

Age-related tooth-wear in African rainforest hunter-gatherers

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1 INTRODUCTION

Tooth-wear refers to the loss of enamel and the gradual exposure of the underlying dentine as a physiological result of mastication. Diet-related abrasion is the predominant tooth-wear mechanism, largely determined by the enamel resistance on working surfaces to food μm -scale indenter particulates (Gügel et al., 2001; Lucas et al., 2013; Romero et al., 2012). Tissues of many edible monocotyledon plants, including various cereal species, contain phytoliths, hydrated silicon dioxide (opal), capable to abraded enamel during tooth-food-tooth contacts (Gügel et al., 2001; Lucas et al., 2014; Piperno, 2006). Other extraneous gritty quartz (crystalline silica) contaminants from grinding, roasted or airborne processing techniques are potential wear agents >2.5 times harder than dental enamel (Lucas et al., 2013; Newesely, 1993). Accordingly, the type and amount of abrasives influence the rate of enamel abrasion (Gügel et al., 2001; Teaford & Lytle, 1996; Smith, 1984).

Tooth enamel wear is also an age-dependent process. However, tooth-wear reports based on known-chronological age from living hunter-gatherers are scarce. Studies conducted on foragers retaining traditional diets from Brazil (Vieira et al., 2015) and Greenland (Davies & Pederson, 1955) found a common pattern of extremely rapid and greater postcanine enamel lost rates relative to age than groups exposed to a diet based on less abrasive and more refined carbohydrate-rich foods. Other studies on Australian aborigines from native settlements provided a longitudinal source of tooth-wear data on a transitional diet during dental development (Richard & Brown, 1981; Molnar & Molnar, 1990; Molnar et al., 1983). A significant age-wear correlations are found and a rapid molar-wear rate and cusp height reduction was attributed to gritty contaminants introduced by maintained traditional cooking methods, since the bulk of their diet was obtained from low-abrasive modern western foods (Molnar et al., 1983). Therefore, the age-diet dependence should have a very strong effect on tooth-wear

behavior amongst populations according to different ecological and dietary proclivities (Richards & Brown, 1981; Tomenchuk & Mayhall, 1979).

Plant-animal subsistence largely varies in proportions among environmentally diverse modern-day hunter-gatherers (Cordain et al., 2000). Ethnographic and ecological data indicate that underground storage organs (USOs) such as roots and tubers are major sources of food year-round for African hunter-gatherers from semi-desert (Crittenden et al., 2017; Laden & Wrangham, 2005) and rainforest habitats (Heymer, 1986; Sato et al., 2012), consumed either raw or briefly thermally processed (Dominy et al., 2008; Laden & Wrangham, 2005). Most edible USOs are tough and fibrous despite being cooked to reduce fracture stress and, should contain also digging-derived grit and dust abrasive contaminants (Dominy et al., 2008; Romero et al., 2013). Overall, a diet premised on energy-rich geophytes is expected to require laborious chewing loadings for breakdown and a significant enamel-wear agent (Dominy, 2012; Dominy et al., 2008; Zink et al., 2014).

A reliance on USO-bearing plant consumption has been suggested as far-reaching adaptive shift for early Pleistocene hominin radiation (Laden & Wrangham, 2005). Particularly, effectiveness of meat and starch-rich tuber dry roasting for reducing masticatory demands and energetic yield increases should largely impact on evolutionary apomorphic cranio-dental changes in *early* Homo (Lucas, 2004; Zink & Lieberman 2016; Zink et al., 2014). Nonetheless, softened foods mechanically processed does not necessarily reflect nonabrasive potential for enamel (Romero et al., 2012) and, differences in foraging behavior determine specific wear patterns (Galbany et al., 2014; Richards & Brown, 1981). Yet molar wear signatures for African early *Homo* reflect dietary versatility including mechanically challenging foods during fallback episodes (Martínez et al., 2016; Ungar & Scott, 2009). However, the USO

abrasive effect on tooth wear-behavior among modern foragers is poorly understood and should greatly contribute to delineate wear-related dietary histories for early *Homo*.

