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Molar enamel thickness distribution and hominid taxonomy

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There is considerable evidence from extant and extinct primates that the structural organization of the mineralized dental tissues holds a significant amount of (paleo)biological information suitable for assessing taxonomy, phylogenetic relationships, functional and adaptive strategies, and for reconstructing the evolutionary history of various primate clades [1]. Enamel thickness (ET) variation patterns in hominids stem from an evolutionary compromise between functional/adaptive constraints and strict control mechanisms of the morphogenetic program, though variability is also presumably affected by a number of biological and environmental factors [2]. ET is useful for tracking diet-related structural adaptations, and for exploring life-history trajectories, phylogenetic relationships and evolutionary trends [1-3]. However, considering the number of factors at play, the value of the ET's taxonomic signal remains unclear, particularly at sub-genus taxonomic levels.

ET is commonly assessed using either bi-dimensional measurements directly performed on fractured crowns or physical ground sections, or non-invasive bi-/three-dimensional approaches such as microtomography [1]. The most common variables used to quantify hominid ET, the average and relative enamel thickness indices, only partially discriminate among extant apes and show overlap among fossil and extant hominin taxa [3]. On the contrary, examining enamel distribution across the whole crown avoids average estimates (generally limited to a gradient scale of single values) and allows a characterization of ET in relation to crown morphology. Indeed, topographic patterning based on qualitative descriptions of ET cartographies suggests that australopiths exhibit thick enamel over the cusp tips, while in *Homo* relatively thicker enamel is found at the cusp base [1,2,4]. In order to quantify ET distribution patterns in a more comprehensive and statistically robust manner, we developed a new analytical approach based on advanced virtual imaging [5] and tested it on a selected sample of fossil and extant hominids.

The study sample includes unworn/minimally worn upper/lower first permanent molars (M1) of extant apes (*Pan*=10/10, *Gorilla*=10/10, *Pongo*=10/10), Plio-Pleistocene non-human hominins (*Australopithecus africanus*=6/10, *Paranthropus robustus*=6/10), and representatives of our own genus (Neanderthals=10/10, extant humans=10/10). The method used here enables statistical comparisons of ET maps by performing a registration using morphological features between a reference surface and the occlusal surfaces of each crown.

Using PCA, cross-validated between-group PCA and cross-validated LDA, our results show that the extant taxa are well discriminated from each other (classification accuracy for bgPCA CV=97.5%/92.5% and for LDA CV=92.5%/92.5%). The Plio-Pleistocene hominin

genera (*Australopithecus* and *Paranthropus*) are well discriminated from the human representatives. While having relatively thinner enamel compared to modern humans, Neanderthals plot close to or within their range.

Our tests indicate that, even where absolute or relative ET indices do not sufficiently discriminate among *Australopithecus*, *Paranthropus*, and *Homo* (usually to the exception of Neanderthals) [3,4], the ET distribution patterns have high taxonomic significance.

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