Buccal dental microwear analyses support greater specialization in consumption of hard foodstuffs for *Australopithecus anamensis*

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Summary - Molar occlusal microwear texture and anisotropy analyses of 3 Australopithecus anamensis fossil specimens have shown complexity values similar to those of Au. afarensis, indicating that neither of these hominin species had a diet dominated by hard food. However, many researchers have suggested that these were some of the earliest hominins to have such diets. Here we examine buccal microwear patterns of 5 Au. anamensis, 26 Au. afarensis, 48 Hominoidea and 80 Cercopithecoidea primate specimens for independent evidence of dietary adaptations of Au. anamensis. The buccal microwear results obtained suggest that the diet of Au. anamensis relied heavily on hard, brittle food, at least seasonally. This is similar to the diet of the extant Cercopithecoidea primates, including Papio anubis and Chlorocebus aethiops, both of which live in wooded, seasonal savannah environments and have diets that include fruit and grasses, but also underground storage organs (USOs), such as corms or blades, as well as leaves and seeds, and also Mandrillus and Cercocebus, from forested environments with frugivorous-granivorous diets. Furthermore, the buccal microwear patterns of Au. anamensis and Au. afarensis clearly differed – in clear contrast to occlusal enamel texture observations – which support previous dietary interpretations based on both anatomical and palaeocological reconstructions.

Keywords - Hominin, Diet, Feeding ecology, Buccal microwear, Fallback food, Australopithecus anamensis.

Introduction

Diet has been considered the major diversifying factor affecting primate life history and evolution (Fleagle, 1999). However, it has been difficult to reconcile data from palaeoecological and dietary reconstructions. During the Pliocene (5.3-2.6 million years ago, *ma*) climatic conditions in East Africa became progressively cooler and drier (Ravelo *et al.*, 2004), with increasing seasonality (Cerling *et al.*, 1997). At the Miocene/Pliocene boundary, C4 ecosystems (grasslands) expanded due to a decrease of atmospheric CO₂ (Cerling *et al.*, 1993, 1997), and a retreat in C3 plants (trees and shrubs)

throughout the Pliocene has been documented (Cerling, 1992; Morgan *et al.*, 1994; Ségalen *et al.*, 2007; Cerling *et al.*, 2010). In East Africa, these climatic and ecological changes led to a significant faunal shift (Cerling *et al.*, 1997). The most documented hominin remains from this period, classified into the *Ardipithecus* genus, come from Ethiopia and date back to 4.4 *ma* (WoldeGabriel *et al.*, 1994, 2009; White *et al.*, 2006, 2009a). Their dental and masticatory morphology, as well as their occlusal microwear patterns and stable isotopes content, suggest that *Ardipithecus ramidus* was an omnivorous, though mainly frugivorous species (Suwa *et al.*, 2009a,b; White *et al.*, 2009a), with a less abrasive diet than

Australopithecus afarensis, that included small amounts of ¹³C-enriched-plants, or animals that fed on them. This dietary reconstruction fits well with the general palaeoenvironmental framework inferred for Ardipithecus ramidus: a closed, semi-deciduous wooded habitat (WoldeGabriel et al., 1994, 2009; Louchart et al., 2009; White et al., 2009b) that included areas of closed to grassy woodlands as well as true forests (White et al., 2009b) with abundant palms (WoldeGabriel et al., 2009). However, it has been argued that neither the faunal assemblage (Benefit, 1999; Leakey, 1999) or the stable isotope data (Cerling et al., 2010, p. 1105-d) reveal the predominance of closed wooded conditions, but of 'tree or bush savannahs'. If Ardipithecus is 'the probable ancestral morphotype of Pliocene Australopithecus' (Suwa et al., 2009a, p. 68e7), it might also represent the ancestral dietary condition for the australopithecine species Au. anamensis and Au. afarensis, who inhabited the palaeo-Solali-Masai province (Brandy et al., 1980). Their first occurrence in the fossil record predates the mid-Pliocene cooling (2.95-2.52 ma) which caused increasing aridity and the expansion of open habitats (Burckle, 1995; deMenocal, 1995; Denton, 1999; Bobe et al., 2002).

Palaeoenvironmental reconstructions have suggested that Au. anamensis inhabited a wide range of environments, including open woodlands and bushlands with abundant grasses (Andrews & Humphrey, 1999) and gallery forests, both at Kanapoi and Allia Bay, in a close relationship with the proto-Omo river (Leakey et al., 1995) and with significant climatic seasonality (Brown & Feibel, 1991). Up to 3.5 ma the climate was wet (Denys, 1999) and despite the later expansion of arid savannahs (Denton, 1999; Foley, 1999), the palaeoecological reconstructions for Au. afarensis are similar to those described for Au. anamensis, with a whole range of habitats, from grassland savannahs to wooded bushlands or woodlands (White et al., 1993; Reed, 1997; Wood & Richmond, 2000; Bonnefille et al., 2004; Grine et al., 2006b). These reconstructions indicate that both species inhabited more open and dryer environments than Ardipithecus *ramidus* and lived under significantly fluctuating climatic conditions (Denton, 1999) with marked seasonality (Macho *et al.*, 2003).

The anatomical differences in the masticatory complex (Suwa et al., 2009a), especially in dental enamel thickness and megadontia (Suwa et al., 2009b), between Ardipithecus ramidus and Australopithecus anamensis make it unlikely that the two species had similar dietary habits. Australopithecus anamensis and Au. afarensis would not have shared a common diet either, since the robust mandibular corpus and enlarged, low-crowned thick-enamelled postcanine teeth of Au. afarensis have traditionally been associated with the progressive expansion of savannah environments and a reduction of the tree coverage (Leakey et al., 1995; Ward et al., 1999, 2001; Teaford & Ungar, 2000), forcing Au. afarensis to greater consumption of hard food, either brittle or tough, as the availability of soft food decreased through time. However, the similarities in the palaeoecological reconstructions of the two species and their close phylogenetic relationship (Strait & Grine, 2004; Kimbel et al., 2006) may suggest that they would have inhabited similar environments and, thus, shared dietary habits. Occlusal dental microwear (Grine et al., 2006a,b), buccal dental microwear (Estebaranz et al., 2009), and occlusal texture (Ungar et al., 2010) analyses have consistently shown that Au. afarensis would have been an active fruit pursuer relying also on fallback food during the dry season. Thus, the distinct dental morphology, enamel microstructure and megadontia of Au. anamensis (Ward et al., 1999; Macho et al., 2005; White et al., 2006) have been considered responses to the mechanical properties of the fallback food consumed by this ancestral, hard object feeder (Grine et al., 2006a), despite the fact that recent occlusal enamel texture analyses have brought this view into question, suggesting that neither Au. anamensis or Au. afarensis had a diet dominated by hard foods (Ungat et al., 2010).

The aim of this research was to further elaborate on the dietary adaptations of *Au. anamensis* from the independent analysis of the buccal dental microwear patterns of fossil specimens and to compare the results obtained with the various reconstructions and conclusions, especially from occlusal microwear analyses, that have been proposed in relation to the dietary adaptations of this hominin species.

Materials and Methods

The Au. anamensis hominin dental sample studied consisted of 59 casts of teeth moulded from the original specimens during the course of an international collaborative project (Galbany et al., 2004a). The teeth belong to 18 fossil specimens (Tab. 1), 4 from Kanapoi and 14 from Allia Bay (East Rudolf), both in Kenya. The sample studied was identical to that described in Grine et al., (2006a, 2010), and included all the Au. anamensis dental remains recovered before 2003. The Asa Issie dental remains were published later (White et al., 2006), but we agree with Grine et al. (2006a) that the teeth from that site (White et al., 2006) might not show well-preserved enamel surfaces. As for the Aramis remains, the ARA-VP-2/334 molars are completely cracked (White et al., 2006) and, as far as can be seen in the published images, they seem to show altered buccal surfaces. However, the ARA-VP-14/1 specimen might have well-preserved buccal surfaces on LM3 and RM2-M3 teeth; but it was not possible to include them in the present buccal microwear comparison, as was also the case for the Ardipithecus specimens, whose buccal microwear has not yet been analysed.

A large primate (both *Hominoidea* and *Cercopithecoidea*) comparative sample was also analysed, which represents various ecological and environmental dietary adaptations. The *Hominoidea* sample included *Gorilla gorilla gorilla (N=32)*, and *Pan troglodytes troglodytes* (N=10), both from Cameroon, as well as *Pan troglodytes verus* (N=7) from Liberia (Galbany *et al., 2009*), since their habitat preferences might be similar to that inferred for Allia Bay (Schoeninger *et al., 2003*), including from closed forests to semi-open wooded habitats, and with dietary habits ranging from succulent soft fruit

to leafs, stems and bark. Gorillas have highly selective diets year-round, consisting mainly of staple piths, leaves, roots and shoots from abundant monocotyledonous plants, from either firm forests or swampy areas. Their diet also includes seasonal ripe fruit, from a wide variety of species, and fallback food, often of lower nutritional quality, such as leaves, bark and fibrous fruit (Doran & McNeilage, 1998; Doran et al., 2002; Rogers et al., 2004). Chimpanzees occupy tropical forests and dry arboreal savannahs. They frequently feed on the ground, walking from one feeding site to another, mainly consuming fruit and nuts, which account for up to 70-80% of their total food intake; other resources, such as leaves and stems, account for up to 20% of the chimpanzee's total food intake, although these proportions vary greatly among populations (Estes 1997; Tutin et al., 1997).

