

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 ^{13}C -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 (Estebanz *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 (Ungar *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 leaf, 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; Wiczakowski, 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 (Coltène™) and positive casts were made with the two-component polyurethane Feropur PR-55 (Fero™) and epoxy resin Epo-Tek 301 (Epoxy Technologies™), 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 thermofusible gum and sputter coated with a 400-Å gold layer for SEM observation (Galbany *et al.*, 2004b; Estebanz *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 Nikon™ 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; Estebanz *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 Photoshop™ 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; Estebanz *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

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

Kanapoi					
KNM-KP-29283	RI ² , RM ² , RC ¹ , RP ³ , RM ² , LI ¹ , LM ² , LC ¹ -M ¹ , LM² , LI ²				
KNM-KP-29287	LI ₁ , LI ₂ , RI ₂ , RP ₃ , RP ₄ , LP ₄ , RM ₁ , LM ₁ , RM 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 , LM ₂ , Li ² , Lm ₁ , LP ₃ , LI ₁				
Allia Bay					
KNM-ER-19981	?	KNM-ER-20420	LM ²	KNM-ER-20421	RM ³
KNM-ER-20422	LM ₁	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	RM₂
KNM-ER-35232	RM ²	KNM-ER-35233	LM₂	KNM-ER-35325	RM ₂
KNM-ER-35236	LM³	KNM-ER-35238	RM ¹		

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-occlusal 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 Estebanz, (Estebanz *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 intra-observer measuring errors of the two researchers were similar and their interobserver error was

small (Galbany *et al.*, 2005b; Estebanz *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 (Estebanz *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 well-preserved buccal microwear patterns (Tab. 1). However, since specimen KNM-KP-347235

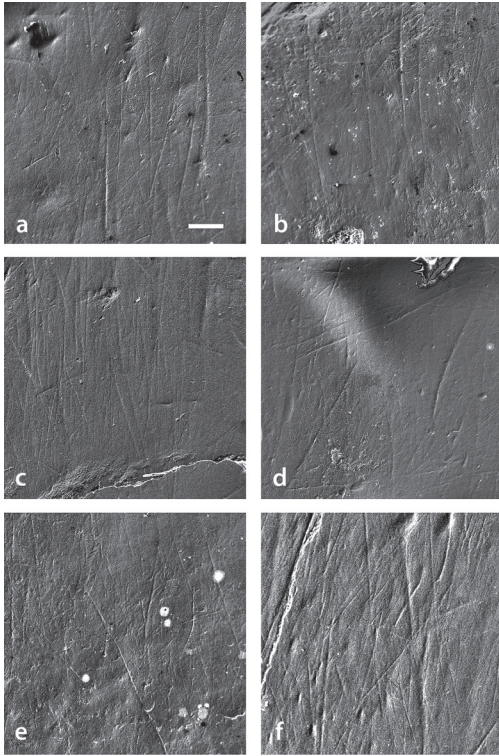


Fig. 1 - Well-preserved buccal microwear SEM images of the 5 *Au. anamensis* samples analysed (a: KNM-KP-29287, b: KNM-KP-29283, c: KNM-ER-35231, d: KNM-ER-35233, e: KNM-ER-35236) and of one *Au. afarensis* specimen (f: LH 4). Scale bar is 100 μ m.

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; Estebanz *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) (Estebanz *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 \pm 46.68), in the same range as the frugivorous and seed-eater *Cercopithecoidea* samples: *Cercocebus* (NT=249.33 \pm 18.23), *Chlorocebus aethiops* (NT=210.60 \pm 9.90), *Mandrillus sphinx* (NT=213.75 \pm 7.56) and *Cercopithecus sp.* (NT=244.00 \pm 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 \pm 52.51), though the density of the horizontal striations in *Au. anamensis* (NH=38.4 \pm 40.74) was similar to that of *Au. afarensis* (NH=41.80 \pm 16.49) and *Gorilla g. gorilla* (NH=40.10 \pm 22.61). However, the density of its vertical striations (NV=77.6 \pm 34.79) more closely resembled *Papio anubis* (NV=85.82 \pm 5.01), *Chlorocebus aethiops* (NV=81.00 \pm 6.57), and even *Cercopithecus sp.* (NV=108.80 \pm 4.74), than *Au. afarensis* (NV=28.31 \pm 24.01), *Gorilla* (NV=53.26 \pm 29.58) or *Pan* (NV=40.40 \pm 23.82 for *P. t. troglodytes* and NV=20.14 \pm 8.45 for *P. t.*