Currently, tooth-wear studies on known-age African foragers are limited and the impact of USO consumption on wearing patterns remains to be elucidated. For instance, dental physiological reports conducted on San (van Reenen, 1966), Hadza (Berbesque et al., 2012; Crittenden et al., 2017) and forest-dwelling Pygmies (Heymer, 1986; Walker & Hewlett, 1990) are mainly based on estimated individual age from life-history events or long-term demographic data. Otherwise, most studies have used simple ordinal scales based upon dentin exposure to record the extent of molar wear according age-cohorts. Because tooth-wear occurs slowly as a progressive development with age, scoring scales resulting in a lack of finer-grained quantitative detail resolution of enamel loss (Gorka et al., 2016; Molnar et al., 1983; Richard & Brown, 1981). Further, the food-tooth interaction by which dental tissue is lost remains overestimated unless individual age is independently known.

Here, we conduct the first quantitative analysis of tooth-wear based on dentine exposure ratios in living known-age Baka Pygmy hunter-gatherers from southern Cameroon (Central Africa). We chose to analyze Baka Pygmies because their dental eruption timing (Ramirez-Rozzi, 2016) and growth patterns (Ramirez-Rozzi, 2018; Ramirez-Rozzi et al., 2015) have been accurately established. Further, forest-based foraging activities, based on bushmeat and wild yam tubers (*Dioscorea* spp.) supply the bulk of the Baka diet, and culinary practices are well-documented for the Baka (Heymer, 1986; Sato et al., 2012; Vallois & Marquer, 1976). Dietary behavior is expected to result in specific intra-population dental-wearing patterns which might provide new insights on the tooth-effect of USOs consumption for the evolutionary hominin adaptations.

2 MATERIAL AND METHODS

2.1 Study population

The Baka Pygmies are semi-nomadic hunter-gatherers living in equatorial African rainforest areas (Ramirez-Rozzi, 2018; Vallois & Marquer, 1976). Among western Pygmies, Baka groups show limited effective dispersal ranges probably reinforcing their genetic isolation (Verdu et al., 2010). The Baka subsistence economy is based primarily on hunting and foraging activities (Sato et al., 2012; Vallois & Marquer, 1976). Foraging activities supply the bulk of the diet among Baka Pygmies mainly focused on gathering wild yam tubers (*Dioscoreaceae*), specially the *Dioscorea praehensilis* specie, providing more than 60% of their estimated energy intake. Animal protein from small-and-medium sized hunted mammals provided $\approx 15\%$ -20% of energy intake. Other wild nuts, fish, honey or insect resources play a complementary role (Sato et al., 2012). Overall, yam tubers and bushmeat occupied more than 90% of food weight in dietary composition with few seasonal differences (Hayashi, 2008; Heymer, 1986; Sato et al., 2012). Exchanges of products with their Bantu-speakers neighbors, practicing slash-and-burn farming, influenced their livelihood and important social changes, especially since 1950s-1960s with government-led sedentarization programs and missionaries influences (Gallois et al., 2015; Hayashi, 2008). Nevertheless, Baka continue actually to be highly dependent on wild resources from forest camps (Hagino & Yamahuci, 2016; Sato et al., 2012). The exchanges are limited mainly to manioc or plantain produced by farmers for meat and honey and, commercially packaged foods are rarely consumed due to geographic isolation and cost (Hayashi, 2008; Ramirez-Rozzi, 2018).

2.2 Sample size

In the Baka village of Moango-le-Bosquet (Lomié District, Southeast Cameroon), we recruited 96 Baka individuals (32 males, 64 females), aged from 8 to 33 years, during fieldworks carried out from 2007 to 2017. Only individuals that had the first mandibular permanent molar (M_1) fully erupted and in occlusion were included. Individuals with oral pathologies or developmental anomalies were discarded. We focus our study on the M_1 because it is the first permanent tooth to erupt in the Baka Pygmies and be in full occlusion ≈ 5 years in both sexes (Ramirez-Rozzi, 2016). Further, the M_1 s are expected to show higher occlusal-wear with age than any other permanent tooth (Molnar et al., 1983; Smith, 1984).