The Cercopithecoidea sample included Papio anubis (N=27), Chlorocebus aethiops (N=15), Cercopithecus sp. (N=10) -including C. mitis (N=7) and C. neglectus (N=3)-, Mandrillus sphinx (N=4), Cercocebus torquatus (N=3), and Colobus sp. (N=21) -including C. polykomos (N=11), C. guereza (N=3), C. badius (N=5), and C. angolensis (N=2)- (Galbany & Pérez-Pérez, 2004; Galbany et al., 2005a; Galbany, 2006). The ecological and dietary preferences of the cercopithecoid comparative groups differ significantly. The two species included in the Cercopithecus sp. group live in closed wooded habitats (Schultz, 1970) and are mainly frugivorous, although their diet may also include insects, flowers and other plant parts (Beeson et al., 1996; Fleagle, 1999; Tweheyo & Obua, 2001; Nakagawa, 2003). Chlorocebus aethiops was not included in this group because it has been suggested that its dietary preferences include a large variety of food with a limited number of staple foodstuffs and a wide supplement based on seasonality (Lee, 1984; Lee & Hauser, 1998). Mandrillus sphinx and Cercocebus torquatus, two closely related species (Harris & Disotell, 1998; Fleagle & McGraw, 1999; Page & Goodman, 2001; Gilbert, 2007), are terrestrial monkeys (Nakatsukasa, 1996; McGraw & Bshary, 2002) from forested environments that

share a mainly frugivorous-granivorous diet (Lahm, 1986; Fleagle & McGraw, 1999, 2002; Wieczkowski, 2009). Fruit and seed consumption in Mandrillus represents almost 90% of their diet (Lahm, 1986), but they also forage rotten wood, leaves, fibrous matter, bark and herbaceous plants, as well as nuts and arthropods (Norris, 1988). Despite fruit intake accounting for up to 40% of their diet, hard objects collected from the ground, such as arthropods, seeds, bark, roots and nuts, are frequently consumed (Hoshino, 1985; Norris, 1988; Rogers et al., 1996). They also face seasonality, with a decrease in fruit consumption during the dry season (Lahm, 1986). Colobus is an arboreal genus (Oates et al., 1994), traditionally classified as a genuine leaf-eater (Oates & Davies, 1994), but more recently considered to have a more heterogeneous diet. Despite some groups appear to be clearly folivorous (Chapman et al., 2002; Chapman & Pavelka, 2005), in others fruit and seed consumption might be greater than expected (DaSilva, 1992; Davies et al., 1999, Daegling & McGraw, 2001; Fashing, 2001; Chapman et al., 2002). Finally, the diet of Papio is mainly composed of resources obtained from grasses, including USOs (Underground Storage Organs), such as corms, blades and seeds (Alberts et al., 2005), as well as green Acacia seeds, fruit and leaves (Altmann & Altmann, 1970; Fleagle, 1999; Hill & Dunbar, 2002; Alberts et al., 2005). Flowers and meat constitute a minor category in their diet (Lahm, 1986; Hill & Dunbar, 2002; Kunz & Linsenmair, 2008) and some preferred foodstuffs (fruit, green seeds, flowers and green grasses) are seasonal (Alberts et al., 2005).

Dental casting and buccal microwear procedures

High-resolution negative impressions were made using *President Microsystem Regular Body* polyvinylsiloxane (ColtèneTM) and positive casts were made with the two-component polyurethane Feropur PR-55 (FerocaTM) and epoxy resin Epo-Tek 301 (Epoxy TechnologiesTM), both of which provide excellent microscopic detail (Rose, 1983; Galbany *et al.*, 2004b, 2005a). The hominin dental casts were made by M. Teaford (Baltimore, USA) and those of the primates were made by J. Galbany (Barcelona, Spain). All replicas were mounted on aluminium stubs with term fusible gum and sputter coated with a 400-Å gold layer for SEM observation (Galbany *et al.*, 2004b; Estebaranz *et al.*, 2009). A colloidal silver layer was applied to the gum in order to prevent electron saturation during SEM observation.

Since post-mortem damage is a major concern for dental microwear, all casts were examined under a NikonTM binocular lens at 10-30X magnification before SEM observation, and fossil teeth showing post-mortem physical abrasion or chemical erosion (Hobson et al., 2002) were excluded (Teaford, 1988, 2007b; King et al., 1999; Martínez & Pérez-Pérez, 2004), which generally results in a significant reduction of the final sample available (Galbany & Pérez-Pérez, 2004; Grine et al., 2006a,b; Estebaranz et al., 2009). SEM images of the well-preserved buccal enamel surfaces were obtained using Cambridge Stereoscan 360 and 120 scanning electron microscopes in secondary electron detection mode; the working distance was fixed at 25 mm and the acceleration voltage was set to 15 kV. Buccal enamel surfaces of dental crowns were allocated in the SEM vacuum chamber perpendicular to the electron beam and digital microphotographs were taken at 100X magnification, avoiding the occlusal and cervical rims, and were processed with PhotoshopTM v.6 with a high-pass filter (50 pixels) and automatic level adjustment. The images were then cropped to fit exactly a 0.56 mm² enamel patch (Lalueza et al., 1996; Galbany et al., 2004b; Estebaranz et al., 2009).

Microwear patterns of buccal dental enamel surfaces differ significantly from the microwear features that can be observed on occlusal enamel surfaces, which include both pits and scratches of various shapes and sizes. Pits are rarely present on well-preserved buccal surfaces (Fine & Craig, 1981; Puech & Albertini, 1984; Ungar & Teaford, 1996; Jarosova, 2007; Galbany *et al.*, 2009), on the occlusal rims (Ungar & Spencer, 1999) or on occlusal shearing facets lacking crushing phases (Goswami *et al.*, 2005, Schubert & Ungar, 2005; Williams *et al.*, 2009). Microwear striations >15

Kanapoi					
KNM-KP-29283	RI ² , RM ² , RC ¹ , RP ³ ,	RM [?] , LI ¹ , LM [?] , LC ¹ -N	1 ¹ , LM ² , LI ²		
KNM-KP-29287	LI ₁ , LI ₂ , RI ₂ , RP ₃ , R	P ₄ , LP ₄ , RM ₁ , LM ₁ , R	M ₂ , LM₂ , LM ³ , RM ³		
KNM-KP-30502	RM ₁ , RM ₂ , RM ₃ , LM	3			
KNM-KP-34725	RI_2 , RI^2 , Rdc_1 , RM_1	, RM ² , Rm ₂ , Ldc ₁ , LM	1 ₁ , LM ₂ , Li ² , Lm ₁ , LP ₃	, LI ₁	
Allia Bay					
KNM-ER-19981	?	KNM-ER-20420	LM?	KNM-ER-20421	RM ³
KNM-ER-20422	LM1	KNM-ER-20423	LM _{2?}	KNM-ER-20427	LM ²
KNM-ER-20428	LM ₃	KNM-ER-20432	LP ₃ , LP ₄	KNM-ER-35231	RM ₂
KNM-ER-35232	RM?	KNM-ER-35233	LM ₂	KNM-ER-35325	RM ₂
KNM-ER-35236	LM ³	KNM-ER-35238	RM ¹		

Tab. **1** - *Fossil specimens of* Australopithecus anamensis *analysed* (references in bold indicate specimens with well-preserved buccal microwear patterns).

µm (Galbany et al., 2004b) were counted and classified, and orientation with respect to the horizontal cemento-enamel junction was resolved into four 45-degree categories: horizontal (H), vertical (V), mesio-oclusal to disto-cervical (MD) and disto-occlusal to mesio-cervical (DM) (Galbany et al., 2004b). The striation densities (N), average length (X), and standard deviation of the length (S) were measured for each orientation category and for all observed striations (T), obtaining 15 quantitative variables (striation densities: NT, NV, NH, NMD, NDM; striation lengths: XT, XV, XH, XMD, XDM; and striation length variability: ST, SV, SH, SMD, SDM) (see Pérez-Pérez et al., 1994, 1999, and 2003 for detailed variable definitions).

Statistical analysis

The microwear patterns of the Au. anamensis and Au. afarensis teeth were measured by Ferran Estebaranz, (Estebaranz et al., 2009), and those of the primate comparative samples were measured by Jordi Galbany (Galbany & Pérez-Pérez, 2004; Galbany et al., 2005a, 2009). The intraobserver measuring errors of the two researchers were similar and their interobserver error was small (Galbany et al., 2005b; Estebaranz et al., 2009). All statistical analysis and comparisons were made using SPSS v. 15 and XLSTAT for MS-EXCEL. Despite all buccal microwear variables following normal distributions in both the primate comparative samples and the Au. afarensis teeth analysed (Estebaranz et al., 2009), since the final, well-preserved sample available for Au. anamensis was very small (N=5), and a significant degree of heterogeneity was found within the sample, group comparisons were made with Kruskal-Wallis and Mann-Whitney non-parametric tests, although basic parametric statistics were provided and a descriptive linear discriminant analysis (LDA) was used to show similarities between groups.

Results

The initial *Au. anamensis* sample consisting of 59 teeth from 18 specimens showed significant *post-mortem* damage. Only 14 teeth (24%) belonging to 6 individuals (33%) exhibited wellpreserved buccal microwear patterns (Tab. 1). However, since specimen KNM-KP-347235



Fig. 1 - Well-preserved buccal microwear SEM images of the 5 Au. anamensis samples analysed (a: KNM-KP-29287, b: KNM-KP-29283, c: KNM-ER-35231, d: KNM-ER-35233, e: KNM-ER-35236) and of one Au. afarensis specimen (f: LH 4). Scale bar is 100 µm.

was only represented by two deciduous canines, it was not considered in the dietary reconstruction (only permanent postcanine teeth were used). Thus, only 5 *Au. anamensis* specimens, representing 29% of all the specimens studied, could finally be compared with *Au. afarensis* and the other primate species. This low preservation value is similar to those observed in previous hominin microwear analyses (Grine *et al.*, 2006a; Estebaranz *et al.*, 2009). SEM images of the analysed enamel surfaces of *Au. anamensis* and *Au. afarensis* specimens are shown in Figure 1; and SEM images of a representative specimen of each comparative primate taxa are shown in Figure 2.

The buccal microwear patterns of all the permanent teeth studied (N=12; 2 incisors, 2

premolars, and 8 molars) of *Au. anamensis* are shown in Appendix 1. Homogeneity in microwear patterns by tooth type could not be tested for due to the reduced sample available, though the postcanine teeth showed fairly similar NT and XT values. Interestingly, the central incisor had a large overall microwear density (NT=329) compared to the posterior dentition (NT ranging from 166 to 271), and was much higher than that of the lateral incisor (NT=155) and than the density values observed in *Au. afarensis* (NT=150.69) (Estebaranz *et al.*, 2009).

