Human Palaeontology and Prehistory

Is the deciduous/permanent molar enamel thickness ratio a taxon-specific indicator in extant and extinct hominids?

Le rapport d'épaisseur de l'émail des molaires déciduales/permanentes est-il un indicateur taxinomique chez les hominidés actuels et fossiles ?

Clément Zanolli [a,*], Priscilla Bayle [b], Luca Bondioli [c], M. Christopher Dean [d], Mona Le Luyer [b,e], Arnaud Mazurier [f], Wataru Morita [g], Roberto Macchiarelli [h,i]

[a] UMR 5288 CNRS, Laboratoire AMIS, Université Toulouse-3 Paul-Sabatier, 31062 Toulouse, France
[b] UMR 5199 CNRS, Laboratoire PACEA, Université de Bordeaux, 33615 Bordeaux, France
[c] Sezione di Bioarcheologia, Museo Nazionale Preistorico Etnografico "Luigi Pigorini", Rome, Italy
[d] Department of Cell and Developmental Biology, University College London, London WC1E 6BT, UK
[e] School of Anthropology & Conservation, University of Kent, Canterbury, UK
[f] UMR 7285 CNRS, Institut de chimie des milieux et matériaux de Poitiers, Université de Poitiers, 86073 Poitiers, France
[g] Department of Oral Functional Anatomy, Graduate School of Dental Medicine, Hokkaido University, Hokkaido, Japan
[h] UMR 7194 CNRS, Laboratoire HNHP, Muséum national d'histoire naturelle, 75116 Paris, France
[i] Unité de formation Géosciences, Université de Poitiers, 86073 Poitiers, France

A R T I C L E   I N F O

A B S T R A C T

In Primates, enamel thickness variation stems from an evolutionary interplay between functional/adaptive constraints (ecology) and the strict control mechanisms of the morphogenetic program. Most studies on primate enamel thickness have primarily considered the permanent teeth, while the extent of covariation in tooth enamel thickness distribution between deciduous and permanent counterparts remains poorly investigated. In this test study on nine extant and fossil hominids we investigated the degree of covariation in enamel proportions between 25 pairs of mandibular dm2 and M1 by a so-called "lateral enamel thickness diphyodontic index". The results did not provide an unambiguous picture, but rather suggest complex patterns likely resulting from the influence of many interactive factors. Future research should test the congruence of the "diphyodontic signal" between the anterior and the postcanine dentition, as well as between enamel and the enamel-dentine junction topography.

© 2017 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

R É S U M É

Chez les primates, le patron de variation d'épaisseur de l'émail est issu d'un compromis évolutif entre contraintes fonctionnelles/adaptatives (écologiques) et mécanismes de contrôle morphogénétique. La majorité des études portant sur l'épaisseur de l'émail des primates concerne les dents permanentes, tandis que le degré de covariation de distribution d'épaisseur de l'émail entre les équivalents déciduaux et permanents reste encore

* Corresponding author.
  E-mail address: clement.zanolli@gmail.com (C. Zanolli).

méconnu. Dans cette étude préliminaire, nous explorons le degré de covariation des proportions d'émail entre 25 paires de dm2 et M1 mandibulaires de neuf hominidés actuels et fossiles en élaborant un « indice diphyodonte d'épaisseur de l'émail latéral ». Les résultats ne montrent pas un signal évident, mais suggèrent plutôt des modèles complexes résultant probablement de l'influence d'interactions entre des facteurs variés. De futures recherches sur le sujet devraient tester le degré de congruence du « signal diphyodonte » entre les dents antérieures et post-canines, ainsi qu'entre l'émail et la topographie de la jonction émail–dentine.

1. Introduction

Following the pioneering methodological work developed by L.B. Martin for measurement procedure and standardization (Martin, 1985), the bi-three-dimensional assessment of tooth enamel thickness has become routine in taxonomic and adaptive/evolutionary studies of fossil and extant primates (e.g., Alba et al., 2013; Kono, 2004; Kono et al., 2014; Macchiarelli et al., 2004, 2009, 2013; Olejniczak et al., 2008a, 2008b, 2008c, 2008d; Pan et al., 2016; Skinner et al., 2015; Smith et al., 2003, 2005, 2011, 2012; Suwa et al., 2009; Zanolli et al., 2015, 2016a). Commonly used to infer durophagy and considered as a proxy of the dietary niches exploited by extinct species (e.g., Constantino et al., 2011, 2012; Lucas et al., 2008; Martin et al., 2003; Schwartz, 2000a; Teaford, 2007; Teaford and Ungar, 2015; Vogel et al., 2008), occlusal enamel thickness is seen as intimately related to dietary abrasiveness and selectively responsive to lifetime dental wear resistance (Pampush et al., 2013; Rabenold and Pearson, 2011).