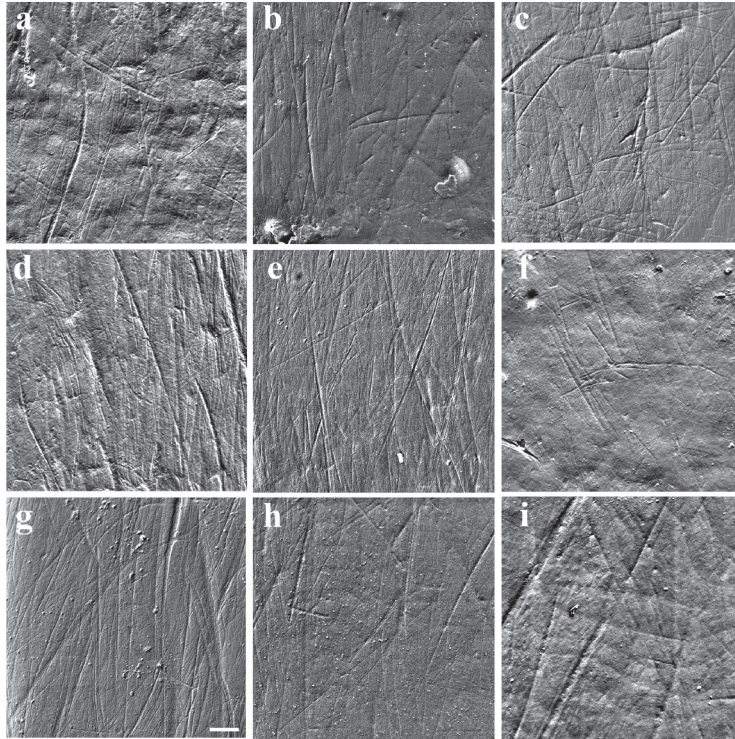


Fig. 2 - SEM images of primate specimens studied: a: *Cercocebus torquatus* IMAZ 9851; b: *Cercopithecus* sp. NMK om7551; c: *Chlorocebus aethiops* NMK om0362; d: *Mandrillus sphinx* HMCZ 34172; e: *Papio anubis* NMK om6992; f: *Colobus* sp. HMCZ 37932; g: *Gorilla gorilla gorilla* NHML 36.7.14.1; h: *Pan troglodytes troglodytes* NHML 50.1863; i: *Pan troglodytes verus* PMAE 7544. (IMAZ: Anthropologisches Institut und Museum Universitaet Zuerich 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* ($NDM=28.00\pm 25.42$) was only comparable to that of *Colobus* sp. ($NDM=30.62\pm 18.36$) and *Papio anubis* ($NDM=20.44\pm 15.69$), 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 non-hominin *Hominoidea*. This was an unexpected result considering the similarities in occlusal microwear patterns between *Au. anamensis* and

Au. afarensis reported by Grine *et al.* (2006a, 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 non-parametric 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

