Stress, life history and dental development: a histological study of mandrills (*Mandrillus sphinx)*

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Thesis submitted for the degree of
Doctor of Philosophy

Department of Anthropology
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September 2017

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Dental development is frequently used to reconstruct life history in primates for which little other information exists. In addition to the regular growth increments visible in histological tooth sections, accentuated lines are thought to form at the time of stressful events in the lives of individual animals. However, our understanding of when, how and why such accentuated lines form in relation to stressful events is limited. In this thesis, I tested the hypothesis that accentuated lines in the enamel and dentine are associated with stressful events in the lives of semi-free-ranging mandrills (*Mandrillus sphinx,* Cercopithecidae) from the Centre International de Recherches Médicales de Franceville, Gabon. I used dates of birth and death to calibrate dental histology to calendar time and individual age. I then reconstructed dental development sequences for individual mandrills, providing a detailed overview of mandrill dental development. I report sex-specific dental development chronologies, crown extension rates and stages of dental development, and compare these to mandrill life history. Based on this dental development data, I matched the observed accentuated lines in the mandrill teeth with the dates of events in the mandrills' lives. My results suggest that accentuated lines can correspond to potentially stressful events, including resumption of reproductive cycling in the mother and menstrual cycles, and in some occasions with parturitions. My results show that male mandrills might form accentuated lines at the time of potentially stressful events too, but most potentially stressful life history events for males take place after dental development is complete. Furthermore, my findings suggest that the number of accentuated lines recorded in teeth varies between individuals in a population, reflecting differences that may influence reproductive success.

Table of Contents

List of Tables

List of Figures

List of Abbreviations

ACTH	=	Adreno-corticotropic hormone
CFT	=	Crown formation time
CIRMF	=	Le Centre international de recherches médicales de Franceville
CRH	=	Corticotropin-releasing hormone
CT- scan	=	Computerised tomography -scan
DSR	=	Daily secretion rate
EDJ	=	Enamel Dentine Junction
EER	=	Enamel extension rate
HPA-Axis	=	Hypothalamic–pituitary–adrenal- axis
IUCN	=	International Union for Conservation of Nature
pH	=	Potential of hydrogen
SE	=	standard error
SEM	=	Scanning Electron Microscope
UV light	=	Ultraviolet light

Statement of Copyright

Acknowledgements

Conducting my PhD research and writing the dissertation is something I have aspired for a long time and it has been a privilege to conduct it at Durham University. However, none of it would have been possible without the help, advice, guidance and encouraging words of a big team of people around me.

First of all, I would like to thank my two supervisors, Jo Setchell and Wendy Dirks. I am so grateful for the chance they have given me to walk on roads I had never taken before, to learn an incredible amount and increasing my passion for microscopy and hard tissue anatomy. Thank you Jo, for the hours and hours we have spent throughout the last years chatting in your office, your thoroughness, your inspiring ideas and all you writing advice. Thanks to you I now share your enthusiasm and devotion to the study of mandrills, what incredible and fascinating creatures they are. Thanks Wendy for sharing your knowledge on primate life history, teeth and microstructure, your enthusiasm for our field, your honest opinions and keeping me sharp, and for your sense of humour too. Both my supervisors have not just guided me through conducting my doctoral studies but have also given me advice and insights from their own 'life history', and I find both women extremely impressive and inspiring. Thank you for giving me the change to work, grow and develop under your wings. I also deeply thank the Leverhulme trust, the Anthropology Department of Durham University, Durham University College and Ruggles Gates Fund for Biological Anthropology for providing the financial support to conduct this doctoral thesis.

I would like to thank my friends and colleagues at CIRMF, Gabon, for their incredible hospitality during my stay, making it possible for me to meet the CIRMF mandrills and for getting to know their beautiful country and its inhabitants; the human and non-human primates. Gabon's got such a big piece of my heart. Thanks to Barthélémy Ngoubangoye and Anaïs Herbert, who facilitated my research visit and allowed me to go through their documentation, assisting me at points where my French was rusty. Big thanks to the other students at CIRMF who made me feel so welcome and with whom I've had an incredible time. Specifically I would like to thank my dear friend Yvan Cyr Moussada Kinga, who's been so kind to me from the first day we met and took me out to see the mandrills every day. I hope our paths will cross again soon.

