3. Quantifying variation in human dental development sequences: An EVO-DEVO perspective

J. BRAGA
Laboratoire d'Anthropologie Biologique
Université Paul Sabatier (Toulouse 3), FRE 2960
39 allées Jules Guesde, 31000 Toulouse, France
braga@cict.fr

Y. HEUZE
Laboratoire d'Anthropologie Biologique
Université Paul Sabatier (Toulouse 3), FRE 2960
39 allées Jules Guesde, 31000 Toulouse, France
heuze@cict.fr

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Abstract

The present paper describes a novel analytical approach to provide a comprehensive description of the complex interactions that exist between the growing permanent mandibular teeth (excluding the third molars), and to quantify variability in sequences of key events during crown and root formation, independent of chronological age. Importantly, our method integrates the fundamental concept of modularity and rejects the old statistical fallacy of analyzing data on the assumption that it contains no information beyond that revealed on a tooth-by-tooth analysis. Indeed, interactions between growing teeth may also contain some information, which enables developmental or evolutionary information to be uncovered. Our training sample is based upon cross-sectional standardized panoramic radiographs of the teeth of a total of 2089 children (1206 girls and 883 boys) of different geographic origins (mainly Western Europe, Southern Iran, and Ivory Coast). We observe that, in extant humans sampled so far, the relative development of the permanent incisors is more plastic and varies more than for other teeth. Therefore, we consider that the quantification of possible variations between onsets, durations and rates of development of different teeth in any given child, within a large sample, is a prerequisite to the analysis of fossil hominids. In particular, we seriously question the assumption that the anterior teeth can serve as a reliable substitute for the other permanent teeth, and in particular for interpretations on somatic maturity and brain size. Our hypothesis of modularity in dental development and our method derived from this concept can serve as a basis for identifying and studying patterns of dental growth and, importantly, for comparisons between extant populations, and/or fossil species. These studies do not need to be hedged with age assessments of unknown accuracy and reliability levels (particularly in fossils), or the assumption of independence between growing teeth.

S.E. Bailey and J.-J. Hublin (Eds.), Dental Perspectives on Human Evolution, 247–261.

Introduction

The aim of our cross-sectional analysis of subadult radiographs is to examine, using an appropriate method and samples from different extant human populations, the variation in the relative sequences (or patterns) of key events during crown and root formation. To date, investigators have focused on the timescale (chronology) of dental development with published median or mean ages of emergence for permanent teeth in different modern human populations (e.g., Kuykendall, 1992; Liversidge, 2003) (in some studies, emergence is often confused with eruption; see Marks and Cahill, 1993 for a definition of the latter term). The debates have focused on the existence of real differences between samples, or on biases due to sampling, rating effects, and statistical procedures (Smith, 1991). However, sequence and timing represent two separate aspects of variation. For example, the first permanent molars of two individuals can mineralize at the same time but in different sequences relative to the other teeth. Compared to variation in timing, variation in patterns is much less documented in the literature. The question of variability in patterns is fundamental to the study of dental developmental processes as a possible foundation for morphological changes during human evolution. For permanent teeth, data are available for variation in sequences of emergence (e.g., Garn et al., 1973; Smith and Garn, 1987; Nonaka et al., 1990) and for differences in sequences of development revealed only between pairs of teeth (e.g., Fanning and Moorrees, 1969; Tompkins, 1996; Liversidge and Speechly, 2001). Variability in sequences of dental development in extant humans is acknowledged by some scholars (Mann et al., 1987; Smith, 1989) but the problem has not properly addressed so far, due to lack of definition, concepts and methods (see below). Little is known of possible shifts in the sequences of formation of teeth that might be due to sex, age, jaw, and geographic origin, among other factors. It is generally assumed that "the pattern of development should be more robust than is age of stage appearance" (Smith, 1989: 77) and that there is little variability in relative sequences of key events during tooth growth. The comparative analyses of the sequences of dental development observed in fossil hominids have led to opposite views regarding their "modern human-like" or "ape-like" status (Smith, 1986, 1989, 1994; Mann et al., 1987; Lampl et al., 1993; Conroy and Kuykendall, 1995). Discrepancies are due to the lack of studies of variability in patterns of dental development both within extant humans and between the two chimpanzee species. In addition to the problem of quantifying variability and the controversy over which standard is the most appropriate, other limitations on the study of dental developmental patterns are mainly methodological: (i) first, the understanding of patterns of developmental relationships should not be age related because non-adult dental age assessment is another complex problem with factors influencing its quality (accuracy and reliability) (Ritz-Timme et al., 2000; Braga et al., 2005); (ii) second, developing teeth do not mineralize randomly with respect to one another. We do not expect partial correlations between the rates of tooth formation to approach zero when controlled for age. Indeed, teeth are topographically, developmentally and functionally associated with each other. Teeth essentially grow as a unit (see below) and should be statistically considered as dependent units which grow within a developmental module (Figure 1).

Figure 1. Modularity in dental development with 126 combinations (numbered as follows, in bold) derived from any sequence comprising 7 permanent teeth.