Individual chronological ages were obtained from birth records held by nursing assistants in the health center at Moango-le-Bosquet (see Ramirez-Rozzi, 2016, 2018; Ramirez-Rozzi et al., 2015; for further details). Baka individuals with unrecorded birth were not included. Participants were nonliterate and provided their oral informed consent for the study. This study obtained approval of the Centre National de la Recherche Scientifique, Agence National de la Recherche (France) and the French Institut de Recherche et Développement (IRD) and was carried out as part of the international agreement between the IRD and the Ministry of Scientific Research and Technology of Cameroon.

2.3 Data collection

High-resolution dental molds of mandibular teeth were first made with hydrophobic polyvinylsiloxanes (Coltène-Whaledent®) using impression trays. Dental replicas were produced from molds using Feropur PR-55 (FeroCa®) polyurethane resin (see Romero et al., 2013, 2018). Digital images (3872×2592 pixels) of M_1 occlusal crown surface replicas were obtained with a digital single-lens reflex camera (Sony α A230 10.2MP) with a focal distance fixed at 50cm. Crown cervical lines were oriented

perpendicular to the focal point of the camera using a leveling device and a millimeter scale was placed near the occlusal plane. Calibrate images were edited using Adobe Photoshop® CS5 to enhance images contrast and dentine areas resolution. Total occlusal area (TOA) and dentin exposure visible as depressed occlusal enamel areas were outlining (Galbany et al., 2014; Gorka et al., 2016) (Figure X). Measurements (in mm²) were recorded using SigmaScan Pro® software (SPSS™, Chicago, IL). When several spots of dentin were present, each one was measured separately (Gorka et al., 2016) and the summed areas account for total dentine exposure (DE). The percentage of dentine exposure (PDE) was computed as $DE/TOA*100$ (Galbany et al., 2014). Measurements were registered two times with at least 4-week interval in twenty-five randomly selected molars to evaluate the technical measurement error (TME). The TME values of TOA (1.771%) and DE (0.308%) less than 5% indicate that the methods is highly precise and repeatable (Gorka et al., 2016).

2.4 Statistical analyses

We tested arcsine-transformed molar PDE as independent linear and quadratic functions of log-transformed individual age covariate and conducted for Baka males and females separately (Galbany et al., 2014; Richard & Brown, 1981). Analyses of covariance (ANCOVA) were also used as needed to estimate the relationship and differences (homogeneity of slopes) between PDE on individual aging by sex. The Akaike Information Criterion (AIC) was used to test the best fit regression models (Galbany et al., 2014). Descriptive (mean \pm SD; standard deviation) and statistical analyses were conducted using PAST 3 (Hammer et al., 2001). The significance level was set at $\alpha=0.01$.

3 RESULTS

We first found a strong linear and quadratic relationship between tooth-wear derived from PDE and chronological age as predictor variable in Baka Pygmies ($r^2 = 0.7$, $p < 0.0001$; PDE = 0.792 ± 1.085 , 8-33 age range, $N = 96$). PDE values were also highly correlated with age for both Baka male ($r^2 = 0.8$, $p < 0.0001$; 8-33 age range, $N = 32$) and female ($r^2 > 0.6$, $p < 0.0001$; 10-30 age range, $N = 64$) individuals (Table 1 and Figure X). Baka males (PDE = 1.036 ± 1.252) generally had teeth that appeared to be rather more worn with age than females (PDE = 0.669 ± 0.979). Likewise, the test for homogeneity of slopes ($F_{1,93} = 0.674$, $p = 0.413$; ANCOVA) revealed non-sexual dimorphic trends in enamel loss with aging. The statistically best model following smaller AIC values corresponds to linear predictions (see Table 1).

Moreover, dentine exposure evidence is commonly detected at ages greater than 16 years, inducing significant intra-population differences in molar wearing patterns between age-ranged individuals ($F_{1,93} = 16.640$, $p < 0.001$; ANCOVA). Baka Pygmies between 8 and 16 years (PDE = 0.208 ± 0.181 , 0-0.6 in range; $N = 56$) wear down their molars at lower linear association ($r^2 = 0.157$, $p = 0.002$) than older individuals ($r^2 = 0.666$; $p < 0.001$) showing heaviest rates of wear (PDE = 1.608 ± 1.284 , 0.20-4.26 in range; 17-33 individual ages; $N = 40$).

