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Primate enamel development with emphasis on South African Plio-Pleistocene fossil hominids

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CHAPTER 1

This dissertation is presented, as per University of the Witwatersrand procedures, in a publication format, in that the bulk of the work that forms the main body of this thesis derives from articles written either wholly by the candidate or under the guidance and assistance from supervisors to the extent reasonably expected. These articles, a total of six, have been accepted in international peer-reviewed journals or peer-reviewed book chapters. The research that these articles cover forms a cohesive body of work that is primarily concerned with the study of the mechanisms of enamel tissue development in South African Plio-Pleistocene hominids, as well as some aspects of the life history. This work includes comparisons to extant hominids. In addition, the only study to date on tooth histology of bonobo (*Pan paniscus*) is presented.

1.1. INTRODUCTION

The study of hominid evolution is a complex process in which biologically based principles studied in living organisms are often applied to individual fossil specimens, or relatively small samples of fossils. This implies therefore that the study of fossils undergoes new interpretative phases not only as samples sizes increase, but also when the underlying growth mechanisms of the skeletal components of living organisms become better known (Lovejoy *et al.*; 1999, 2002; McCollum 1999; Dean *et al.*; 2001; McCollum & Sharpe 2001). This is not surprising given that knowledge of the growth processes that intervene in the development of anatomical structures is important in order to interpret evolutionary changes through time (Atchley 1985; Atchley & Hall 1991; Jernvall & Jung 2000).

Recently, hominid palaeontology has sought new direction in understanding the principles of biological development to better interpret morphological variation (Howell 2002; Hlusko 2004; Lieberman 2004). Assessing the developmental interdependence of

different elements in anatomical complexes is therefore becoming increasingly important (e.g. McCollum 1999). The aim, it appears, is to create a new philosophy in palaeoanthropology based on the new age of discoveries in the field of developmental biology (e.g. Lovejoy *et al*.; 1999, 2002, 2003; McCollum & Sharpe 2001; Howell 2002; Lieberman 2004) in which teeth play a critical role (e.g. Jernvall 1995).

It is very fortunate that in the Plio-Pleistocene hominid fossil record, teeth are one of the most abundantly represented elements. Their external morphology has been thoroughly studied and has been widely used as a taxonomic indicator (e.g. Robinson 1956; Wood & Abbot 1983; Wood *et al*.; 1983; Grine 1985, 1988, 1993; Suwa *et al*.; 1996). In addition, functional, structural and adaptive features have been detailed and have been interpreted within an ecological context (Grine 1981; Turner & Wood 1993; Ramirez Rozzi *et al*.; 1999; Teaford & Ungar 2000; Macho 2001; Kuykendall 2003; Ungar 2004, in press). It is self evident that the importance of teeth is paramount, because an animal's subsistence depends on food processing, and because food processing begins in the mouth, teeth, as "tools", have been adapted in their shapes to perform a variety of activities highly dependent upon the animal's feeding proclivities (e.g. Ungar 1998; Teaford *et al*.; 2000).

Teeth are structures for which an in depth level of knowledge about their biological development is available (Jernvall & Jung 2000; Jernvall & Thesleff 2000; Sharpe 2000; Zhao *et al*.; 2000; Kangas *et al*.; 2004). Thus, it would seem that teeth are exceptionally useful in providing valuable information about evolutionary changes in lineages (Jernvall 1995). Such changes may be discerned at the general level of morphological innovations (Hunter & Jernvall 1995; Jernvall 2000). More specifically, as previous studies in hominid evolution have shown, teeth can provide information about enamel tissue growth in fossil hominid species (e.g. Dean *et al*.; 2001).

Interpretations of hominid dental morphology can be attempted at basic hierarchical levels of organismal biology, the cells. Enamel can be studied at this level because the specific secretory cells that produce enamel matrix, ameloblasts, leave behind mineralised tracks of their direction of movement and metabolic rate (Schour & Massler 1941; Boyde 1964). These tracks can be visualized with various microscopic techniques. Three aspects of dental enamel are of relevance to this study. The first is that once the enamel crown is formed, which is always prior to tooth eruption, ameloblasts cease their secretory activity. During the life of the individual, these cells will not be reactivated and thus enamel will not be subjected to the influence of epigenetic factors or remodelling after eruption, which commonly affect bone (Jernvall & Jung 2000). Second, the growth tracks preserved in enamel tissue (cross striations and striae of Retzius [Boyde 1964]) have been shown to form in time increments which allow calculations of the formation time of this tissue (Dean 1987, 2000; Boyde 1990; Reid & Dean 2006). Cross striations represent daily markers of cell secretions (Boyde 1964; Dean 1987; Bromage 1991; Fitzgerald 1998; Risnes 1998; Smith 2006). Striae of Retzius, and their external manifestations known as perikymata, represent longer term markers. The number of cross striations between striae represents their periodicity. Third, dental development is correlated with certain life history parameters and therefore provides useful information about the palaeobiology of extinct primate taxa (Bromage 1987; Smith 1991; Wood 1996; Macho 2001; Anemone 2002; Kuykendall 2003).

