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How the microstructure of dentine can contribute to reconstructing developing dentitions and the lives of hominoids and hominins

Comment la microstructure de la dentine peut contribuer à reconstruire le développement dentaire et la vie des hominoïdes et homininés

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ABSTRACT

Accounts of dentine microstructure are less well established in the primate life history literature than those of enamel microstructure. The aim of this paper is to draw some basic comparisons between enamel and dentine, but at the same time to show how dentine microstructure can make a major but different contribution to reconstructing past lives than enamel can. Dentine has both an organic and an inorganic component. The organic component contains growth factors, stable isotopes and DNA that survive long after death. The mineral component contains trace elements and preserves an incremental record of tooth growth. These can be used to put a time scale to many past events when the chemistry or microstructure of dentine has become altered during tooth growth. Dentine microstructure allows us to reconstruct tooth root growth in the past and has contributed to a fuller understanding of the modular nature of developing dentitions among hominoids and hominins.

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RÉSUMÉ

Au sein de la littérature sur l'histoire de vie des primates, il existe moins d'études portant sur la microstructure de la dentine que sur celle de l'émail. Le but de cet article est d'extraire des informations à partir de simples comparaisons entre émail et dentine, tout en montrant combien la microstructure de la dentine peut apporter une contribution majeure et différente de celle de l'émail pour reconstruire la vie passée. La dentine présente à la fois une composante organique et une composante non organique. La composante organique contient des facteurs de croissance, des isotopes stables et de l'ADN qui survivent longtemps après la mort de l'individu. La composante minérale contient des éléments traces et enregistre de manière incrémentale les variations périodiques de la croissance dentaire. Toutes ces informations peuvent être utilisées pour retracer la chronologie de nombreux événements passés lorsque la chimie ou la microstructure de la dentine a été altérée au cours

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de la croissance dentaire. La microstructure de la dentine nous permet de reconstruire la croissance de la racine des dents et contribue à mieux comprendre la nature modulaire du développement dentaire chez les hominoïdes et les hominins.

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1. Introduction

As a tissue, dentine predates the origin of teeth. The dermal placodes, or placode scales, of jawless fish evolved as reparative organs able to respond to wear and wounding on the surface of the skin. In all likelihood, their microstructure suggests they were able to detect changes in osmolarity and temperature giving them a protective role comparable to dentine in teeth today. The classic theory is that these structures in the skin at the margins of the mouth gave rise to teeth in the first jawed vertebrates, some 420 million years ago (Smith and Sansom, 2000; Smith et al., 2016). Subsequently, the evolution of an epithelial dental lamina along the jaws enabled what were scattered structures in the skin to become a precisely timed and serially ordered morphogenetic field of developing teeth in the mouth (Smith et al., 2016). The placode dentine of jawless fish, 380 million years ago, contained fine tubules the same size (~2 µm diameter) as human dentine tubules that formed at the periphery of a vascular pulp cavity seated in supporting bone beneath (Smith et al., 2016). The odontoblast cells, whose long cell processes created the tubules as they retreated towards the vascular space within the trabecular bone, also clearly laid down reparative (or secondary) dentine in response to wear and damage (Smith et al., 2016). In mammals, odontoblasts are among the longest-lived of all post-mitotic cells (Couve et al., 2013). For the whole life of a tooth (and an individual), they are capable of predentine and dentine formation.

Dentine makes up the bulk of all teeth. Dentine surrounds the vascular pulp of a tooth and is covered with enamel over the crown and with cementum over the tooth root (Fig. 1). Only 72% by weight of dentine is made up of an inorganic component that is largely hydroxyapatite, compared with enamel where 96% by weight is mineral. Dentine contains 10% water, while enamel contains only 2%. Various organic components make up 20% of dentine by weight compared with only 1 or 2% in enamel. The organic constituents in dentine are largely type I collagen, but there are also other non-collagenous proteins such as proteoglycans (important for collagen fibre assembly), dentine phosphoproteins and sequestered growth factors (Linde, 1984). Dentine phosphoproteins have very high phosphate content and have calcium binding properties that are presumably involved in the mineralisation process (Berkovitz et al., 2002; Linde, 1984). These fundamental compositional differences give dentine and enamel completely different physical properties. While harder than bone and cementum, dentine is less hard than enamel, but it resists crack propagation better than enamel and has greater compressive and tensile strength being both rigid and elastic (Berkovitz et al., 2002).

Dentine is characterised by tubules that pass from the pulp to the enamel dentine junction (EDJ) in the crown and to the cementum dentine junction (CDJ) in the root (Fig. 1). They follow a long sinuous curving path that reflects the changing rate of formation as dentine is laid down from the EDJ pulpwards (Fig. 1). The cell bodies of odontoblasts line the pulp cavity and their cell processes remain embedded within dentine tubules through life. Some accounts (Schroeder, 1991) claim that during life an odontoblast cell process can reach as far as the EDJ, while others suggest it may only extend just a third of the total tubule length (Shellis, 1981). Dentine tubules also contain tissue fluid and some unmyelinated nerve fibres that are largely distributed beneath the crown. This ensures that dentine remains hydrated, vital (alive) and also constantly sensitive and responsive to changes in temperature, osmotic pressure and other external stimuli. Enamel, on the other hand, is a non-vital tissue containing no cells and is completely insensitive to external stimuli and unable to repair itself. Pulp and bone are both richly innervated and vascularised tissues but enamel, dentine and cementum contain no blood vessels at all.

Enamel, dentine and cementum all form incrementally by apposition of one tissue layer secreted upon another and once formed are not replaced or turned over during life. The general incremental pattern of dentine (Fig. 1) is primarily determined by the rate of differentiation of the forming odontoblast cell sheet and was first described by Victor von Ebner (1902). Dentine formation, unlike enamel formation, can continue in various forms after the tooth has fully grown in response to abrasion, attrition, erosion, tooth fracture and caries so long as the pulp has a blood supply and remains vital. At the end of tooth formation, so-called primary dentine formation is complete, but dentine formation continues at an extremely slow rate in the form of regular secondary dentine (Fig. 1). The reduced outline of the pulp chamber, when examined radiographically, gives some indication of the history of how this has occurred, both locally and generally within a tooth. It has even been used to estimate the age of individuals and may proceed at different rates in males and females (Zilberman and Smith, 2001). Irregular secondary dentine and sclerosed dentine (Fig. 1) are protective and/or reactive forms of dentine and are described and discussed further below.

During tooth formation, ameloblasts secrete enamel matrix and odontoblasts secrete dentine matrix but here the similarities end. A layer of predentine between 10 and 40 µm thick remains unmineralised until the organic component of the predentine has become highly organised into a mesh or felt-work of collagen fibres arranged parallel with the forming dentine surface (Fig. 2). The predentine is essentially a working space within which individual

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