The second permanent molar (M2) was the most represented tooth in the Au. anamensis sample (5/12), belonging to 4 different fossil specimens (KNM-KP 29287, KNM-KP 29283, KNM-ER 35231, and KNM-ER 35233); an additional specimen (KNM-ER 35236) was included by selecting its M3 tooth. The buccal microwear patterns of these 5 selected teeth and the sample variable averages and standard deviations are shown in Appendix 1. The average values and standard deviations of all 15 variables for Au. afarensis and the comparative primate samples are shown in Appendix 1. Australopithecus anamensis showed a high overall density of striations (NT=220.60±46.68), in the same range as the frugivorous and seed-eater Cercopithecoidea samples: Cercocebus (NT=249.33±18.23), Chlorocebus aethiops (NT=210.60±9.90), *Mandrillus sphinx* (NT=213.75±7.56) and *Cercopithecus sp.* (NT=244.00±14.18). The average striation density of Australopithecus anamensis was considerably higher than that of the other East African Pliocene hominin Au. afarensis (NT=150.69±52.51), though the density of the horizontal striations in Au. anamensis (NH=38.4±40.74) was similar to that of Au. afarensis (NH=41.80±16.49) and Gorilla g. gorilla (NH= 40.10 ± 22.61). However, the density of its vertical striations (NV=77.6±34.79) more closely resembled Papio anubis (NV=85.82±5.01), Chlorocebus aethiops (NV=81.00±6.57), and even Cercopithecus sp. (NV=108.80±4.74), than Au. afarensis (NV=28.31±24.01), Gorilla (NV=53.26±29.58) or Pan (NV=40.40±23.82 for P. t. troglodytes and NV=20.14±8.45 for P. t.



Fig. 2 - SEM images of primate specimens studied: a: Cercocebus torquatus IMAZ 9851; b: Cercopithecus sp. NMK om7551; c: Chlorocebus aethiops NMK om0362; d: Mandrillus sphinx HMCZ 34172; e: Papio anubis NMK om6992; f: Colobus sp. HMCZ 37932; g: Gorilla gorilla gorilla NHML 36.7.14.1; h: Pan troglodytes troglodytes NHML 50.1863; i: Pan troglodytes verus PMAE 7544. (IMAZ: Anthropologisches Institut und Museum Universitaet Zuercih Irchel; NMK: National Museums of Kenya; HMCZ: The Museum of Comparative Zoology – Harvard University; NHML: Natural History Museum of London; PMAE: Peabody Museum of Archaeology and Ethnology – Harvard University).

verus). The low average NDM value for *Au. anamensis* (NDM=28.00±25.42) was only comparable to that of *Colobus sp.* (NDM=30.62±18.36) and *Papio anubis* (NDM=20.44±15.69), as the NDM values of the *Hominoidea* ranged from 39.90 to 47.42 (Appendix 2). The box-plots of total striation densities (NT) and average striation lengths (XT) for *Au. anamensis, Au. afarensis* and the comparative primate samples (Fig. 3) showed that *Au. anamensis* shared high striation densities with the *Cercopithecoidea* samples, and clearly deviated from *Au. afarensis* and the nonhominin *Hominoidea*. This was an unexpected result considering the similarities in occlusal microwear patterns between *Au. anamensis* and *Au. afarensis* reported by Grine *et al.* (2006*a*, 2010), as well as between those of *Pan* and *Gorilla*, which showed clear dissimilarities with *Colobus* (Grine *et al.*, 2006a).

For the intergroup comparisons with nonparametric tests, outliers for the total density of striations (NT) were removed from the primate samples analysed and, based on dietary and ecological data, 10 groups were finally considered: *Au. anamensis* (N=5), *Au. afarensis* (N=26), *Cercopithecus* (N=8), *Chlorocebus* (N=13), *Papio* (N=25), *Colobus* (N=19), *Mandrillus-Cercocebus* (N=7), *Gorilla* (N=29), *Pan t. troglodytes* (N=10), and *Pan t. verus* (N=7). Kruskal-Wallis analysis revealed statistically significant



Fig. 3 - Box plots of NT (total striation density) and XT (average length of all striations) for Au. anamensis, Au. afarensis and the primate comparative samples (including Cercopithecoidea and Hominoidea). The two australopithecine samples show clearly distinct striation density values (NT), with Au. anamensis more closely resembling those of the cercopithecines than Au. afarensis.

differences between groups for 10 of the 15 buccal microwear variables analysed: NH (H=28.82, P=0.001), XH (H=33.66, P=0.000), SH (H=18.10; P=0.034), NV (H=81.22, P=0.000), SV (H=18.59, P=0.029), NMD (H=23.44; P=0.005), XMD (H=27.16; P=0.001), NDM (H=35.88, P=0.000), NT (H=66.50, P=0.000), and XT (H=22.20; P=0.008). The comparison of Au. anamensis with the other samples, using U-Mann-Whitney tests, revealed statistically significant differences in NT with Au. afarensis (U=15, P=0.007), Pan t. verus (U=1, P=0.007), Papio anubis (U=25, P=0.037), and Colobus (U=6, P=0.003); in NV with Au. afarensis (U=13.5, P=0.006), Pan t. verus (U=2.50; P=0.015), and Colobus sp. (U=10, P=0.008); in NDM with Mandrillus-Cercocebus (U=5, P=0.041); in SV with Pan t. verus (U=5, P=0.042); and in ST also with Pan t. verus (U=2, P=0.012).

Descriptive LDA did not include the length variability variables (ST, SV, SH, SMD, SDM), since significant correlation coefficients (Spearman *rho*) between length variability and density variables were observed for all the samples analysed (N=148; Appendix 3), and the aim was to describe group relationships based only on striation densities and average lengths, which were the most discriminant microwear variables. Uncorrelated discriminant functions (Flury, 1988, p.5) of the 10 original variables were thus obtained. Significant differences in microwear patterns were observed (*Wilk's* λ =0.153, F=3.405, P<0.0001), with all variables showing significant differences between groups (P<0.05) except XDM (P=0.287). The first two discriminant functions (DF) obtained accounted for 72.88% of the total variance (Fig. 4); DF₁ (57.33%) was mainly correlated with NV (r=0.940) and NT (0.653), and DF₂ (15.54%) was correlated with NDM (0.757) and NT (0.635). All the length variables were negatively correlated with DF_1 , with r values ranging from -0.197 to -0.280. The first two DFs were plotted to show group centroid similarities and 95% confidence intervals of the sample means (equiprobable ellipses) (Fig. 4). A clear separation between the Hominoidea and Cercopithecoidea

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Fig. 4 - Descriptive linear discriminant analysis of the 10 groups considered, including Au. anamensis and Au. afarensis. DF1 was mainly correlated with NV and NT; while DF2 was correlated with NDM and NT (see description in the text). Despite its high dispersion range, Au. anamensis clearly clusters with the cercopithecines, whereas Au. afarensis only overlaps with Pan confidence intervals. Ellipses include 95% confidence intervals of the sample means.

groups was observed for DF₁, with the exception of *Colobus* which showed close similarities in microwear pattern with *Pan t. troglodytes*, perhaps reflecting its heterogeneous, non-exclusive folivorous diet. The joint group formed of *Mandrillus* and *Cercocebus* fell between the *Cercopithecoidea* and *Hominoidea* samples for DF₁, though not for DF₂; their mainly frugivorous dietary habits could account for the overlap with *Gorilla* and *Pan t. troglodytes* for DF₁, and their terrestrial behaviour could be responsible for their high and variable DF₂ values (Fig. 4).

In order to show overall similarities between microwear patterns of all the groups considered, Mahalanobis distances (∂) between group centroids were computed within the descriptive LDA. The buccal microwear pattern of Au. anamensis clearly differed from that of Au. afarensis $(\partial = 346.6)$. The best analogues for Au. anamensis were the cercopithecine species *Papio anubis* (∂ = 4.1), a mainly terrestrial, seasonal fruit and seed consumer, and *Chlorocebus aethiops* ($\partial = 5.9$), with a seasonal, very heterogeneous diet. These were followed at greater distances by the terrestrial, forest-dweller Mandrillus and Cercocebus species ($\partial = 98.8$), the non-terrestrial, from wooded habitats, mainly frugivorous Cercopithecus sp. (C. *mitis* and *C. neglectus*) ($\partial = 232.1$), and the folivorous, though also frugivorous Colobus species (d = 232.3). The most distant groups were Gorilla $(\partial = 317.4)$, Pan t. troglodytes ($\partial = 328.6$) and, especially, Pan t. verus ($\partial = 1,763.2$).

A second, predictive LDA was performed to predict group membership of Au. anamensis specimens using all 15 buccal microwear variables of the 9 comparative groups defined. Since the probability of group membership is highly dependent on the sample sizes (Lachenbruch & Goldstein, 1979), the group sizes was considered when assigning the *a priori* probabilities within the LDA (Marks & Dunn, 1974; Lachenbruch & Goldstein, 1979), to avoid overclassification into groups with larger covariances (Chan, 2005). The first two DFs derived explained 69.1% of total variance (DF₁ 46.4%, DF₂ 22.7%), with *Wilks* λ being highly significant even if the first two DFs were removed (P=0.002). DF₁ was significantly correlated with NV (r=0.874) and NT (r=0.568), and DF₂ was mainly correlated with XH (r=0.389), XMD (r=0.377), and SV (r = -0.336). The overall *post-hoc* probability of correct classification was 62.5% (41.7% after a leave-one-out cross-validation test), and the groups showed highly variable percentages of correct classification: 20.0% Pan t. troglodytes, 38.5% 42.9% Chlorocebus. Mandrillus-Cercocebus, 57.9% Colobus, 58.6% Gorilla, 71.4% Pan t. verus, 75.0% Cercopithecus, 76.9% Au. afarensis, and 84.0% Papio. All 5 Au. anamensis specimens showed buccal microwear patterns similar to those of the cercopithecines: 2 were classified as Papio (ER-35233, 71.5% post-hoc classification probability; and ER-35236, 76.4%), 1 as Chlorocebus (KP-29287, 89.2% probability), 1 as Cercopithecus (ER-35231, 95.3%), and 1 as Mandrillus-Cercocebus (KP-29283, 60.7%): none of them was classified as Gorilla, Pan or Au. afarensis. This suggests that Au. anamensis shows a buccal microwear pattern that is clearly distinct from those of the Hominidea groups compared, including Au. afarensis.

Discussion

The buccal microwear pattern of Au. anamensis showed higher striation densities than any Plio-Pleistocene hominin analysed to date, including not only Au. afarensis (Estebaranz et al., 2009) but also Paranthopus boisei and Homo (Martínez, 2010). Given the similarities in palaeoecological reconstructions of Au. anamensis and Au. afarensis (Brown & Feibel, 1991; Leakey et al., 1995; Andrews & Humphrey, 1999), similarities in microwear patterns (and, by extension, of the African great apes) would also be expected. However, clear differences between Au. anamensis and the Hominoidea were observed, which is in agreement with the assumption of Macho & Shimizu (2010, p. 23) that "it is more parsimonious to conclude that the habitual diet of Au. anamensis differed considerably from that of the extant African great apes". Furthermore, the robustness of the mandibular corpus of Au. anamensis has been seen to suggest a distinct diet for this species from those of both the Plio-Pleistocene hominins and the extant apes (Teaford & Ungar, 2000).