Furthermore, my gratitude goes out to all my colleagues at Level 7 of the Dental School of Newcastle University. Colleagues… or should I say flatmates? The words of my fellow Dutchman Van Leeuwenhoek seem quite fitting here: "*I've spent more time than many will believe [making microscopic observations], but I've done them with joy*". I can't believe how much time I have spent

in that department and in that microscopy room. I can still hear staff members walking by the room in the evening, peaking in, saying “still here”? Yep. Still here. And the next day, and the next... Sometimes it seemed that there would be no end to it, and I confess, I had moments of despair when not finding any matches in my material, but at some point.. they started coming! And my colleagues were always there, encouraging me too keep going when I couldn’t find what I was looking for, and dancing with me through the tea-room once I actually found it. Pam Walton, thank you for helping me with all those mandrill thin sections, as well as for being a ‘lab-mum’ to all of us. Thanks to my close friends Syatirah Abdullah, Nieka Adhera, Anas Al Aubaydi and especially Nadia Rostami, who are extremely intelligent and inspiring researchers, and incredible friends.
Although I spend a lot less time at the Anthropology department in Durham, luckily in my final year I had the chance to see a bit more of my colleagues there. Thank you to all of my fellow primatologists, for your comments and advice at Primatology group on chapter drafts, conference posters and for the brainstorm-sessions. It has been a great community to be part of and I have learned a lot from listening and chatting to all of you. Many thanks to Trudi Buck for the chats and for giving me a sense of direction when I lost focus. I thank Stefano Vaglio for his healthy perspective on (academic) life and for our catch-ups and diners. I thank Don Reid and Chris Dean for their advice and encouraging words, they meant a lot to me! I thank John Forster and Kate Payne for being patient with me every time I came by with paperwork and thanks to my progression panel for their advice. I also thank my friends down in the Bio-Anth/Physical Activity lab for their companionship. I’ll miss that office!

Additional to friends and colleagues from research related settings, I also owe a lot of gratitude to my flatmates (The Moorlands Family), my friends at University College, Jaqui and Terry McDonough, and everybody that made me feel so at home in The North East. You made me fall in love with this part of the world. A special mention here goes out to my closest friend Jason Nadell who I met the first week of my arrival in Durham, but it feels like we grew up in the same street. This guy deserves a statue.
Furthermore I thank my Dutch friends for the many visits, calls and cards, ‘out of sight, out of mind’ is anything but true. Thanks for sticking it out with me.
And last, but all but least; I would like to thank team Lemmers: My parents Charles and Carien, my sister Jacqueline and my brother Daan, to whom I dedicate this thesis. Thank you for encouraging me to follow my dreams, for your advice and unconditional love and support, while always reminding me of Ithaca.

To my loving family: Charles, Carien, Jacqueline and Daan

"As you set out on your journey to Ithaca,
pray that your journey filled with adventure,
filled with discovery.
May there be many summer mornings
when with what pleasure, with what joy,
you enter harbors never seen before.
And may you go to many cities to learn
and learn from those who know.
But always keep Ithaca in your mind.
You are destined to arrive there."

- On Odysseus' travels -
Excerpt from C.P. Cavafy's "Ithaca", 1911

Chapter 1: Introduction

1.1 Life history theory

Life history theory explains the scheduling of key life history events in species, such as age at weaning, age at menarche in females and age at first reproduction, but also gestation period, length of inter-birth intervals and overall lifespan, as being shaped by the forces of natural selection (Charnov & Berrigan, 1993; Janson & Van Schaik, 1993; Promislow & Harvey, 1990). Individuals have finite resources and the scheduling of key events in the life course is determined by natural selection, optimising the allocation of resources to competing requirements of growth, reproduction and maintenance (Stearns, 1989). Trade-offs between competing demands for resources create a unique assemblage of characteristics for every species, in response to environmental conditions, mortality schedules, and the abundance of resources. For example, trade-offs occur between effort invested in current and future reproduction, and between the quality and the quantity of offspring (Hill & Kaplan, 1999). Life history strategies lie on a continuum between early, frequent and prolific reproduction on the one hand and delayed, infrequent and limited reproduction on the other.