4 DISCUSSION

We provide the first model of the age-related tooth-wear progression in Central African Baka Pygmy foragers. A strong linear association of molar-wearing with aging was found in agreement with early reports on living foraging groups from arctic (Davies & Pedersen, 1955; Tomenchuk & Mayhall, 1979) and more temperate climates (Molnar et al., 1983; Richards & Brown, 1981; Vieira et al., 2015). However, Baka Pygmies show surprisingly lower tooth-wear rates than expected for foraging diets (Gorka et al., 2015; Molnar et al., 1983).

Central African small-scale foragers subsist primarily on hunting game activities and wild plant-food gathering. Particularly, USOs are staple resources and supply year-round over 50% the nutritional requirements for both bush dwelling Hadza from savanna woodlands (Marlow & Berbesque, 2010; Crittenden et al., 2017) and forest-dwelling Baka (Sato et al., 2012) foragers. Likewise, the greater diversity of edible USO-bearing species in savanna notably contribute to include in dietary more species (65%) that are edible without cooking than occur in rainforest (<10%) habitats (Laden & Wrangham, 2005). Most USOs are highly resistant to fracture when raw and outer tunic quartz particles potential enamel indenters (Dominy, 2012; Lucas et al., 2014). While roasting significantly reduce the tuber toughness and masticatory effort, increasing also starch digestibility and energy gain (Zink et al., 2014), the mechanical challenge for human molars is still too excessive (Dominy et al., 2008). However, little is known about USOs mechanical hardness and long-term effects on enamel decline in volume with age for forager populations.

We found that Baka individual age was able to explain 70% of tooth-wear variability. Nonetheless, maximum PDE values no greater than 5% found in older ≈ 30 aged individuals correspond mainly to buccal cusps removal and moderate to large spots of dentine exposure (wear stages 3-4; Smith, 1984). No straightforward comparison is

possible between PDE rates obtained in Baka Pygmies and qualitative wear patterns previously reported among other African Pygmy foragers (Heymer, 1986; Walker & Hewlett, 1990). Likewise, this negligible tooth-wear is in complete contrast to the usual pattern of abrasion found among Hadza at early ages, since $\approx 50\%$ of the maxillary molars at estimated individual age ≥ 18 years exhibit flat surfaces with considerable exposed dentin (Crittenden et al., 2017). Consequently, the lower molar-wear rates with age among the Baka Pygmies than Hadza dentitions (Berbesque et al., 2012; Crittenden et al., 2017) might be mainly caused by differences in mechanical and physical properties of chewed foods.

Abrasive wear is as likely due to repetitive loading of phytolith-rich plant foods as exogenous grit (Lucas et al., 2014). However, while enamel lost increased with silica content, the abrasive potential estimates for opal-phytoliths are way below those of siliceous grit and dust >10 times higher for enamel abrasively (Gugel et al., 2001; Newesely, 1993). Raw meat-consumption is not hard enough to scratch enamel surfaces when compared to plant foods (Lucas, 2004; Romero et al., 2013) and the abrasive effect for enamel of animal-based foods is only dependent on silica-based grittiness adhered during meat roasting that Baka directly grill on the fire (Vallois & Marquer, 1972). Otherwise, Baka Pygmies consumed foraged plant foods with reduced etching particles compared to Bantu harvested foods (Romero et al., 2013), since no phytoliths exist in yam and manioc starch grains from tropical environments (Piperno, 2006). Further, yam-like tubers, especially the annual plant *Dioscorea praehensilis*, before being eaten are soaked in water for a few days for detoxification and boiled in pottery pots or cooked in hot ashes wrapped in leaves (Heymer, 1986; Sato et al., 2012; Vallois & Marquer, 1972). In contrast, *Vigna frutescens* tubers are consumed by Hadza preferably raw or briefly open air roasting and, flour derived from baobab hard seeds open-rock grinding

incorporate high amounts of grit-soil particles as potential factors in Hadza dental abrasion (Berbesque et al., 2012). However, Baka Pygmies grinding tubers and seeds to obtain flour using wood mortars and, other harvested fruits are cooked to obtain porridges (Heymer, 1986; Vallois & Marquer, 1976). Overall, mechanical and thermal food processing in Baka culture appears to contribute to ingest generally less abrasive and tenderer foods (Dominy et al., 2008; Romero et al., 2013; Zink et al., 2014).