The similarities observed in the buccal microwear pattern between Au. anamensis and the extant Cercopithecoidea species Papio and Chlorocebus indicate that Au. anamensis might have exploited gritty savannah and woodland resources (Wynn, 2000); its dietary preferences would have included, in addition to succulent fruit, hard items such as seeds, nuts, tubers, bark, and roots similar to those consumed by the papionini. The buccal microwear results reported here support the prior assumptions that the diet of Au. anamensis probably included hard foodstuffs (Teaford & Ungar, 2000; Macho et al., 2005; White et al., 2006), including hard foods, such as sedges and USOs, and brittle resources, such as seeds and nuts. Some seeds (such as Brachystegia) and nut bearing trees, from which Au. anamensis could have fed, might have been present at Allia Bay (Schoeninger et al., 2003). The palaeoenvironmental reconstructions also indicate that fossil remains of Au. anamensis are associated with fluvial and lacustrine environments, both at Kanapoi (Leakey et al., 1995, 1998) and Allia Bay (Feibel et al., 1991), which are typical of gallery woodlands. These habitats could also have provided Au. anamensis with soft food resources, such as fruit similar to those consumed by extant baboons, mangabeys and mandrills (Lahm, 1986; Lambert et al., 2004;

Wieczkowski, 2009). However, fruit would not have constituted the great bulk of its diet (Macho & Shimizu, 2010), as is the case for the extant *Pan* and *Gorilla* species (Williamson *et al.*, 1990).

Australopithecus anamensis dental traits have been interpreted as adaptations to crushing hard food (Ward et al., 1999, 2001; Teaford & Ungar, 2000; White et al., 2006; Macho & Shimizu, 2010), which would be consistent with the highly scratched buccal enamel surfaces observed, in contrast to Au. afarensis (Estebaranz et al., 2009). In addition, Macho et al. (2003) have pointed out that Au. anamensis lived in seasonal environments, similar to those seen in the present-day Masai-Mara region in Kenya, which constitute a great challenge due to food scarcity during the dry season, when dietary habits need to rely on fallback food: highly abundant, poor quality non-preferred food (Marshall & Wrangham, 2007; Altmann, 2009; Marshal et al., 2009). Nevertheless, items collected from the ground, such as nuts or seeds, are less susceptible to seasonality (Norris, 1986), and baboons depend heavily on them during the dry season (Hoshino, 1985; Lahm, 1986; Altmann, 2009). Yet the intake of leaves and insects of Mandrillus increases during the dry season (Hoshino, 1985); Papio's fallback food items are mainly corms of grasses and sedges (Alberts et al., 2005; Altmann, 2009); and Mangabeys consume hard seeds and bark as fallback food when their preferred food is not available (Lambert et al., 2004). Taking the papionini as a model for Au. anamensis, it is feasible to consider that its diet might have also been affected by seasonality. However, it is difficult to assess the nature of the fallback food that it might have relied on, since this early australopithecine species might have been a more extreme ecological generalist than the baboons (Codron et al., 2008). Dry seeds, sedges, grass corms and other USOs are good candidates for Au. anamensis fallback food (Macho & Shimizu, 2010). The biomechanical demands of sedges and corms on teeth fit well with Au. anamensis' microenamel structure adaptations (Macho & Shimizu, 2010). The importance of USOs in human evolution has already been highlighted (Laden & Wrangham,

2005; Dominy et al., 2008), and analysis of stable isotopes has suggested that grasses and sedges (C4 plants and/or animals that fed on them) were consumed by the australopithecines along with forest food (Sponheimer & Lee-Thorp, 2003). In fact, the consumption of C4 food and the C3:C4 proportion in the baboons are similar to those of early hominins (Codron et al., 2008). Although Au. anamensis was contemporary to the expansion of open C4 grasslands (Cerling et al., 1992, 1997, 2010), some studies point out that C4 grasses remained a minor part (circa 15%) of the environment until the Late Pliocene (Haywood & Valdes, 2006; Ségalen et al., 2007). Nevertheless, the consumption of green blades of grass (a seasonal preferred food for the baboons) and corms of grasses (a non-preferred USO) might constitute the consumed C4 food detected by stable isotope analysis in hominins. Despite all these considerations, the analyses of Au. anamensis' dental microstructure (Macho & Shimizu, 2010) and occlusal microwear patterns (Grine et al., 2006a; Ungar et al., 2010) have excluded hard, brittle items from the diet of Au. anamensis. Various reconstructions of the diet of Au. anamensis have been reported, though (Teaford & Ungar, 2000; Macho et al., 2005; Grine et al., 2006a; Macho & Shimizu, 2010). Despite the fact that Macho & Shimizu (2010) argue that such differences could be due to methodological limitations, they might just as well be interpreted as "different dietary/lifestyle regimes at different periods over the human lifespan" (Nystrom, 2010, p. 215).

Previous microwear analysis has shown that buccal and occlusal patterns reflect the same dietary tendencies in recent human populations (Nystrom, 2010), Pliocene hominin *Au. afarensis* (Grine *et al.*, 2006a; Estebaranz *et al.*, 2009) and Pleistocene *P. boisei* (Ungar *et al.*, 2008; Martínez, 2010). However, the results reported here do not support previous interpretations of similarities in microwear patterns between *Au. anamensis* and *Au. afarensis*, or with those of *Pan* and *Gorilla*, based on occlusal microwear texture analysis, which led to the suggestion that the two hominin species "*did not have diets dominated by hard, brittle foods*" and "*did not have diets* dominated by tough foods either" (Ungar et al., 2010, p. 3345), despite the fact that it was "perhaps surprising that the occlusal microwear data" suggested "that chimpanzees and gorillas constitute the best modern analogues for dietary preferences in Au. anamensis" (Grine et al., 2006a, p. 301).

The non-coincident buccal microwear interpretation made here could be attributed to differences in sample size or composition. However, the original sample studied in both analyses (occlusal and buccal microwear) was the same and two specimens (KNM-ER-35236 and KNM-KP-29287) were included in both the buccal (N=5) and the occlusal (N=3) analyses; KNM-KP-34725 had no permanent teeth with well-preserved buccal microwear pattern, and KNM-ER-35231 and KNM-ER-35233 were not preserved enough for occlusal microwear analysis (Grine et al., 2006a). However, specimens KNM-ER-35236 and KNM-KP-29287 behaved congruently in both buccal and occlusal surface research: KNM-ER-35236 had low feature densities, below the species average, and KNM-KP-20287 showed highly featured surfaces in both analyses. Although the trend might be the same, the two techniques do not necessarily explain exactly the same phenomenon (Nystrom, 2010). Buccal microwear long-term stability, both in human populations (Romero et al., 2012) and in Papio cynocephalus from Amboseli (J. Galbany, unpublished data), contrast with the faster turnover of occlusal microwear patterns (Teaford & Oyen, 1989; Teaford & Tylenda, 1991), described as the "Last Supper Effect" (Grine, 1986; Ungar, 2009). Occlusal dental microwear patterns in primates record the effects of the diet from only the previous days or weeks before death (Teaford, 2007a), which makes analysis of large samples necessary (Ungar, 2009). In contrast, although buccal microwear may also be affected by significant, short-term dietary changes, the overall population buccal microwear pattern will remain unchanged unless dietary shift homogeneously affected most of the specimens analysed over a long time period before death (Romero et al., 2012). Thus, the analyses of the two enamel surfaces could be

complimentary, since they may be providing dietary reconstructions on different time scales (Nystrom, 2010). The simultaneous study of both buccal and occlusal microwear patterns of Pliocene samples, such as Cercopithecoidea primates from East Africa (Leakey et al., 1995; Frost & Delson, 2002), would provide relevant information that would help to interpret the observed microwear discrepancies between occlusal and buccal patterns for Au. anamensis, since the palaeoenvironmental changes affected the two groups in similar ways, forcing them to include C4 food in their diets (Codron et al., 2008). The Kanapoi fossil assemblage includes over 30 mammalian taxa (Leakey et al., 1995), although only Parapapio cf. ado and two colobine primate species were recovered (Leakey et al., 1995). Dietary reconstructions for both groups have indicated that their diet included leaves (Teaford & Leakey, 1992; Lucas & Teaford, 1994), although Parapapio from Kanapoi was supposed to have been more frugivorous than those from Laetoli and East Rudolf (Benefit, 1999). Until a detailed comparison between the two techniques is made on identical fossil specimens, with large samples, the significance of the non-coincident results cannot be fully ascertained.

Our buccal microwear results suggest that Au. anamensis would have had a significantly specialized diet that included food from open environments, such as grasses or sedges, as proposed for later hominin species (Sponheimer et al., 2005, 2006a), although it could also have consumed resources from gallery forests. Moreover, cercopithecines (mainly papionini) constitute the best modern dietary analogue for Au. anamensis based on buccal dental microwear striation density (Fig. 5). This interpretation enhances previous studies that proposed baboons as a model for early hominin evolution (Sponheimer et al., 2006b), based on habitat preferences (Reed, 1997; Jolly, 2001), functional morphology (Jolly, 1970, 2001), and their association with C4 environment expansions (Lee-Thorp et al., 2003; Sponheimer et al., 2006a; Codron et al., 2008). Preliminary results on the occlusal microwear of Ardipithecus have shown that its diet was less



Fig. 5 - Overall microstriation density (NT) and main dietary specificities of the primate comparative taxa analysed (open dots) compared to those for Au. anamensis and Au. afarensis (black dots). The images stand for main foodstuffs consumed by the extant taxa: fruits, seeds and nuts, leaves, grass blades, and USOs. Dietary data was obtained from Schultz (1970), Hoshino (1985), Lahm (1986), McGrew et al. (1988), Oates & Davies (1994), Beeson et al. (1996), Tutin et al. (1997), Harris & Disotell (1998), Lee & Hauser (1998), Fleagle & McGraw (1999), Page & Goodman (2001), Tweheyo & Obua (2001), Doran et al. (2002), Nakagawa (2003), Rogers et al. (2004), Alberts et al. (2005), Chapman & Pavelka (2005), Gilbert (2007), Harris & Chapman (2007), and Cooke & McGraw (2010).

abrasive than that of Australopithecus (Suwa et al., 2009b), and Ardipithecus dental enamel thickness is consistent with such an interpretation: it is intermediate between Pan and Australopithecus (Leakey et al., 1995; Suwa et al., 2009b), revealing a soft or omnivorous diet (Ward et al., 1999; Suwa et al., 2009b), chimpanzee-like (Ward et al., 1999; Laden & Wrangham, 2005), with consumption of C3 plants (White et al., 2009a). The diet of Au. anamensis could therefore be interpreted as an adaptation to more demanding, colder and dryer environments. The diverging buccal microwear patterns of Au. anamensis and Au. afarensis, which might constitute an anagenetically evolving lineage (Kimbel et al., 2006), suggest that Au. afarensis would have returned (compared to its predecessor) to softer dietary habits, closer to those of Gorilla and Pan (Grine et al., 2006b; Estebaranz et al., 2009), at least during the favourable season, consuming fallback food, such as seed, bark or corms, during the dry season, although the high turnover

and remodelling observed on buccal enamel surfaces (Romero *et al.*, 2012) might not allow to discriminate seasonal diets. An alternative view would be that *Au. anamensis* represents a dietary specialized stage from which *Au. afarensis* could have not derived. Still, the comparison of the buccal microwear pattern of *Ardipithecus ramidus* (which could differ from the occlusal one) with those of *Au. anamensis* and *Au. afarensis* will certainly shed more light on the Pliocene *hominin* dietary adaptations and speciation processes.