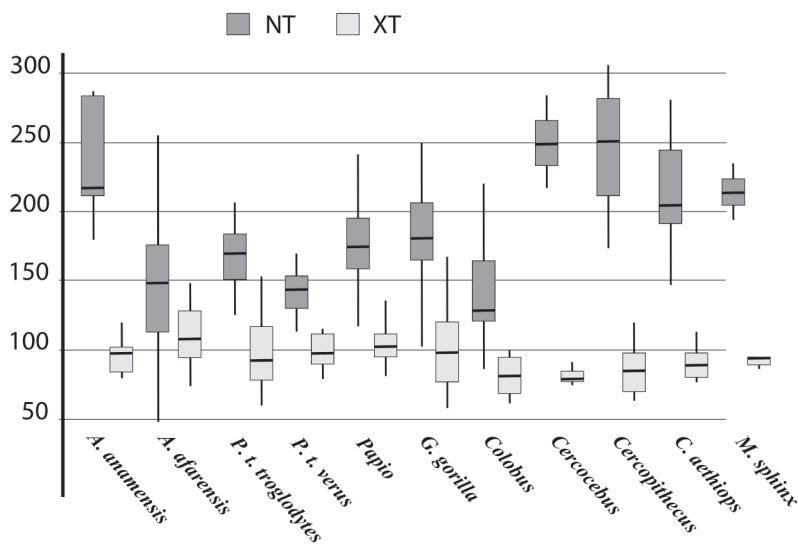


Fig. 3 - Box plots of NT (total striation density) and XT (average length of all striations) for *Au. anamensis*, *Au. afarensis* and the primate comparative samples (including *Cercopithecoidea* and *Hominoidea*). The two australopithecine samples show clearly distinct striation density values (NT), 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-Cercopithecus* ($U=5$, $P=0.041$); 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 ρ) 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* $\lambda=0.153$, $F=3.405$, $P<0.0001$), 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); DF_1 (57.33%) was mainly correlated with NV ($r=0.940$) and NT (0.653), and DF_2 (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*

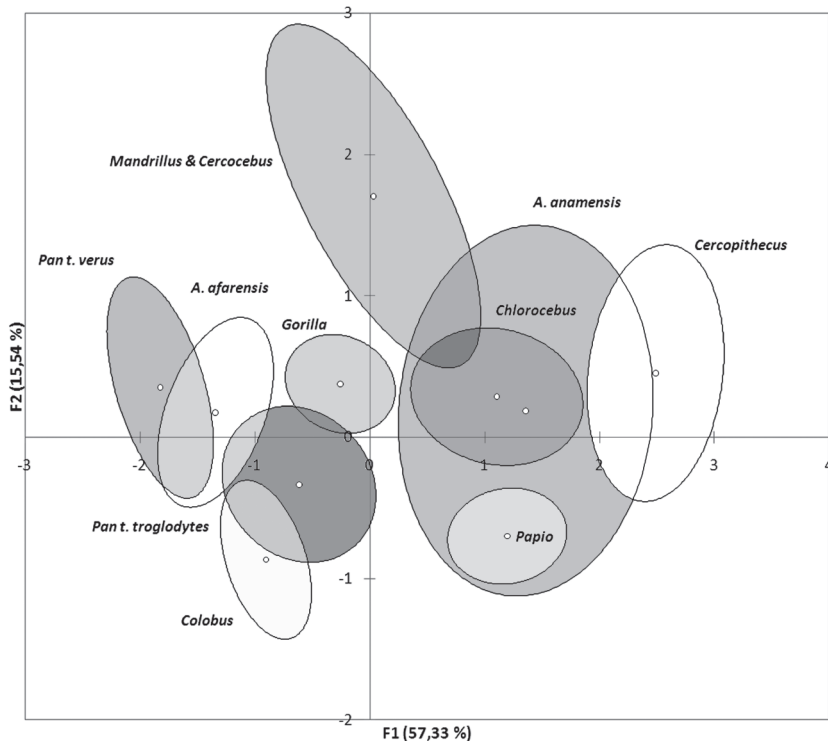


Fig. 4 - Descriptive linear discriminant analysis of the 10 groups considered, including *Au. anamensis* and *Au. afarensis*. DF_1 was mainly correlated with NV and NT; while DF_2 was correlated with NDM and NT (see description in the text). Despite its high dispersion range, *Au. anamensis* clearly 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 DF_1 , 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 DF_1 , though not for DF_2 ; their mainly frugivorous dietary habits could account for the overlap with *Gorilla* and *Pan t. troglodytes* for DF_1 , and their terrestrial behaviour could be responsible for their high and variable DF_2 values (Fig. 4).