Moreover, tooth-eruption and life-history events in comparison to worn surfaces are considered particularly relevant factors (Molnar & Molnar, 1990; Molnar et al., 1983). Minimal tooth-wear found among Baka Pygmies indicates significant implications in terms of the individual's age and suggest that wearing patterns could be also attributed to inter-individual masticatory function and dietary changes that occur during periods of growth and development. In this context, our findings reveal no evidence of sexual dimorphism of PDE rates controlling for age, suggesting equal enamel loss process and bite dynamics during individual growth affecting both males and females. Full lower-upper first molar occlusion occurs in the Baka between 5.2-5.5 years, with negligible sex differences in age ranges (see Ramirez-Rozzi, 2016, for further details). Lack of gender-based differences in molar wear patterning is similarly reported among other foraging populations (Crittenden et al., 2017; Richard & Brown, 1981). Otherwise, despite documented sexual division in subsistence activities (Gallois et al., 2015; Vallois & Marquer, 1976), Baka males and females consume similar foods and acquire equal daily energy intakes (Sato et al., 2012). Further, Baka children participate in the same food procurement activities than adults (Gallois et al., 2015; Hagino & Yamahuci, 2016). However, we found significant increases in wear values up to age 16 years. In the Baka at Le Bosquet, first pregnancy occurs at 16 years and adult size reached at around 20 years of age for both sexes when body muscle and fat increase (Ramirez-Rozzi, 2018; Ramirez-

Rozzi et al., 2015). As Baka move into adolescence are considered socio-culturally adults and their social role changes to include execution of the main part of subsistence-related activities (Gallois et al., 2015; Vallois & Marquer, 1976), which require the increase of food intake for physical development (Hagino & Yamahuci, 2016). Thereby, greater metabolic demands and occlusal loading during adulthood might be sufficiently explaining age-related trends of wear rates observed.

Meat and starch-rich USOs are considered keystone resources for early *Homo* and their mechanical processing involved adaptive smaller masticatory features (Laden & Wrangham, 2005; Lucas, 2004). Cheek-teeth occlusal-microwear evidence suggests that *H. ergaster* might have relied more on hard-brittle foods (Ungar & Scott, 2009). Further, the highly abraded buccal enamel support also the consumption of a wide range of abrasive food items including mechanically demanding USOs (Martínez et al., 2016). However, our findings challenge the view about the long-term abrasive impact of USOs consumption on enamel damage with important implications about cooking methods on hominin tooth-wear behaviors (Dominy et al., 2008; Laden & Wrangham, 2005; Zink & Lieberman, 2016).

Unprocessed raw edible tubers are too tough force-limited foods for human consumption (Dominy et al., 2008; Zink & Lieberman, 2016). Roasting significantly decrease both tuber toughness and fracture stress for chewing (Zink & Lieberman, 2016; Zink et al., 2014), while food acquisition and processing may actually introduce gritty contaminants that encourage tooth-wear (Dominy et al., 2008; Romero et al., 2012). Previous buccal-microwear findings denote that Baka Pygmies mainly consume foods with reduced abrasiveness (Romero et al., 2013). Thence, Baka cooking modes in which both meat and USOs resources are thermally-processed should also impact in reducing enamel abrasive foreign materials influencing slower rates of dentine exposure. Instead,

minimally processed grit-laden foods appear to be the major cause of higher enamel wearing for Hadza foragers (Berbesque et al., 2012). On the basis of these findings, we suggest that tooth-wear behavior is culturally specific among African foragers relying on USO-based diets and certain patterns are unique to particular food-processing. Therefore, non-cooked mechanically processing foods (slicing meat and pounding USOs) abrasive effects on enamel wear within early *Homo* species (Martínez et al. 2016; Ungar & Scott, 2009) should not be dismissed and favored similarly adaptive selection for smaller jaws and teeth (Zink & Lieberman, 2016). Because the mechanical properties of foods differently impact on occlusal morphology as the enamel wears down (Smith, 1984; Ungar & Scott, 2009), further studies are needed to explore dental topographic changes with wear among known-age living foraging groups.

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