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Tertiary dentine frequencies in extant great apes and fossil hominins

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Tertiary dentine forms when an odontoblast is directly affected by stimuli, commonly through occlusal wear. In this study the presence of tertiary dentine is recorded in three South African fossil hominin species (*Australopithecus africanus*, *Homo naledi* and *Paranthropus robustus*), and two extant great ape species (*Gorilla gorilla gorilla* and *Pan troglodytes*). Frequencies of tertiary dentine were calculated for each species based on macroscopic observations of teeth with dentine exposed through occlusal wear. Overall, the three hominin species have similar tertiary dentine frequencies ranging from 12% to 16.13%. In contrast, over 90% of gorilla teeth with dentine visible show tertiary dentine. Chimpanzees fall between these extremes with 47.21% of teeth affected. Species variances are not related to differences in occlusal wear. Instead, some species appear predisposed to produce tertiary dentine earlier and/or faster than other species. Therefore, tertiary dentine formation has the potential to provide useful information on fossil specimens. For example, the uniformly low rate of tertiary dentine formation in hominins may be due to thick enamel having a similar role in preventing loss of function of teeth, i.e., extending the life of a tooth. In contrast tertiary dentine is clearly an important mechanism for normal dental function in gorillas, and may have evolved to maintain sheering surfaces for masticating tough vegetation.

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Tertiary dentine frequencies in extant great apes and fossil hominins

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Abstract

Tertiary dentine forms when an odontoblast is directly affected by stimuli, commonly through occlusal wear. In this study the presence of tertiary dentine is recorded in three South African fossil hominin species (*Australopithecus africanus*, *Homo naledi* and *Paranthropus robustus*), and two extant great ape species (*Gorilla gorilla gorilla* and *Pan troglodytes*). Frequencies of tertiary dentine were calculated for each species based on macroscopic observations of teeth with dentine exposed through occlusal wear. Overall, the three hominin species have similar tertiary dentine frequencies ranging from 12% to 16.13%. In contrast, over 90% of gorilla teeth with dentine visible show tertiary dentine. Chimpanzees fall between these extremes with 47.21% of teeth affected. Species variances are not related to differences in occlusal wear. Instead, some species appear predisposed to produce tertiary dentine earlier and/or faster than other species. Therefore, tertiary dentine formation has the potential to provide useful information on fossil specimens. For example, the uniformly low rate of tertiary dentine formation in hominins may be due to thick enamel having a similar role in preventing loss of function of teeth, i.e., extending the life of a tooth. In contrast tertiary dentine is clearly an important mechanism for normal dental function in gorillas, and may have evolved to maintain sheering surfaces for masticating tough vegetation.

Key words: dentine formation, hominid diet, dental properties, gorillas

1. Introduction

Primary dentine is produced during tooth formation and is succeeded by secondary dentine, which is an ongoing slow process (Rutherford et al., 1995; Dean, 2017). Tertiary dentine forms as protection against insult, caused commonly by excessive wear, microbial infection, and caries (Bjørndal, 2001; Fischer et al., 1970; Foster et al., 2013; Mjör & Karlsen, 1970; Ricucci et al., 2014; Stanley et al., 1966; Wennberg et al., 1983). There is often confusion as to what to call this process, referred to in this study as 'tertiary dentine' following Foster et al. (2013). The terms 'secondary dentine', 'irregular secondary dentine' and 'reparative dentine' have all also been used in the literature to describe this phenomonon (e.g., Ortner, 2003; Hillson, 2005; Dean, 2017).

Tertiary dentine can be formed in two ways. Reactionary, in which new dentine forms from the pre-existing odontoblast, and reparative, in which new odontoblast cells are formed (Ricucci et al., 2014; Dean, 2017). Both types can only be formed when an odontoblast is directly affected by stimuli, and so the position and structure depends on the type and intensity of the force (e.g., occlusal wear and caries). The colour of tertiary dentine is distinct from the surrounding primary dentine, and usually darker in appearance (Hillson, 2005).