Enamel thickness of the permanent dentition is also an important character of the adult phenotype which features prominently in taxonomic studies within the Hominoidea (Robinson 1956; Martin 1985; Grine & Martin 1988; Macho & Thackeray 1992; Schwartz 2000; Smith *et al.*; 2005). The development of enamel thickness is a function of the number of active secretory cells, daily secretion rates, and the timing of pre-programmed cell death (apoptosis) (e.g. Grine & Martin 1988; Beynon *et al*.; 1991; Macho 1995; Dean

2000; Dean *et al*.; 2001), factors that need not be directly correlated with each other. This has been clearly indicated in recent studies by Dean and co-workers where a wide array of extant and extinct primate taxa is shown to follow different trajectories in occlusal enamel development (Dean 1998; 2000; Dean *et al.*; 2001). Enamel thickness is therefore better understood at cellular levels where variation in daily secretion rates has the potential to show mechanistic differences of its development (Dean 2000). However, the determination of the role played by tooth function with regards to differences in developmental mechanisms of enamel thickness, remain unresolved (Dean 2000).

In spite of the importance of understanding enamel tissue growth, research in Plio-Pleistocene hominid enamel has been, until very recently, limited to relatively few studies. This is due, for the most part, to the intrusive nature of the requirements of microscopic procedures which commonly require sectioning of the specimens. Thus, some studies have focused on perikymata counts and/or perikymata distribution as these features can be studied without the use of intrusive methods. However, these studies do not provide a complete picture to understanding mechanisms of growth. Alternatively, researchers usually resort to making replicas of the original material to be analysed under SEM, which reduces the array of features that can be studied (e.g. striae of Retzius) (Dean 1988; Beynon & Dean 1988). In addition, studies of enamel microstructure are typically time-consuming.

Despite these difficulties, in recent years there has been a vast increase in comparative studies on the histology of anterior and posterior tooth growth from Miocene hominoids to modern humans and great apes (e.g. J.H.E. vol 35, 1998). These studies have provided a more robust base from which to understand and contextualize hominid enamel growth, which was much needed. In addition, Dean *et al.*; (2001) has sparked renewed interest in understanding the mechanisms of enamel growth in early hominids.

The study of Dean and co-workers analysed daily growth rates in 13 fossil hominid teeth. However, 11 specimens were sectioned for this study.

The constraint to limit histological studies of enamel growth in fossil hominids is obvious, and thus a new technology was needed to access more specimens without making use of sections. One such technology now exists, and is presented in the form of a portable confocal scanning optical microscope (PCSOM). This instrument has been under development since early 2000 by T.G. Bromage, A. Perez-Ochoa and A. Boyde. These researchers managed to develop a microscope purposefully designed for the study of hominid remains that permits the analysis of bone and tooth microstructure without requiring that the specimens be sectioned, but benefiting from natural breaks present in many specimens (Bromage *et al.*; 2003, 2005).

This thesis is largely based on the application of this new technological tool, which has been used to study Plio-Pleistocene hominid enamel. Fundamental differences therefore exist between this study and previous works. First, no sectioning of fossil material was required. Second, we were able to image specimens directly to observe, for example, daily enamel secretions which range in length between 3 and 7 microns. Third, we can greatly increase the number of specimens in which daily secretion rates can be studied as these features can be imaged directly in natural fractures of teeth. Finally, because both cross striations and striae of Retzius can be simultaneously observed, we can study the periodicity of striae in large samples of teeth. With time and patience, there is virtually no enamel microstructural feature that cannot be imaged with the PCSOM. For the most part, the PCSOM was applied to the question of the possible differences in mechanisms of molar growth between Plio-Pleistocene hominid species from the cave sites of South Africa, in order to explore and explain the observed differences in enamel thickness and absolute molar size between taxa (Robinson 1956; Grine & Martin 1988).