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References

- Alberts S.C., Hollister-Smith J., Mututua R.S., Sayialel S.N., Muruthi P.M., Warutere J.K. & Altmann J. 2005. Seasonality and long-term change in a savannah environment. In D.K. Brockman & C.P. Van Schaik (eds): Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates, pp. 157-196. Cambridge University Press. Cambridge, UK.
- Altmann S.A. 2009. Fallback foods, eclectic omnivores, and the packaging problem. Am. J. Phys. Anthropol., 140: 615-629.
- Altmann S.A. & Altmann J. 1970. Baboon ecology. Bibliotheca Primatologica, 12. University of Chicago Press, Chicago.
- Andrews P., & Humphrey L. 1999. African Miocene environments and the transition to early hominines. In T.G. Bromage & F. Schrenk (eds): *African Biogeography, Climate Change and Human Evolution.* Oxford University Press, New York.
- Beeson M., Tame S., Keeming E. & Lea S.E.G. (1996). Food habits of guenons (*Cercopithecus* spp.) in Afro-montane forest. *Afr. J. Ecol.*, 34: 202-210.
- Benefit B.R. 1999. Biogeography, dietary specialization and the diversification of African Plio-Pleistocene monkeys. In T. Bromage & F. Schrenk (eds): *African Biogeogrpahy, Climate Change and Human Evolution*, pp. 172-188. Oxford University Press, New York.
- Bobe R., Behrensmeyer K. & Chapman R.E. 2002. Faunal change, environmental variability and late Pliocene hominin evolution. *J. Hum. Evol.*, 42: 475-497.
- Bonnefille R., Potts R., Chalie F., Jolly D. & Peyron O. 2004. High-resolution vegetation and climate change associated with Pliocene *Australopithecus afarensis. Proc. Natl. Acad. Sci.* U.S.A., 101: 12125–12129.

- Brandy L.D., Sabatier M. & Jaeger J.J. 1980. Implications phylogénétiques et biogéographiques des dernières découvertes de Muridae en Afghanistan, au Pakistan et en Ethiopie. *Géobios Lyon* 13: 639-643.
- Brown F.H. & Feibel C.S. 1991. Stratigraphy, depositional environments and paleogeography of the Koobi Fora Formation. In Harris J.M. (ed): *Koobi Fora Research Project. Stratigraphy, Artiodactyls and Paleoenvironments, vol. 3,* pp.1-10. Clarendon Press, Oxford.
- Burckle L.H. 1995. Current issues in Pliocene Paleoclimatology. In E.S. Vrba & G. H. Denton T.C. Partridge & L.H. Burckle (eds): *Paleoclimate and Evolution, with Emphasis on Human Origins*, pp. 37-44. Yale University Press, New Haven.
- Cerling T.E. 1992. Development of grasslands and savannas in East Africa during the Neogene. *Palaeogeograph. Palaeoecl.*, 97: 241-247.
- Cerling T.E., Wang Y. & Quade J. 1993. Expansion of C4 ecosystems as an indicator of global ecological change in the late Miocene. *Nature*, 361: 344-345.
- Cerling T.E., Harris J.M., MacFadden B.J., Leakey M.G., Quade J., Eisenmann V. & Ehleringer J.R. 1997. Global vegetation change through the Miocene/Pliocene boundary. *Nature*, 389: 153-158.
- Cerling T.E., Levin N.E., Quade J., Wynn J.G., Fox D.L., Kingston J.D., Klein R.G. & Brown F.H. 2010. Comment on the Paleoenvironment of *Ardipithecus ramidus. Science*, 328: 1105-d.
- Chan Y.H. 2005. Biostatistics 303. Discriminant analysis. *Singapore Med. J.*, 46: 54-61.
- Chapman C.A. & Pavelka M.S.M. 2005. Group size in folivorous primates: ecological constraints, and the possible influence of social factor. *Primates*, 46: 1-9.
- Chapman C.A., Chapman L.J. & Gillespie T.R. 2002. Scale issues in the study of primate foraging: Red colobus of Kibale National Park. Am. J. Phys. Anthropol., 117: 349-363.
- Codron D., Lee-Thorp J.A. Sponheimer M., de Ruiter D. & Codron J. 2008. What insights can baboon feeding ecology provide for early hominin niche differentiation? *Int. J. Primatol.*, 29: 757-772.

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- Cooke C. & McGraw S. 2010. Diet, food hardness and tooth use in red-capped mangabeys from Sette Cama, Gabon. *Am. J. Primatol.*, 72S: 38.
- Daegling D.J. & McGraw W.S. 2001. Feeding, diet, and jaw form in West African *Colobus* and *Procolobus. Int. J. Primatol.*, 22: 1033-1055.
- Dasilva G.L. 1992. The western black-and-white colobus as a low-energy strategist: activity budgets, energy expenditure and energy intake. *J. Anim. Ecol.*, 61: 79-91.
- Davies A.G., Oates J. & Dasilva G.L. 1999. Patterns of frugivory in three West African colobine monkeys. *Int. J. Primatol.*, 20: 327-357.
- DeMenocal P.B. 1995. Plio-Pleistocene African Climate. *Science*, 270: 53-59.
- Denton G. H. 1999. Cenozoic climate change. In T.G. Bromage & F. Schrenk (eds): African biogeography, climate change and human evolution, pp. 94-115. Oxford University Press, New York.
- Denys C. 1999. Of mice and men. Evolution in East and South Africa during the Plio-Pleistocene times. In T.G. Bromage & F. Schrenk (eds): *African Biogeography, Climate Change & Human Evolution,* pp. 226-252. Oxford University Press, New York.
- Dominy N., J., Vogel E.R., Yeakel J.D., Constantino P. & Lucas, P.W. 2008. Mechanical properties of plant underground storage organs and implications for dietary models of early hominins. *Evol. Biol.*, 35: 159-175.
- Doran D., & McNeilage A. 1998. Gorilla ecology and behaviour. *Evol. Anthropol.*, 6:120–131.
- Doran D., Mc Neilage A., Greer D., Bocian C., Mehlman P. & Shah N. 2002. Western lowland gorilla diet, resource availability: new evidence, cross-site comparisons, reflections on indirect sampling methods. *Am. J. Primatol.*, 58:91–116.
- 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.
- Estes R.D. 1997. *The behaviour guide to African mammals*. Russel Friedman Books, Halfway House Estate, Johannesburg.

- Fashing P.J. 2001. Feeding ecology of guerezas in the Kakamega Forest, Kenya: The importance of Moraceae fruit in their diet. *Int. J. Primatol.*, 22: 579-609.
- Feibel C.S., Harris J.M. & Brown F.H. 1991. Neogene paleoenvironments of the Turkana basin. In J.M. Harris (ed): Koobi Fora Research Project. Stratigraphy, Artiodactyls, and Paleoenvironments, vol.3, pp. 321-346. Clarendon Press, Oxford.
- Fine D. & Craig G.T. 1981. Buccal surface wear of human premolar and molar teeth: A potential indicator of dietary and social differentiation. *J. Hum. Evol.*, 10: 335-344.
- Foley R.A. 1999. The evolutionary geography of Pliocene hominids. In T.G. Bromage & F. Schrenk (eds): *African biogeography, climate change, and hominid evolution,* pp. 327-348. Oxford University Press, Oxford.
- Fleagle J.G. 1999. *Primate adaptation and evolution*. 2nd Edition. Academic Press, New York.
- Fleagle J.G. & McGraw W.S. 1999. Skeletal and dental morphology supports diphyletic origin of baboons and mandrills. *Proc. Natl. Acad. Sci.* U.S.A., 96: 1157-1161.
- Fleagle J.G. & McGraw W.S. 2002. Skeletal and dental morphology of African papionins: unmasking a cryptic clade. *J. Hum. Evol.*, 42: 267-292.
- Flury B., 1988. Common principal components and related multivariate methods. In V. Barnett R.A. Bradley, Hunter S., Kadane J.B., Kendall D.G., Smith A.F.M., Stigler S.M. & Watson G.S. (eds): Wiley Series in Probability and Mathematical Statistics. Wiley Liss, New York.
- Frost S.R. & Delson E. 2002. Fossil Cercopithecidae from the Hadar Formation and surrounding areas of the Afar Depression, Ethiopia. *J. Hum. Evol.*, 43: 687-748.
- Galbany J. 2006. *El patró de microestriació dental de primats Catarrhini: un model ecològic per primats fòssils i homínids.* Ph. D. Dissertation. Universitat de Barcelona, Barcelona. http:// www.tdx.cat/handle/10803/802
- Galbany J. & Pérez-Pérez A. 2004. Buccal enamel microwear variability in Cercopithecoidea Primates as a reflection if dietary habits in

forested and open savanna environments. *Anthropologie*, XLII: 13-19.

