5. A computerized model for reconstruction of dental ontogeny: A new tool for studying evolutionary trends in the dentition

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Abstract

All hominid molars show the same sequence of cusp initiation, but differ in the later stages of development. The topography of the dentin-enamel junction (DEJ) represents the outcome of differential growth between cusps. Since the cusps grow in an orderly sequence from tip to base (defined by the plane of coalescence with adjacent cusps), quantification of cusp volume and relationships can be used to reconstruct successive stages in development and their contribution to the morphometry of the crown surface. Their volume and spatial relationships at the DEJ enable us to partition cell proliferation in relation to cusp initiation, while quantification of the amount and distribution of enamel overlying the DEJ provides the necessary discrimination between cell proliferation and cell function, expressed in enamel matrix apposition. We have developed a three-dimensional

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computerized model of a lower molar tooth that enables us to identify and quantify the different stages of tooth development defined above. The model is based on serial micro-computed tomography (microCT) images of human teeth that provide accurate quantification of the outer and inner enamel and dentin boundaries of individual cusps. We have used this model to compare morphogenesis in the lower second deciduous molar and lower first permanent molar. Spatial relationships of the cusps, expressed by the topography of the DEJ showed that shape differences were established in the early stages of morphogenesis by differential proliferation within the developing tooth germ and that cusp size and proportions were modified at the crown surface by enamel apposition. Reduction of the hypoconulid in the permanent molar shown at the DEJ was largely masked by the exceptional thickness of enamel on this cusp. We propose that this model provides a novel contribution to the identification of ontogenetic trajectories and their contribution to evolutionary trends in tooth size, shape and enamel thickness.

Introduction

All hominid lower molars are variants of the 5-Y Dryopithecine molar pattern (Gregory and Hellman, 1926; Dahlberg, 1945). The observed variation in tooth size, cusp number and outline (steep versus rounded, large versus small, groove pattern and enamel thickness) that has traditionally been used in phylogenetic studies has however, recently been questioned on the grounds of homoplasy (Collard and Wood, 2000; Finarelli and Clyde, 2004). Enamel thickness, in particular, varies independently of tooth size. In a recent study of enamel thickness variation of inbred baboons Hlusko (2004) proposed that rapid change in this feature could occur under appropriate selective pressures. Thus, variation in enamel thickness may account for much of the homoplasy shown at the crown surface. As it is the last tissue to be completed, enamel modifies the template of the tooth laid down during morphogenesis. For this reason, examination of the earlier stages of tooth development, represented in the completed tooth by the dentin-enamel junction (DEJ), has long been considered a more reliable representation of the underlying phenotype in phylogenetic studies (Kraus, 1952; Korenhof, 1960; 1979; Smith et al., 1997; Sasaki and Kanazawa, 1999; Smith et al., 2000).

While we cannot directly study developmental processes in fossil teeth, the sequential pattern of tooth development means that many early developmental stages are conserved in the structure of completed teeth and can be identified using appropriate imaging systems. The meristic variation shown along the molar tooth row of modern humans, whose developmental pattern is well established, provides an excellent model for examining the extent to which ontogenetic pathways are modified in teeth of different size and rates of development.

The mandibular molars develop along a mesio-distal gradient in which their size and complexity increase and decrease differentially. The size changes are associated with mesio-distal gradients in the duration of development and enamel thickness as well as in overall tooth size and cuspal relationships. All molars show the same order of cusp initiation (protoconid>metaconid>hypoconid> entoconid> hypoconulid), but differ in subsequent amount and rate of growth (Kraus and Jordan, 1965; Butler, 1967, 1999; Winkler et al., 1991; Avishai et al., 2004). In large toothed hominids, the distal cusps are larger relative to other cusps than in small toothed hominids, with the differences most pronounced in the M2 and M3. The cusps develop as infoldings of the inner enamel epithelium initiated by the enamel knots. They develop apically from tip to base. Differentiation of the cells of the inner enamel epithelium into ameloblasts and underlying cells of the dental papilla and odontoblasts follows the same sequence. Cusp size and shape is therefore a function of the temporal