Since the pioneering study of Bromage and Dean (1985) in which incremental lines, in this case perikymata, were used to study growth of modern humans and fossil hominid enamel, this and subsequent studies have revealed a series of differences between hominids and modern humans (e.g. Dean & Reid 2001 a & b). Differences were also observed among fossil taxa, which are discussed in more detail in the following chapter.

An interesting paradox was noted: in spite of the much larger crowns of some fossil hominid teeth (Figure 1) - which in the case of molars may double the size of modern human molars - they nevertheless formed their teeth in the same or less amount of time (Bromage & Dean 1985; Beynon & Wood 1987, Ramirez Rozzi 1993, 1995; Dean *et al.*; 2001).

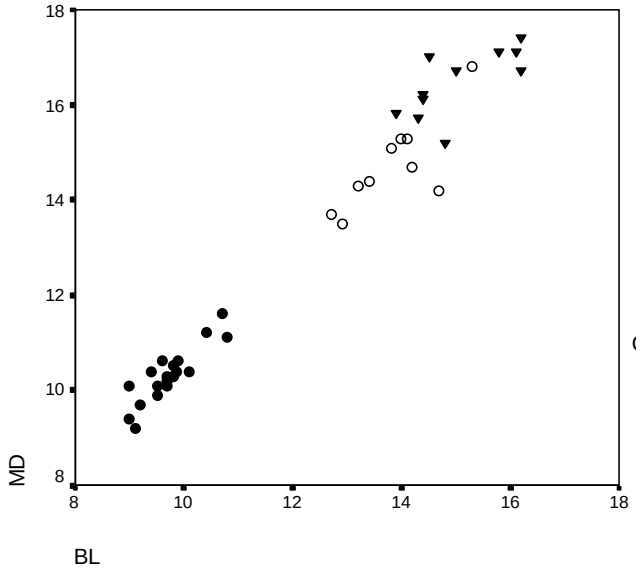


Figure 1. Box plot of MD/BL measurements of second permanent molars of *A. africanus* (n= 10) (open circles), *P. robustus* (n= 11) (triangles) and modern humans (n= 20) (closed circles). It is noticeable that the occlusal area of *P. robustus* is larger than in the other two species, although there is some overlap with *A. africanus* for this tooth type.

In addition, it has been known for some time that Plio-Pleistocene hominids in general had faster growth trajectories than modern humans (Bromage & Dean 1985;

Bromage 1987; Smith 1989, 1991). These two interesting facts, the rapid overall dental development and fast tooth crown formation, implied that the mechanism by which these species accomplished tooth development in a timely manner was different to that of modern humans.

A few studies have shed light into the nature of these mechanisms. For example, some hominid taxa showed faster daily rates of enamel secretion and a higher number of ameloblasts cells involved in secreting enamel at any given time (Beynon & Wood 1986, 1987; Ramirez Rozzi 1993, 2002). Differences can be observed in growth trajectories between fossil hominids and modern humans. Occlusal enamel development in modern humans is formed at lower daily rates which are maintained for longer periods of time (Beynon & Wood 1987; Dean *et al*.; 2001). These studies, with a few exceptions, were mainly conducted on samples derived from East African sites, which created a gap in our knowledge concerning growth processes in South African taxa. For example, only two studies (Dean *et al*.; 1993; Moggi-Cecchi *et al.*; 1998) had been carried out on crown formation time in four molars of South African early hominid taxa, while over 50 specimens had been sampled from East African early hominids. Grine & Martin (1988) and later Beynon (1992) and Dean *et al.*; (1993a) were the only three studies, until the present series of studies, in which some limited knowledge was presented on the mechanisms of molar growth of *Australopithecus africanus* and *Paranthropus robustus*[§]*.* This thesis was designed to bridge that gap and to allow a more complete picture of hominid evolution at this level.

[§]Moggi-Cecchi *et al*.; (1998) study of Stw 151 was not conclusive about the taxonomic attribution of this specimen, showing both *Homo* and *A. africanus* features.

1.2. HYPOTHESES TESTED IN THIS STUDY

There are two primary areas of understanding relating to hominid dentition that drove the research of this thesis. First is that for many years, it has been noted that enamel thickness and occlusal crown area of molars (Figure 1) appear to be different between *A. africanus* and *P*. *robustus* (Robinson 1954; Grine & Martin 1988; Macho & Thackeray 1992). In addition, the limited information available on some enamel microstructural characters of these taxa indicate that there are some noticeable differences at this level (Grine & Martin 1988).