In comparison to mammals of similar body size, primates have slow life histories (Charnov & Berrigan, 1993; Harvey & Clutton-Brock, 1985; Lindstedt & Calder, 1981; Mumby & Vinicius, 2008; Stearns, 1983; van Schaik & Isler, 2012; Zimmerman & Radespiel, 2007). They have long juvenile periods, low fertility and mortality, large neonates, large costly brains and long life spans (Ross, 1998). Although earlier maturity and high fertility would seem better for fitness (Lewontin, 1965; Cole, 1954), delayed maturity allows for an extended period of brain growth and learning (Bogin, 1990; Leigh, 2004; Leigh & Park, 1998). Primates have large brains relative to their body size which are extremely costly and may serve as a regulator of their slow life history (Martin, 2003, review in Jones, 2011). Primates' delayed maturity and low fertility can also be understood as adaptations to uncertainty in juvenile recruitment (Charnov, 1991; Gadgil & Bossert 1970; Jones, 2011; Schaffer 1983). By delaying reproduction, mothers invest in their own survival and reduce their reproductive effort at any given age to achieve more reproductive events overall (Jones, 2011). Furthermore, primates' low risk of death before reproduction and general low mortality favour a prolonged period of growth investment (Charnov & Berrigan, 1993).

Although generally classified as 'slow', there is also distinct variation in life history pace among primates. The cercopithecoids, the Old World monkeys, are a good example of being 'fast among the slow'. Compared to hominoids, who are known for their slow paced life histories (van Schaik & Isler, 2012), cercopithecoids have short gestation periods, wean their infants early and have short interbirth intervals, meaning they have a high intrinsic rate of population increase (Napier & Napier, 1970). This makes them good at producing offspring successfully under unstable, highly seasonal environments with changes in food abundance (Ross, 1988). Cercopithecoids have eclectic diets, and their bilophodont dentition indicates increased dependence on folivory (Napier & Napier, 1970; Temerin & Cant, 1983; Walker & Murray, 1975), which allows them to subsist on generally lower quality foods (e.g., Bennett & Davies, 1994; Temerin & Cant, 1983) and with that, flexibility in their geographic distribution (Jablonski et al., 2000). Due to limited phylogenetic differentiation, cercopithecoids acquired fewer diverging specialisations than any other major group of primates, including their fast life histories relative to other primates (Jablonski & Kelley, 1997). The number of cercopithecoid species, their dense populations and their geographic distribution shows how successful they have been in adapting to demanding environments (Andrews, 1981).

Life history trajectories can vary distinctly among individuals of a single species according to their strategies for optimize growth, maintenance and reproduction (Lee, 1996; Borries et al., 2001), such as for males and females (Dixson, 2012). Life history variables such as gestation length and neonatal mass and the timing of weaning often show limited variation among the sexes of a species (van Schaik & Isler, 2012). However, sexual differences may arise during growth and development which in some species can be extreme (e.g., Clutton-Brock, 1988; Setchell et al., 2001). These differences are generally the result from the differences in strategies and priorities between the sexes for passing on genes to the next generation (Hrdy, 1979; Palombit, 2014; Smuts & Smuts, 1993; van Schaik & Janson, 2000; van Schaik & Isler, 2012). Female primates carry the energetic burden of gestation and lactation, as conventional among mammals, but additionally keep on investing in their infants through a long period of physical and social care (van Noordwijk, 2012). In contrast, the amount of male parental care is highly variable among primates (Wright, 1990). In many group living primates, male-infant investment post-siring, if any, is limited to protecting offspring from threats as infanticide (Hrdy, 1979; Laidre & Yorzinski, 2008; Palombit et al., 2000; van Schaik & Janson, 2000). When a primate species is sexual dimorph, a result of differences between the sexes in the duration or rates of growth, or a combination of these (Leigh, 1992; Shea, 1986), there will be differences between the sexes in age- specific reproductive output and mortality profiles, and there will be more variation in reproductive success among males than among females (Clutton-Brock, 1988). This leads to a large difference between male in female timing of investment in own growth compared to

investment in reproduction. As a result, the timing of life history events as reaching sexual maturity and first reproduction can vary drastically between a male and female of the same species.

Studying primate life history is fundamental to understanding primate evolution (e.g., Lee, 1996; Borries et al., 2001; Setchell 2006), but the sequence and timing with which life history adaptations arose remains subject to debate (e.g., Macchiarelli et al., 2006; Smith, 1991). We can determine some aspects of the scheduling of life history events, such as weaning and first reproduction, from observations of live animals (e.g., Setchell et al., 2002a, 2005, 2006), but this is difficult for primates living in dense rain forests, and impossible for extinct primates. We therefore need proxies from which data on the scheduling of life history events can be approximated. One such proxy is the dentition.