- Galbany J., Martínez L.M., Hiraldo O., Espurz V., Estebaranz F., Sousa M., Martínez López-Amor H., Medina A. M., Farrés M., Bonnin A., Bernis C. Turbón D. & Pérez-Pérez. 2004a. A. Pérez-Pérez (ed.): *Teeth: Catálogo de los moldes de dientes de homínidos de la Universitat de Barcelona*. Universitat de Barcelona, Barcelona.
- Galbany J., Martínez L.M. & Pérez-Pérez A. 2004b. Tooth replication techniques, SEM imaging and microwear analysis in primates: methodological obstacles. *Anthropologie*, XLII: 5-12.
- Galbany J., Moyà-Solà S. & Pérez-Pérez A. 2005a. Dental microwear variability on buccal tooth enamel surfaces of extant Catarrhini and the Miocene fossil *Dryopithecus laietanus* (Hominoidea). *Folia Primatol.*,76: 325-341.
- Galbany J., Martínez L.M., López-Amor H.M., Espurz V., Hiraldo O., Romero A., de Juan J. & Pérez-Pérez A. 2005b. Error rates in buccaldental microwear quantification using scanning electron microscopy. *Scanning*, 27: 23-29.
- Galbany J., Estebaranz F., Martínez L.M. & Pérez-Pérez A. 2009. Buccal dental microwear variability in extant African Hominoidea: taxonomy *versus* ecology. *Primates*, 50: 221-230.
- Gilbert C.C. 2007. Craniomandibular morphology supporting the diphyletic origin of mangabeys and a new genus of the *Cercocebus/ Mandrillus* clade, *Procercocebus. J. Hum. Evol.*, 53: 69-102.
- Goswami A., Flynn J., Ranivoharimanana L. & Wyss A.R. 2005. Dental microwear in Triassic Amniotes: implications for paleoecology and masticatory mechanics. *J. Vertebr. Paleonto.*, 25: 320-329.
- Grine F. E. 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: a quantitative qnalysis of permament molar microwear. *J. Hum. Evol.*, 15: 783-822.
- Grine F., Ungar P.S. & Teaford M.F. 2006a. Was the Early Pliocene hominin 'Australopithecus' anamensis a hard object feeder? S. Afr. J. Sci., 102: 301-310.
- Grine F., Ungar P.S., Teaford M.F. & El-Zaatari S. 2006b. Molar microwear in *Preanthropus*

afarensis: evidence for dietary stasis through time and under diverse palaeoecological conditions. *J. Hum. Evol.*, 51: 297-319.

- Harris T.R. & Chapman C.A. 2007. Variation in diet and ranging of black and white colobus monkeys in Kibale National Park, Uganda. *Primates*, 48: 208-221.
- Harris E.E. & Disotell T.R. 1998. Nuclear gene trees and the phylogenetic relationships of the mangabeys (Primates: *Papionini*). *Mol. Biol. Evol.*, 15: 892–900.
- Haywood A.M. & Valdes P.J. 2006. Vegetation cover in a warmer world simulated using a dynamic global vegetation model for the Mid-Pliocene. *Palaeogeogr Palaeocl*, 237: 412-426.
- Hill R.A. & Dunbar R.I.M. 2002. Climatic determinants of diet and foraging behavior in baboons. *Evol. Biol.*, 16: 579-593.
- Hobson R.S., Rugg-Gunn A.J. & Booth, T.A. 2002. Acid-etch patterns on the buccal surface of human permanent teeth. *Arch. Oral Bio.*, 47: 407-412.
- Hoshino J. 1985. Feeding ecology of mandrills (*Mandillus sphinx*) in Campo Animal Reserve, Cameroon. *Primates*, 26: 248-273.
- Jarosova I. 2007. Dental buccal microwear of the medieval population from Dolní Vestonice, Czech Republic. *Anthropologie*, 45: 71-80.
- Jolly C.J. 1970. The seed-eaters: a new model of hominid differentiation based on a baboon analogy. *Man*, 5: 1-26.
- Jolly C.J. 2001. A Proper Study of Mankind: Analogies from the papionin monkeys and their implications for human evolution. *Yearb. Phys. Anthropol.*, 44: 177-204.
- Kimbel W.H., Lockwood C.A., Ward C.V., Leakey M.G., Rak Y. & Johanson D.C. 2006. Was Australopithecus anamensis ancestral to A. afarensis? A case of anagenesis in the hominin fossil record. J. Hum. Evol., 51: 134-152.
- King T., Andrews P. & Boz B. 1999. Effect of taphonomic processes on dental microwear. *Am. J. Phys. Anthropol.*,108: 359-373.
- Kunz B.K. & Linsenmair K.E. 2008. The disregarded West: diet and behavioural ecology of Olive Baboons in the Ivory Coast. *Folia Primatol.*, 79: 31-51.

- Laden G. & Wrangham R. 2005. The rise of the hominids as an adaptive shift in fallbacks foods: Plant underground storage organs (USOs) and australopith origins. *J. Hum. Evol.* 49: 482-498.
- Lachenbruch P.A. & Goldstein M. 1979. Discriminant Analysis. *Biometrics*, 35: 69-85.
- Lalueza C., Pérez-Pérez A. & Turbón D. 1996. Dietary inferences through buccal microwear analysis of Middle and Upper Pleistocene human fossils. *Am. J. Phys. Anthrop.*, 100: 367-387.
- Lahm S.A. 1986. Diet and habitat preferences of Mandrillus sphinx in Gabon: implications of foraging strategy. Am. J. Primat., 11: 9-26.
- Lambert J.E., Chapman C.A., Wrangham R.W. & Conkin-Brittain N.L. 2004. Hardness of cercopithecine foods: implications for the critical function of enamel thickness in exploiting fallbacks foods. *Am. J. Phys. Anthropol.*, 125: 363-368.
- Leakey M.G., Feibel C.S., McDougall I. & Walker A. 1995. New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature*, 376: 565-571.
- Leakey M.G., Feibel C.S., McDougall I., Ward C. & Walker A. 1998. New specimens and confirmation of an early age for *Australopithecus anamensis*. *Nature*, 393: 62-66.
- Leakey M.G. 1999 Introduction. Part IV: Hominid Evolution. In Bromage F. & T. Schrenk (eds): African Biogeography, Climate Change, and Human Evolution, pp. 271-275. Oxford University Press, New York.
- Lee P.C. 1984. Ecological constraints of the social development of the vervet monkeys. *Behaviour*, 91: 245-262.
- Lee P.C. & Hauser M.D. 1998. Long-term consequences of changes in territory quality on feeding and reproductive strategies of vervet monkeys. J. Animal Ecol., 67: 347-358
- Lee-Thorp J.A., Sponheimer, M. & van der Merwe. 2003. What do stable isotopes tell us about hominid dietay and ecological niches in the Pliocene? *Int. J. Osteoarchaeol.*, 13: 104-113.
- Locuhart A., Wesselman H., Blumenschine R.J., Hlusko L.J., Njau J.K., Black M.T., Asnake M. & White T.D. 2009. Taphonomic, avian, and

small-vertebrate indicators of *Ardipithecus ramidus* habitat. *Science*, 326: 66, 66e1-66e4.

- Lucas P.W. & Teford M.F. 1994. Functional morphology of colobine teeth..In A. G. Davies & J. F. Oates (eds) *Colobine monkeys: their ecology, behaviour and evolution,* pp. 173-203. Cambridge University Press, Cambridge.
- Macho G.A., Leakey M.G., Williamson D.K. & Jiang Y. 2003. Palaeoenvironmental reconstruction: evidence for seasonality at Allia Bay, Kenya, at 3.9 million years. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 199: 17-30.
- Macho G.A., Shimizu D., Jiang Y. & Spears I. 2005. *Australopithecus anamensis*: a finite-element approach to studying the functional adaptations of extinct hominins. *Anat. Rec. Part A*, 283: 310-318.
- Macho G.A. & Shimizu D. 2010. Kinematic parameters inferred from enamel microestructure: new insights into the diet of *Australopithecus anamensis. J. Hum. Evol.*, 58: 23-32.
- Marks S. & Dunn O.J. 1974. Discriminant functions when covariance matrices are unequal. J. Am. Stat. Assoc., 69: 555-559.
- Marshall A. J. & Wrangham R.W. 2007. Evolutionary consequences of fallback foods. *Int. J. Primatol.*, 28: 1219-1235.
- Marshall A.J., Boyko C.M., Feilen K., Boyko R. H. & Leighton M. 2009. Defining fallback foods and assessing their importance in primate ecology and evolution. *Am. J. Phys. Anthropol.*, 140: 603-614.
- Martínez L.M. 2010. Variabilidad del patrón de microdesgaste dental en Homininos Plio-Pleistocénicos del este y sur de África. PhD. Dissertation, Universitat de Barcelona.
- Martínez L.M. & Pérez-Pérez A. 2004. Postmortem wear as indicator of taphonomic processes affecting enamel surfaces of hominin teeth from Laetoli and Olduvai (Tanzania): implications to dietary Interpretations. *Anthropologie*, 42: 37–42.
- McGraw W.S. & Bshary R. 2002. Association of terrestrial mangabeys (*Cercocebus atys*) with arboreal monkeys: Experimental Evidence for the Effects of Reduced Ground Predator Pressure on Habitat Use. *Int. J. Primatol.*, 23: 311-325.

- McGrew W.C., Baldwin P.J. & Tutin C.E.G. 1988. Diet of wild chimpanzees (*Pan troglodytes verus*) at Mt. Assirik, Senegal: I. Composition. *Am. J. Primatol.* 16: 213-226.
- Morgan M.E.J., Kingston J.D. & Marino B.D. 1994. Carbon isotope evidence for the emergence of C_4 plants in the Neogene of Pakistan and Kenya. *Nature*, 367, 162-165.
- Nakagawa N. 2003. Differences in food selection between patas monkey (*Erythrocebus patas*) and tantalus monkeys (*Cercopithecus aethiops tantalus*) in Kala Maloue National Park, Cameroon, in relation to nutrient content. *Primates*, 44: 3-11.
- Nakatsukasa M. 1996. Locomotor differentiation and different skeletal morphologies in mangabeys (Lophocebus and Cercocebus). Folia Primatol., 66: 1-4.
- Norris J. 1988. Diet and feeding behavior of semifree ranging mandrills in an enclosed gabonais forest. *Primates*, 29: 449-463.
- Nystrom P. 2010. Dental microwear as indicator of diet in recent human populations. A case study from an early Neolithic site in the Czech Republic. *Am. J. Phys. Anthropol.*, 141 S50: 125.
- Oates J.F. & Davies A.G. 1994. What are the colobines? In A.G. Davies, J.F. Oates (eds): *Colobine monkeys: their Ecology, Behaviour and Evolution*, pp. 1-10. Cambridge University Press, Cambridge.
- Oates J.F., Davies A.G. & Delson E. 1994. The diversity of living colobines. In A.G. Davies & J.F. Oates (eds): *Colobine monkeys: their ecology*, *behaviour and evolution*, pp.45-74. Cambridge University Press, Cambridge.
- Page S.L. & Goodman M. 2001. Catarrhine phylogeny: noncoding DNA evidence for a diphyletic origin of the mangabeys and for a humanchimpanzee clade. *Mol. Phylogenet. Evol.*, 18: 14-25.
- Pérez-Pérez A., Lalueza C. & Turbon D. 1994. Intraindividual and intragroup variability of buccal tooth striation pattern. *Am. J. Phys. Anthropol.*, 94, 175–187.
- Pérez-Pérez,A., Bermúdez de Castro J.M. & Arsuaga J.L. 1999. Nonocclusal dental microwear analysis of 300,000-year-old *Homo*

heilderbergensis Teeth from Sima de los Huesos (Sierra de Atapuerca, Spain. Am. J. Phys. Anthropol., 108: 433-457.

