramat & Heim [2003].

Powierzchnie policzkowe zębów były skanowane SEM zgodnie ze standardową procedurą [Pérez-Pérez *et al.* 2003, Galbany *et al.* 2009]. Z obrazów SEM wycięte zostały fragmenty szkliwa o powierzchni 0,56 mm², na których zliczano rysy przy pomocy półautomatycznego oprogramowania. Uwzględniano gęstość, długość i odchylenie standardowe długości wszystkich zauważonych prążków w kategoriach ich orientacji (pionowe, poziome, mezjo-dystalne i dysto-mezjalne oraz wszystkich orientacji łącznie). Przedstawiana analiza dotyczy jednak tylko ogólnej gęstości prążkowania. W analizie statystycznej wykorzystano SPSS 15.

Ponieważ gęstość prążkowania ma rozkład normalny, do porównań międzygrupowych zastosowano testy parametryczne (ANOVA). We wszystkich trzech badanych populacjach osobniki w wieku poniżej 5 lat wykazywały gęstość prążków podobną do osobników dorosłych. Choć u neandertalczyków w wieku 6-13 lat gęstość prążkowania wyraźnie malała, co mogło korespondować z wyrzynaniem się M1, w grupie AMH dzieci miały rzadsze prążki niż starsze osobniki i wykazywały ciągły wzrost gęstości z wiekiem. Zmienność mikrostartarcia u osobników w wieku dziecięcym może być związana z procesem przechodzenia na pokarm stały, który u AMH polegał na stopniowym włączaniu do diety twardszych składników, jak również obróbki termicznej [Haddingham 1979, Pfeiffer 1986, Nakazawa *et al.* 2009].

Z tej pracy płyną następujące wnioski: Wzór policzkowego mikrostartarcia jest charakterystyczny dla każdej populacji i odzwierciedla długotrwałe zwyczaje żywieniowe. Uwzględnić należy wiek w chwili śmierci, szczególnie dla osobników przed 13 rokiem życia. Przejście od diety dziecięcej na dorosłą mogło zachodzić stopniowo u AMH, podczas gdy u neandertalczyka wcześniej ujawnia się wzrost gęstości prążków, prawdopodobnie odzwierciedlając przechodzenie na dietę z produktami wywołującymi większą abrazję. Zmienność wewnątrzpopulacyjna – czasowa, geograficzna i klimatyczna – może oznaczać, że te czynniki mogły wpływać na dostępność różnych składników pokarmu.