Only a few studies have looked at tertiary dentine in detail (e.g., Geissler et al., 2015; Pampush et al., 2016; Dean, 2017). Clinical studies have researched the speed and properties of tertiary dentine formation, usually from an oral health perspective (Cox et al., 1992; Smith et al., 1994; Tarim et al., 1998; Ivanovic and Santini, 1989). Furthermore, it is rarely recorded in the archaeological literature, and cross-species studies have yet to be carried out on hominins, although its presence has been noted (Margvelashvili et al., 2013). It is not known how the frequency and speed of tertiary dentine formation varies between wild primate groups or if certain groups may start to produce this form of dentine in response to stimuli earlier than others. In this exploratory macroscopic study these processes are tested by comparing tertiary dentine rates in different species of extant great apes and fossil hominins. The aim is firstly to see how variable hominids are in terms of tertiary dentine frequencies and secondly to see if differences in formation rates may relate to diet or phylogeny across the five species studied.

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2. Materials and methods

Data was collected on South African fossil hominins and two extant primate species. The hominin species studied were *Paranthropus robustus*, *Australopithecus africanus* and *Homo naledi* and extant great apes *Gorilla gorilla gorilla* and *Pan troglodytes*. The fossil hominin samples are curated at The Ditsong National Museum of Natural History and the University of the Witwatersrand. The extant primate material is curated at the Powell-Cotton Museum in Kent, UK, and specimens were wild shot in the first half of the 20th century (Guatelli-Steinberg and Skinner, 2000; Macho and Lee-Thorp, 2014). In the text when stated as chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla gorilla*) this refers to these species/subspecies.

Dentine is exposed through antemortem wear on half of the teeth studied. A major issue in comparing frequencies of tertiary dentine is the amount of postmortem discoloration on many hominin teeth. Particularly common is for dentine islands on the occlusal surface to be stained but for the surrounding enamel to appear relatively unaffected. Teeth with such staining are excluded from analysis. However, the large size of the three fossil hominin species studied means there is still a large sample for each.

Only teeth that have dentine exposed on the occlusal surface through wear, and are not damaged or obscured by post-mortem damage, were included in analysis. Tertiary dentine is then marked as present or absent for each of these teeth. Obvious coloration changes that are clearly antemortem in nature are recorded as tertiary dentine (Figure 1). Only clear areas of tertiary dentine that are visible with the naked eye, and caused by wear rather than other stimuli, are included. The severity of occlusal wear for each tooth was recorded following Scott (1979) for molars and Smith (1984) for all teeth as part of a separate study (Towle, 2017a), allowing differences in wear between species to be examined.

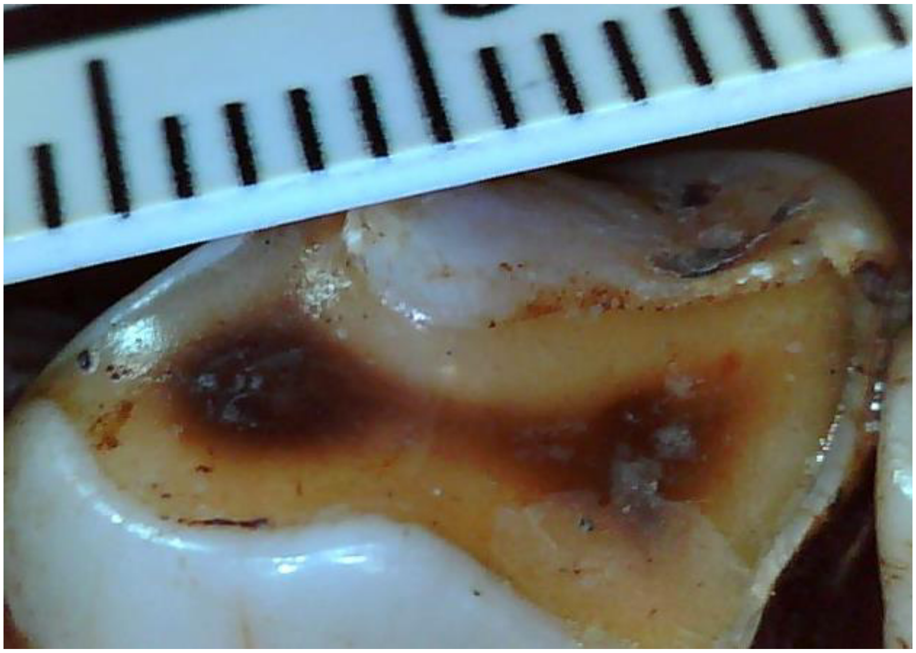

Figure 1. *Gorilla gorilla gorilla* lower left first premolar showing tertiary dentine formation (specimen M 786).