- Pérez-Pérez A., Espurz V., Bermúdez de Castro J.M., de Lumley M.A. & 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.
- Puech P.F. & Albertini H. 1984. Dental microwear and mechanisms in early hominids from Laetoli and Hadar. *Am. J. Phys. Anthropol.*, 65, 87–91.
- Ravelo A.C., Andreasen D.H., Lyle M., Olivarez Lyle, A. & Wara M.W. 2004. Regional climate shifts caused by gradual global cooling in the Pliocene epoch. *Nature*, 426: 263-267.
- Reed K.E. 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. *J. Hum. Evol.*, 32: 289–322.
- Rogers M.E., Abernethy K.A., Fontaine B., Wickings E.J. & White L.J.T. 1996. Ten days in the life of a mandrill horde in the Lopé Reserve, Gabon. *Am. J. Primatol.*, 40: 297-313.
- Rogers M.E., Abernethy K., Bermejo M., Cipolletta C., Doran D., McFarland K., Nishihara T., Remis M., Tutin C.E.G. 2004. Western Gorilla diet: a synthesis from six sites. *Am. J. Phys. Anthropol.*, 64:173–192.
- Romero A., Galbany J., De Juan J. & Pérez-Pérez A. 2012. Brief Communication: Short and long-term *in vivo* human buccal dental-microwear turnover. *Am. J. Phys. Anthropol.*, (in press) DOI 10.1002/ajpa.22054.
- Rose J.J. 1983. A replication technique for scanning electron microscopy: applications for anthropologists. *Am. J. Phys. Anthropol.*, 62: 255-261.
- Schoeninger M.J., Reeser H. & Hallin K. 2003. Paleoenvironment of *Australopithecus anamen*sis at Allia Bay, East Turkana, Kenya: evidence from mammalian herbicore enamel stable isotopes. J. Anthropol. Archaeol., 22: 200-2007.
- Schultz A.H. 1970. The comparative uniformity of the Cercopithecoidea. In J. R.: Napier & P.H. Napier (eds): *Old world Monkeys*, pp. 39-51. Academic Press, New York.

- Schubert B.W. & Ungar P.S. 2005. Wear facets and enamel spalling in tyrannosaurid dinosaurs. *Acta Palaeontol. Pol.*, 50: 93-99.
- Ségalen L., Lee-Thorp J.A. & Cerling T. 2007. Timing of C4 grass expansion across sub-Saharan Africa. *J. Hum. Evol.*, 53: 549-559.
- Sponheimer M. & Lee-Thorp J.A. 2003. Differential resource utilization by extant great apes and australopithecines: towards solving the C4 conundrum. *Comparative Biochemistry and Physiology Part A*, 136: 27-34.
- Sponheimer M., Lee-Thorp J., de Ruiter D., Codron D., Codron J., Baugh A.T. & Thackeray F. 2005. Hominins, sedges, and termites: new carbon isotope data from the Sterkfontein valley and Kruger National Park. *J. Hum. Evol.*, 48: 301-312.
- Sponheimer M., Passey N.J., de Ruiter D., Guatelli-Steiberg D., Cerling T.E. & Lee-Thorp J.A. 2006a. Isotopic evidence for dietary variability in the early hominin *Paranthropus robustus. Science*, 314: 980-982.
- Sponheimer M., Loudon J.E., Codron D., Howells M.E., Pruetz J.D., Codron J., de Ruiter & D.J. & Lee-Thorp J.A. 2006b. Do "savanna" chimpanzees consume C4 resources? *J. Hum. Evol.*, 51: 128-133.
- Strait D.S. & Grine F.E. 2004. Inferring hominoid and early hominid phylogeny using craniodental characters: the role of fossil taxa. *J. Hum. Evol.*, 47: 399-452.
- Suwa G., Asfaw B., Kono R.T., Kubo D., Lovejoy C.O. & White T.D. 2009a. The Ardipithecus ramidus skull and its implications for hominid origins. Science, 326: 68e1-68e7.
- Suwa G., Kono R.T., Simpson S.W., Asfaw B., Lovejoy C.O. & White T.D. 2009b. Paleobiological implications of the Ardipithecus ramidus dentiton. Science, 326: 94-99.
- Teaford M.F. 1988. Scanning electron microscope diagnosis of wear patterns versus artifacts on fossil teeth. *Scanning Microscopy*, 2: 1167-1175.
- Teaford M.F. 2007a. What do we know and not know about dental microwear and diet? In P.S. Ungar (ed): *Evolution of the human diet: the* known, the unknown and the unknowable, pp. 106-132.Oxford University Press, New York.

- Teaford M.F. 2007b. Dental microwear and Paleoanthropology: Cautions and possibilities. In S.E. Bailey & J. J. Hublin (eds): *Dental Perspectives on Human Evolution: State of the Art Research in Dental Paleoanthropology*, pp. 345-368. Springer, Dordrecht.
- Teaford M.F. & Leakey M.G. 1991. Dental microwear and diet in Plio-Pleistocene cercopithecoids from Kenya, Am. J. Phys. Anthropol. 14 (Suppl.): 160-161.
- Teaford M.F. & Oyen O.J. 1989. *In vivo* and *in vitro* turnover in dental microwear. *Am. J. Phys. Anthropol.* 80, 447-460.
- Teaford M.F. & Tylenda C.A. 1991. A new approach to the study of tooth microwear. *J. Dent. Res.*, 70: 204–207.
- Teaford M.F. & Ungar P.S. 2000. Diet and the evolution of the earliest human ancestors. *Proc. Natl. Acad. Sci. U.S.A.*, 97: 13506-13511.
- Tutin C.E.G., Ham R.M., White L.J.T., Harrison M.J.S. 1997. The primate community of the Lope' Reserve, Gabon: diets, responses to fruit scarcity, and effects of biomass. *Am. J. Primatol.*, 34:1–24.
- Tweheyo M. & Obua J. 2001. Feeding habits of chimpanzees (*Pan troglodytes*), red-tail monkeys (*Cercopithecus ascanius schmidti*) and blue monkeys (*Cercopithecus mitis stuhlmanii*) on figs in Budongo Forest Reserve, Uganda. *Afr. J. Ecol.*, 39: 133-139.
- Ungar P.S. 2009. Tooth form and function: insights into adaptation through the analysis of dental microwear. In: *Comparative dental morphology*, T. Koppe, G. Meyer & K.W. Alt (eds): pp. 38-43. Front Oral Biol. Basel., Karger, vol 13.
- Ungar P.S. & Spencer M.A. 1999. Incisor microwear, diet, and tooth use in three amerindian populations. *Am. J. Phys. Anthropol.*, 109: 387-296.
- Ungar P.S., Teaford M.F. 1996. Preliminary examination of non-occlusal dental microwear in anthropoids: implications for the study of fossil primates. Am. J. Phys. Anthropol., 100: 101-114.
- Ungar P.S., Grine F.E. & Teaford M.F 2008. Dental microwear and diet of the Plio-Pleistocene hominin *Paranthropus boisei*. *PLoS one*, 3: 1-6.

- Ungar P.S., Scott R.S., Grine F.E. & Teaford M.F. 2010. Molar microwar textures and the diets of *Australopithecus anamensis* and *Australopithecus afarensis*. *Philosophical Transactions of the Royal Society of London*, 365: 3345-3354.
- Ward C., Leakey M. & Walker A. 1999. The new hominid species *Australopithecus anamensis*. *Evol. Anthropol.*, 7: 197-205.
- Ward C., Leakey M. & Walker A. 2001. Morphology of *Australopithecus anamanesis* from Kanapoi and Allia Bay, Kenya. *J. Hum. Evol.*, 41: 255-368.
- White T.D., Suwa G., Hart W.K., Walter R.C., WoldeGabriel G., de Helnzelin J., Desmond Clark J., Asfaw B. & Vrba E. 1993. New discoveries of *Australopithecus* at Maka in Ethiopia. *Nature*, 366: 261–265.
- White T.D., WoldeGabriel G., Asfaw B., Ambrose S., Beyene Y., Bernor R.L., Boisserie J.R., Currie B., Gilbert H., Haile-Selassie Y., Hart W.K., Hlusko L., Howell F.C., Kono R.T., Lehmann T., Locuhart A., Lovejoy C.O., Renne P.R., Saegusa H., Vrba E.S., Wesselman H. & Suwa G. 2006. Asa Issie, Aramis and the origin of *Australopithecus. Nature*, 440: 883-889.
- White T.D., Asfaw B., Beyene Y., Haile-Selassie Y., Lowejoy C.O., Suwa G. & WoldeGabriel G. 2009a. Ardipithecus ramidus and the paleobiology of early hominids. Science, 326:64-86.
- White T.D., Ambrose S.H., Suwa G., Su D.F., DeGusta D., Bernor R.L., Boisserie J.R., Brunet M., Delson E., Frost S., García N., Giaourtsakis I. X., Haile-Selassie Y., Clark Howell F., Lehmann T., Likius A., Pehlevan C., Saegusa H., Semprebone G., Teaford M. & Vrba E. 2009b. Macrovertebrate Paleontology and the Pliocene Habitat of Ardipithecus ramidus. Science, 326: 87-93.