In order to show overall similarities between microwear patterns of all the groups considered, Mahalanobis distances (\bar{d}) between group centroids were computed within the descriptive

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

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% *Chlorocebus*, 42.9% *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* (Estebanz et

al., 2009) but also *Paranthropus 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* (Estebanz *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; Marshall *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; Estebanz *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

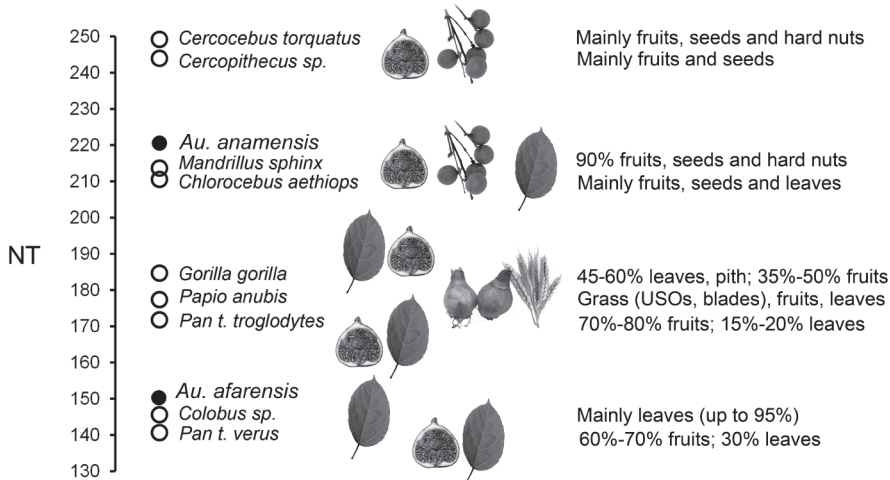


Fig. 5 - Overall microstriation density (NT) and main dietary specificities of the primate comparative taxa analysed (open dots) compared to those for *Au. anamensis* and *Au. afarensis* (black dots). The images stand for main foodstuffs consumed by the extant taxa: fruits, seeds and nuts, leaves, grass 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; Estebarez 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.

Acknowledgements

We are grateful to M.F. Teaford for the casting of *Au. anamensis*' teeth and to P.S. Ungar for allowing J. Galbany to obtain dental casts of some Hominoidea teeth, as well as to F. Grine for his advice and warnings concerning conservation of *Au. anamensis* dental remains. This research was funded by the Spanish Ministerio de Educación y Ciencia via projects

CGL2004-00775, CGL2007-60802, CGL2010-15340, CGL2011-22999 and SGR2009-884; and an FPU grant from the Spanish Government to FE. The SEM analysis was performed at the SCiT of the University of Barcelona.

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Associate Editor, Rita Vargiu

Appendix 1 - Average buccal microwear values by tooth type for the *Au. ananensis* sample.

	LI ₁	LI ₂	LP ₃	LM ₁	LM ₂	RP ₄	RM ₁	RM ₂	LVP ₂	LVP ₁	RM ₂	LM ₂	LM ₂	A. ananensis		
N	1	1	1	1	2	1	1	2	29283	35236	35231	35233	29287	5		
	X _i	X _i	X _i	X _i	mean	std	X _i	X _i	mean	std	X _i	X _i	X _i	X _i	mean	std
NH	88	43	24	17	32.00	9.89	15	52	27.00	25.45	108	11	9	39	38.40	40.74
NV	79	26	111	47	82.50	17.67	97	67	108.50	14.85	25	79	119	70	77.60	34.79
NMD	133	13	79	143	111.00	39.59	40	49	17.50	9.19	92	58	11	83	76.60	46.96
NDM	29	73	2	2	6.50	3.53	29	55	98.00	49.49	46	18	63	4	28.00	25.42
NT	329	155	216	209	232.00	50.91	181	223	251.00	69.29	271	166	202	196	220.60	46.68
XH	102.74	120.41	68.57	52.31	78.94	24.60	91.52	87.75	87.84	26.59	80.94	116.48	106.25	96.34	92.27	21.59
XV	112.59	200.47	136.31	99.54	109.13	3.57	122.98	88.57	127.64	14.32	89.49	119.18	137.78	106.61	112.93	17.65
XMD	87.17	169.13	81.14	90.06	79.70	14.38	151.18	121.72	93.69	16.24	80.92	66.61	105.19	89.88	82.43	15.75
XDM	79.42	78.22	163.17	62.43	73.82	14.76	75.88	64.44	79.04	11.33	75.17	127.53	87.06	84.26	87.48	24.22
XT	96.76	118.05	108.85	88.86	90.27	9.55	119.06	89.71	102.74	22.66	80.74	101.51	118.77	97.02	96.31	15.31
SH	96.03	104.34	42.66	39.47	73.08	12.92	60.35	83.78	48.78	14.59	84.86	51.82	38.47	82.22	64.26	19.79
SV	89.21	166.85	118.36	62.77	92.56	8.10	84.60	72.81	91.76	9.70	88.94	106.79	84.90	86.83	93.19	9.26
SMD	82.97	232.19	98.91	65.93	81.75	42.13	132.92	89.55	71.77	0.32	68.85	32.61	72.01	111.55	67.39	29.24
SDM	46.61	44.09	17.54	30.11	31.00	11.56	39.18	36.05	58.31	6.00	77.24	140.02	62.56	22.83	68.37	45.19
ST	86.19	121.32	108.60	64.08	85.76	14.96	93.64	74.99	77.85	2.16	78.49	92.87	79.38	96.35	84.45	9.48