3. Results

The three hominin species have very similar tertiary dentine frequencies, ranging from 12.00% to 16.13% (Table 1), with no statistically significant differences among them (*e.g., P. robustus* vs. *H. naledi*: X^2= 0.326, 1 df, p= 0.5679). The extant primate samples have substantially higher rates than the hominins, with gorillas standing out with over 90% of teeth with dentine exposed through occlusal wear displaying tertiary dentine. The same order for the extant great ape samples is present in deciduous teeth, with gorillas having the highest frequency (Table 2). There were not enough complete deciduous teeth with dentine exposed for the hominin samples for comparisons. The more worn a tooth is the more likely it will display tertiary dentine. However, differences in wear between species do not explain the large differences in tertiary dentine frequencies, with wear score proportions similar among all species studied (Towle, 2017a).

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Table 1. Frequencies of tertiary dentine in permanent teeth, as a percentage of all teeth with dentine exposed through wear on the occlusal surface.

Species	Tertiary dentine present	No tertiary dentine	Tertiary dentine %
A. africanus	12	78	13.33
P. robustus	9	66	12.00
H. naledi	5	26	16.13
Chimpanzees	448	501	47.21
Gorillas	917	67	93.19

Table 2. Frequencies of tertiary dentine in deciduous teeth, as a percentage of all teeth with dentine exposed through wear on the occlusal surface.

Species	Tertiary dentine present	No tertiary dentine	Tertiary dentine %
Chimpanzees	113	128	46.89
Gorillas	131	61	68.23

4. Discussion

Differences in formation properties of tertiary dentine are at present not well understood. However, it is known that this material forms as a response to stressors, including heavy wear (Bjørndal, 2001; Foster et al., 2013; Mjör & Karlsen, 1970; Stanley et al., 1966; Wennberg et al., 1983). Why species differences may exist has rarely been explored. Presumably as well as the type of stimuli causing the tertiary dentine formation, the intensity of the stimuli and dental properties are important factors (Ricucci et al., 2014; Dean, 2017).

The results of this study show that diverse hominin species, from three genera, have similar tertiary dentine rates. This is despite disparity in other dental properties, and dietary differences between these three genera (e.g., Towle et al., 2017b; Ungar and Grine, 1991; Grine et al., 2012; Smith et al., 2015; Daegling et al., 2013). Tertiary dentine is much more common in other great apes. This may relate to evolving to cope with different diets, or different ways to cope with similar dietary items. For example, tertiary dentine formation may be less important in hominins, with thick enamel potentially more important for extending tooth functionality, most notably in species such as *P. robustus*.

The differences between species is not related to differences in tooth wear, with all species represented by a wide range, and similar proportions, of wear stages that all cluster around the same mean (Towle, 2017a). The deciduous teeth for the extant primate sample follow the same pattern as the permanent teeth; again suggesting genuine species differences in the speed tertiary dentine is formed. Differences in the speed of wear between species has been suggested as potentially influencing formation, with wear that is too fast potentially not allowing enough time for tertiary dentine to form (Fischer et al., 1970; Foster et al., 2013; Mjör & Karlsen, 1970; Ricucci et al., 2014; Stanley et al., 1966; Wennberg et al., 1983). The results of this study suggest the main factor is dentine/tooth properties, with certain species, such as gorillas, laying down tertiary dentine faster and/or earlier than other species. Further histological studies on different species is needed to support this finding, as this will allow the true extent of differences to be studied (Smith et al., 1994; Tarim et al., 1998; Ivanovic and Santini, 1989).

A potential explanation for the substantially different rates of tertiary dentine formation in hominids is evolving dental properties to cope with different diets. The high speed of tertiary dentine formation in gorillas has potentially evolved as a consequence of their diet high in tough vegetation, in which fast and early tertiary dentine formation keeps the tooth functioning for longer. When frequencies for different hominin groups have been researched further conclusions on what the low rate may mean in terms of diet can be explored. Additionally, once more extant primate species have been studied, and presuming dietary differences explain variation in tertiary dentine rates, inferences into the diet of fossil samples may be possible. The large differences between hominid species also suggests tertiary dentine may also be a useful tool for phylogeny studies.

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