- Wieczkowski J. 2009. Brief communication: Puncture and crushing resistance scores of Tana River mangabey (*Cercocebus galeritus*) Diet Items. Am. J. Phys. Anthropol., 140: 572-577.
- Williams V.S., Barrett P.M. & Purnell M.A. 2009. Quantitative analysis of dental microwear in hadrosaurid dinosaurs, and the implications for hypotheses of jaw mechanics and feeding. *Proc. Natl. Acad. Sci. U.S.A.*, 106: 11194-11199.
- Williamson E.A., Tutin C.E.G., Rogers M.E. & Fernandez M., 1990. Composition of the diet of lowland gorillas at Lopé, Gabon. Am. J. Primatol., 21: 266–277.
- WoldeGabriel G., White T.D., Suwa G., Renne P., de Heinzelin J., Hart W.D. & Heiken G. 1994. Ecological and temporal placement of early Pliocene hominids at Aramis, Ethiopia. *Nature*, 371: 330-333.
- WoldeGabriel G., Ambrose S.H., Barboni D., Bonnefille R., Bremond L., Currie B., DeGusta D., Hart W.K., Murray A.M., Renne P.R., Jolly-Saad M.C., Stewart K.M. & White T.D. 2009. The geological, isotopic, botanical, invertebrate, and lowe vertebrate surroundings of *Ardipithecus ramidus. Science*, 326: 65-65e5.
- Wood B. & Richmond B.G. 2000. Human evolution: taxonomy and paleobiology. J. Anat., 196: 19–60.
- Wynn J.G. 2000. Paleosols, satable carbon isotopes, and *including opened woodlands and bushlands including opened woodlands and bushlands* interpretation of Kanapoi, Nothern Kenya. J. Hum. Evol., 39: 411-432.

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Appendix

	ц		ĽЪ	LM		×	Р 4	RM_1	RM_2		LM ²	LM ³	RM_2	LM_2	LM_2	Au. anan	rensis
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	×	×	×	×	mean s	td	×	×	mean	std	×	×	×	×	×	mean	std
HN	88	43	24	17	32.00 9.8	68	15	52	27.00 2	5.45	108	11	6	39	25	38.40	40.74
N	79	26	111	47	82.50 17.0	25	97	67 1	08.50 1	4.85	25	79	119	70	95	77.60	34.79
DMN	133	13	79	143	111.00 39.	20	40	49	17.50	9.19	92	58	11	83	139	76.60	46.96
MDM	29	73	2	2	6.50 3.5	53	29	55	98.00 4	9.49	46	18	63	4	6	28.00	25.42
NT	329	155	216	209	232.00 50.	31 16	81	223 2	51.00 6	9.29	271	166	202	196	268	220.60	46.68
НX	102.74	120.41	68.57	52.31	78.94 24.	50 91.	52 87	7.75	87.84 2	6.59	80.94	116.48	106.25	96.34	61.54	92.27	21.59
XV	112.59	200.47	136.31	99.54	109.13 3.	57 122.9	98 86	8.57 1	27.64 1	4.32	89.49	119.18	137.78	106.61	111.65	112.93	17.65
MDX	87.17	169.13	81.14	90.06	79.70 14.	38 151.	18 12:	1.72	93.69 1	6.24	80.92	66.61	105.19	89.88	69.53	82.43	15.75
ХDМ	79.42	78.22	163.17	62.43	73.82 14.	76 75.8	88 64	4.44	79.04 1	1.33	75.17	127.53	87.06	84.26	63.38	87.48	24.22
¥	96.76	118.05	108.85	88.86	90.27 9,	55 119.(06 85	9.71 1	02.74 2	2.66	80.74	101.51	118.77	97.02	83.51	96.31	15.31
SH	96.03	104.34	42.66	39.47	73.08 12.9	32 60.2	35 8,	3.78	48.78 1	4.59	84.86	51.82	38.47	82.22	63.94	64.26	19.79
SV	89.21	166.85	118.36	62.77	92.56 8.:	10 84.(60 72	2.81	91.76	9.70	88.94	106.79	84.90	86.83	98.29	93.19	9.26
SMD	82.97	232.19	98.91	65.93	81.75 42.	13 132.9	92 8	9.55	71.77	0.32	68.85	32.61	72.01	111.55	51.96	67.39	29.24
SDM	46.61	44.09	17.54	30.11	31.00 11.	56 39.	18 3(6.05	58.31	6.00	77.24	140.02	62.56	22.83	39.18	68.37	45.19
ST	86.19	121.32	108.60	64.08	85.76 14.	96 93.(64 74	4.99	77.85	2.16	78.49	92.87	79.38	96.35	75.18	84.45	9.48
* Each	individu	al is repr	esented t	y a single	s tooth (colur	nns in bolc	(j										

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Appendix 2 - Microwear pattern derived from the 15 microwear variables studied for each fossil specimen of Au. anamensis considered: average values for the complete sample (N=5).

	Au. afaren N=26	sis	Pan trogloc trogloc N= 10	dytes tytes	Pan troglod verus N= 7	lytes	Gorilla gorilla gorilla N= 31		Papio anubis N=27		Chlorocc aethiop: N=15	snqa	Cercoce torquat N=3	snqa sn.	Mandril sphinx N=4	snj	Colobus sp. * N=21	10	Cercopith sp.** N=10	ecus
	mean	std	mean	std	mean	std	mean	std	mean	std	mean	std	mean	std	mean	std	mean	std	mean	std
HN	41.80	16.49	52.80	33.15	28.43	6.95	40.10	22.61	21.44	9.14	34.67	19.38	52.67	26.00	46.00	17.45	42.48	28.50	34.80	21.50
HX	111.91	28.34	92.34	36.10	87.32	19.57	83.14	38.39	90.78	22.52	73.22	15.80	73.37	8.03	77.68	9.29	79.41	17.17	83.88	31.81
SH	93.47	35.45	77.80	46.20	81.74	39.86	64.90	45.19	72.77	32.33	60.79	27.27	55.56	17.03	74.04	8.08	62.17	30.20	67.21	43.08
N	28.31	24.01	40.40	23.82	20.14	8.45	53.26	29.58	85.81	26.07	81.00	25.46	45.67	19.55	60.25	25.50	35.57	18.16	108.81	14.99
X	124.19	46.62	126.89	16.62	153.81	44.89	128.93	34.51	118.28	18.26	112.13	20.94	109.03	10.71	116.77	9.33	112.22	31.31	99.81	18.41
SV	89.15	36.53	119.50	30.42	138.77	44.85	117.24	42.34	108.97	23.74	101.01	23.30	94.67	26.83	114.26	2.29	103.87	46.49	81.89	26.13
MMD	39.38	19.58	38.80	11.04	50.14	17.07	44.32	22.21	49.78	25.05	56.4	24.84	66.67	13.32	54.50	7.23	37.05	21.89	60.60	25.71
MDX	109.28	31.80	79.01	26.72	98.68	43.29	83.56	38.85	88.79	19.28	75.22	12.09	68.14	24.01	86.22	13.59	74.91	24.47	74.37	19.36
SMD	89.94	34.77	68.68	37.71	102.96	56.71	76.97	50.08	80.71	28.89	64.16	17.16	62.82	44.42	82.79	24.08	67.67	43.1	66.61	28.99
MDM	47.42	34.26	39.90	13.54	42.00	9.52	47.03	21.16	20.44	15.69	38.53	15.38	84.33	35.38	53.00	15.14	30.62	18.36	39.80	20.75
XDM	93.85	19.85	94.31	38.24	106.58	23.26	90.99	26.79	86.25	21.74	80.92	18.25	81.64	10.11	78.38	17.02	85.26	29.29	76.00	21.48
SDM	70.94	23.64	84.60	51.36	111.73	22.32	84.97	45.10	66.21	33.61	70.38	26.95	73.54	21.63	74.85	21.94	76.01	58.30	56.89	35.17
NT	150.69	52.21	171.90	31.81	140.71	18.07	184.71	32.29	177.48	34.32	210.60	38.36	249.33	31.56	213.75	15.13	145.71	34.37	244.00	44.84
¥	111.56	24.86	98.31	28.24	105.94	26.93	100.81	26.63	103.78	14.29	90.32	9.76	82.13	7.73	92.41	3.84	89.40	16.92	87.36	18.36
ST	92.98	22.19	94.63	35.94	111.80	26.68	101.74	33.11	96.96	18.81	85.77	12.04	77.16	21.51	92.67	3.06	84.91	22.66	75.87	22.51

* Colobus sp. (N=21) included C polykomos (N=11), C. badius (N=5), C. guereza (N=3) and C. angolensis (N=2);

**Cercopithecus sp. (N=10) included C. mitis (N=7) and C. neglectus (N=3)

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ST	-0.201**	0.442**	0.459**	-0.77	0.678**	0.690**	-0.083	0.620**	0.641**	-0. 078	0.615**	0.590**	-0.176*	0.850**	1
¥	-0.243**	0.612**	0.494**	-0.076	0.635**	0.478**	-0.165*	0.792**	0.675**	-0.156	0.685**	0.493**	-0.242*	1	
NT	0.290**	-0.156	-0.026	0.530*	-0.166	-0.006	0.511**	-0.228*	-0.149	0.285**	-0.195*	-0.139	1		
SMD	-0.067	0.332**	0.351**	-0.195*	0.320**	0.309**	-0.102*	0.315**	0.328**	0.216**	0.822**	1			
CIMX	-0.104	0.482**	0.427**	-0.203*	0.402**	0.294**	-0.175*	0.456**	0.422**	0.097	1				
MDM	0.366**	-0.020	0.064	-0.224**	-0.066	-0.029	-0.231**	-0.138	-0.131	1					
SMD	-0.089	0.437**	0.439**	-0.117	0.321*	0.280**	0.046	0.894*	1						
CIMX	-0.124	0.524**	0.433**	-0.161*	0.362**	0.241**	-0.061	1							
OMN	0.198*	-0.025	0.070	0.122	-0.016	0.087	1								
SV	-0.120	0.070	0.084	0.05	0.849*	Ч									
×	-0.156	0.146	0.109	-0.098	1										
N	-0.467**	-0.266**	-0.220*	1											
SH	0.141	0.859**	Ħ												
HX	0.065	Ч													
HN	H														
	HN	HX	SH	N	×	SV	MMD	MD	SMD	MDM	XDM	SDM	M	¥	ST

^{*:} significant correlation at p<0.05 **: significant correlation at p<0.01