Based on this information as well as factors influencing enamel thickness, described above, we can advance the following main testable hypotheses:

1- Mechanisms of enamel development differ between modern humans and South Plio-Pleistocene fossil hominids

2- Mechanisms of enamel molar growth differ between *A*. *africanus* and *P*. *robustus.*

To test these hypotheses, a number of studies had to be developed, which included work in fossil and extant taxa. Differences in number of lateral striae, daily secretion rates, striae periodicity, and angles formed between the striae and the enamel dentine junction (EDJ), were studied in South African taxa to assess inter-specific differences. These features where then compared to available data on other Plio-Pleistocene fossil and extant hominids.

1.3. STRUCTURE OF THE THESIS

Chapter 2 presents a broad background to the study of enamel, from aspects of its developmental biology to life history implications of enamel growth in hominids. Here, detailed descriptions of tooth development from a developmental perspective as well as current theories on the appearance of morphological novelties are discussed.

The basic structures of enamel in primates are examined, and how some of these features have been used to assess the formation of the crown in modern humans and early hominids. Finally, the implications for life history within the hominid lineage are discussed.

Chapter 3 presents the materials and methods used in the ensuing chapters, although some aspects may be repeated in the individual publications. The portable confocal scanning optical microscope (PCSOM) used in this study is described in detail. Features recorded in the enamel of the different samples of primates are detailed and each fossil specimen is described. This chapter also includes a wide range of images taken with the PCSOM on enamel features of fossil taxa to show the capabilities of this instrument. As this technology has not been applied to enamel studies prior to this study, the protocols that were developed during this dissertation are detailed for each image.

Chapter 4 is an overview of the geological, environmental and taxonomic context of the fossils studied as much of this literature is only referenced in the articles presented. Chapter 5 presents some results of the comparative studies carried out in modern human samples.

Chapters 6 to 11 consist of the body of work which has been submitted for publications in peer-reviewed journals or book chapters, and these works are synthesized in Chapter 12, the final chapter of this thesis. To maintain uniformity throughout the text, these chapters are presented here in the same format as the remaining chapters of the thesis, instead of using the corresponding formatting requirements of the individual journals. References used in each publication are presented at the end of each paper. A general reference list is also included at the end of the thesis.

The publications section begins with a comparative histological study of the upper dentition of a bonobo (*Pan paniscus*) individual (Chapter 6). This work was carried

out for two reasons: firstly, no histological work on enamel growth of the bonobo was known; and secondly, given the close genetic relationship between bonobo and the common chimpanzee (*P. troglodytes*) (Raaum *et al*.; 2005), this would be a good reference to understand growth differences between closely related taxa. In addition, it allowed the author to use laboratory methods specific to this type of histological study.

The second paper (Chapter 7) was a unique opportunity to investigate life history events in one of the most widely studied fossil hominids, the Taung child. During the course of this thesis, it was noted that enamel defects were present in the permanent molars of the Taung child. These defects, known as hypoplasias, are formed during phases of high physiological stress. This research provided the opportunity to make and use high resolution replicas and casts of an original fossil, which were subsequently studied using scanning electron microscope (SEM).

Chapters 8 – 11 made use of the PCSOM to investigate various aspects of the enamel microstructure of several fossil hominid species, and to test the usefulness of criteria derived from enamel microstructural features in taxonomy. Specifically, Chapter 8 introduces the microscope and its wide range of applications in studies of enamel microstructure in natural breaks on fossil teeth. Chapter 9 presents a comparative study of measurements of daily cell secretions along certain areas of the cusps in the largest sample of any fossil hominid species to date. The results were then compared to other primates, including modern humans.

Chapter 10 compares various aspects of enamel development in two of the best known Plio-Pleistocene fossil taxa, *Australopithecus africanus* and *Paranthropus robustus*. This study was considered by the candidate to be encompassing and included analysis of the largest sample of striae periodicity for any fossil taxa to date, as well as crown formation times for three molars. Chapter 11 tests the usefulness of criteria derived from studies of enamel microstructure in a specimen derived from the site of

Kromdraai which was originally classified as *Paranthropus,* but later placed in the genus *Homo*. Finally, Chapter 12 summarizes the research presented in the previous chapters and discusses how this combined body of research revises our knowledge of the mechanisms of hominid enamel growth, while also suggesting further areas of study.