In primates, enamel thickness variation stems from an evolutionary interplay between functional/adaptive constraints (ecology) and strict control mechanisms of the morphogenetic program (Horvath et al., 2014; Kelley and Swanson, 2008; Kono, 2004; Simmer et al., 2010; Smith et al., 2012; Vogel et al., 2008). It appears to respond relatively quickly in evolutionary time to dietary/ecological changes (Grine and Daegling, 2017; Hlusko et al., 2004; Le Luyer and Bayle, 2017), thus being prone to homoplasy (Smith et al., 2012; rev. in Macho, 2015).

Most studies on enamel thickness have primarily considered the permanent teeth, especially the molar series, while the extent of covariation in tooth enamel thickness between deciduous and permanent counterparts has been the object of limited quantitative analyses, including in hominids (for a recent synthesis and review of studies on deciduous enamel thickness in humans, see table 1 in Mahoney, 2013; additionally, among other contributions, see Benazzi et al., 2011; Fornai et al., 2014, 2016; Macchiarelli et al., 2006, 2013; Peretto et al., 2015; Zanolli, 2015a; Zanolli et al., 2010a, 2012, 2014). Accordingly, quantitative support to answer a number of questions remains so far elusive. More specifically: whenever, in a comparative intertaxonomic assessment, we score a permanent hominid tooth as relatively "thinly"- or "thickly-enamelled" and order it accordingly within a series of investigated specimens, does the primary element score similarly and does it (tend to) occupy a comparable position within the same deciduous series? Can we confidently predict an enamel thickness "category" for a hominid deciduous crown based on the measure of the permanent tooth (or vice versa)? Does a predictable deciduous-permanent pattern exist for tooth enamel thickness in hominids? If so, is it taxon-specific?

The second deciduous (dm2) and the first permanent (M1) molars are part of the same developmental molar series (rev. in Bailey et al., 2014, 2016; see also Evans et al., 2016), i.e., they are meristic elements with a similar and serially repeated structure within the same organism (Butler, 1956, 1967; Kraus and Jordan, 1965). In this study on some extant and fossil hominids, we thus investigate the degree of covariation in enamel proportions between the dm2 and the M1 (for the extant human condition, see Gantt et al., 2001; Grine, 2005; Huszár, 1972; Mahoney, 2010; Rossi et al., 1999). In order to perform intertaxonomic comparisons, we established a so-called "lateral enamel thickness diphyodontic index" (LETDI; see § Materials and methods) as a measure of the proportions in the amount of non-occlusal enamel (Macchiarelli et al., 2016; Zanolli, 2015b). Even if the mandibular dm2 and the M1 specifically used in this study are not successional elements, we introduced the wider concept of "diphyodontic index" referring to their usual differential use-life. Given the exploratory nature of this study, whose main goal is to capture a tendency or trend, if any, and not to assess intraspecific variation, or evolutionary trends, or phylogenetic relationships, the number of cases examined for each taxon (ranging from 1 to 5 tooth pairs) is just minimal. By definition, at this stage of the research the underlying assumption is that the signal revealed by each dm2-M1 crown pair used here, all from mandibular dentitions, represents the average condition of its own taxon, i.e., is taxon-representative.

Apart from some intertaxonomic differences in developmental timing and patterning between the dm2 and the M1 (Dean, 2000, 2006, 2010; Dean and Cole, 2013), given that the dm2 is in functional occlusion for a much shorter time and commonly experiences lower functional constraints at least until the weaning process begins (Fleagle, 2013; Swindler, 2002), we expect that, independently from their relative qualitative "category" ("thinner" vs. "thicker"), the dm2/M1 enamel relative volume ratios are < 1.

2. Materials and methods

The hominid taxa considered in this study include the four extant genera *Homo* (HOM), *Pan* (PAN), *Gorilla*