* Each individual is represented by a single tooth (columns in bold)

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).

	<i>Au. afarensis</i> N=26		<i>Pan troglodytes troglodytes</i> N= 10		<i>Pan troglodytes verus</i> N= 7		<i>Gorilla gorilla gorilla</i> N= 31		<i>Papio anubis</i> N=27		<i>Chlorocebus aethiops</i> N=15		<i>Cercocebus torquatus</i> N=3		<i>Mandrillus sphinx</i> N=4		<i>Colobus sp.*</i> N=21		<i>Cercopithecus sp.**</i> N=10	
	mean	std	mean	std	mean	std	mean	std	mean	std	mean	std	mean	std	mean	std	mean	std	mean	std
NH	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	17.45	42.48	28.50	34.80	21.50	
XH	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
NV	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
XV	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
NMD	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
XMD	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
NDM	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
XT	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)

Appendix 3 - Rho Spearman correlation coefficients and significance for the 15 variables considered in the analysis for the whole sample (N=148).

	NH	XH	SH	NV	XV	SV	NMD	XMD	SMD	NDM	XMD	SMD	NT	XT	ST
NH	1	0.065	0.141	-0.467**	-0.156	-0.120	0.198*	-0.124	-0.089	0.366**	-0.104	-0.067	0.250**	-0.243**	-0.201**
XH		1	0.859**	-0.256**	0.146	0.070	-0.025	0.524**	0.437**	-0.020	0.482**	0.332**	-0.156	0.612**	0.442**
SH			1	-0.220*	0.109	0.084	0.070	0.433**	0.439**	0.064	0.427**	0.351**	-0.026	0.494**	0.459**
NV				1	-0.098	0.05	0.122	-0.161*	-0.117	-0.224**	-0.203*	-0.195*	0.530*	-0.076	-0.77
XV					1	0.849*	-0.016	0.362**	0.321*	-0.066	0.402**	0.320**	-0.166	0.635**	0.678**
SV						1	0.087	0.241**	0.280**	-0.029	0.294**	0.309**	-0.006	0.478**	0.690**
NMD							1	-0.061	0.046	-0.231**	-0.175*	-0.102*	0.511**	-0.165*	-0.083
XMD								1	0.894*	-0.138	0.456**	0.315**	-0.228*	0.792**	0.620**
SMD									1	-0.131	0.422**	0.328**	-0.149	0.675**	0.641**
NDM										1	0.097	0.216**	0.285**	-0.156	-0.078
XDM											1	0.822**	-0.195*	0.685**	0.615**
SDM												1	-0.139	0.493**	0.590**
NT													1	-0.242*	-0.176*
XT														1	0.850**
ST															1

*: significant correlation at p<0.05

** : significant correlation at p<0.01