Teeth are the hardest tissue in a species' body and due to their highly mineralised character, they can stay preserved for a long time after death and under extreme conditions (e.g., Guatelli-Steinberg, 2016; Hillson, 1996, 2014; Irish & Scott, 2015). Once formed, teeth remain unchanged throughout life, apart from wear, breakage or pathology since, unlike bone, teeth do not remodel (Chiego, 2014; Nanci, 2003). Teeth have a daily clock built into the layered structure of their tissues, recording incremental growth (e.g., Asper, 1916; Boyde 1963, Boyde, 1989, Antoine et al., 2009; Dean & Lucas, 2009; Dean, 2006; Dean et al., 1993; Dirks, 1998, 2018; Reid & Dean, 2006; Reid & Ferrell, 2006). The timing of tooth development and eruption is closely linked to mammalian life history, and has long been a topic of interest in primatology (Smith, 1991; Smith, 1991; Smith, 2000). To attain a better understand of how the analysis of primate teeth can be used as a proxy for investigating primate life history, and how it can contribute to the wider debate on the evolution of life history, I direct this thesis to studying markers in primate enamel and dentine visible on a microscopic level that may relate to stress related to life history events. When physiological and hormonal homeostasis (the bodies' optimal state) is disrupted, for example during a period of illness or psychological stress, the hypothalamic-pituitary-adrenal axis is activated, and hormones such as glucocorticoids are released into the bloodstream, enabling the individual to cope with demanding and novel situations (Sapolsky et al., 2000; Sapolsky, 1987). The rhythmically deposited dental matrix is sensitive for disruption to homeostasis and can record stress in the shape of accentuated lines visible in enamel and dentine (Asper, 1916; Dirks et al., 2002; Goodman & Rose, 1990; Macho et al., 1996; Risnes, 1998; Wilson & Shroff, 1970). Teeth might therefore also be able to contain signs of stress related to life history events (Dirks et al., 2002). I focus my thesis on a well studied cercopithecoid primate, the mandrill (*Mandrillus sphinx*), analysing the dentitions of individuals with known life histories (e.g., Setchell, 2016; Setchell & Wickings, 2004; Setchell et al., 2006). To explain the context of this study, I will first give an in-depth review of tooth anatomy and the incremental markers of tooth growth (1.1), with a

focus one type of marker visible in tooth sections, known as accentuated lines, which are thought to relate to various types of stress (1.2). After that, I will review how tooth development relates to life history and how it has been employed to study the evolution of life history through fossil remains (1.3). After that, I will introduce how stress related to life history might show up in teeth, and how these accentuated lines therefore might function as a proxy for interpreting life history from teeth (1.4). After that, I will set out why I choose mandrills as the species for this study and review the literature on mandrill life history (1.5). I finish this introduction by setting out the structure of this thesis and how I intend to examine the correlation between stress, life history and dental development in mandrills (1.6).

1.2 Tooth anatomy and dental development

The timing of the development of a whole dentition is linked to a species' life history (Dirks & Bowman, 2007; Dirks, 2018; Smith, 1991; 2000; Smith, 2013). However, to explain this link, I first introduce general primate tooth anatomy. Enamel and dentine develop through rhythmic matrix secretions by enamel- and dentine-forming cells. This rhythmic patterning is similar to the shell formation of marine organisms and the layered structure visible in tree trunks (Neville, 1967). Primate dentitions consist of deciduous and permanent teeth whereby deciduous teeth commonly develop prenatally, and crowns mineralise before birth, whereas all permanent teeth, except the first permanent molars, start to form after birth (Swindler, 2002). Numerous specific aspects of odontogenesis are not yet fully understood, but its general pattern is well understood (Chiego, 2014; Nanci, 2003).

Apart from timing and duration, the general process of tooth development (odontogenesis) of deciduous and permanent teeth are very similar (Chiego, 2014). All teeth develop as single anatomically distinct units with four types of tissue: enamel, dentine, pulp and cementum (Figure 1.1). Enamel is the protective material covering the crown of a tooth and is the hardest tissue in the body (Figure 1.1). It consists of 95% inorganic hydroxyapatite and 4% water and 1% organic matter (Eisenmann, 1994). Hydroxyapatite is a crystalline calcium phosphate, also present in dentine, cementum and bone. The organic component of enamel is the protein enamelin, comparable to the protein keratin in skin. This composition makes enamel very resistant to fractures during food processing. Enamel is the only part of the tooth exposed to the oral environment and protects the softer and more vulnerable underlying tissues (Nanci, 2003; Newman et al., 2011). Once fully mineralised, enamel does not undergo any changes and can only break or decay. Dentine makes up

the body of the tooth (Figure 1.1). It is a living, sensitive tissue generally not exposed to the oral environment; crown dentine being covered by enamel and root dentine covered by cementum, periodontal ligaments and the alveolar bone. Once mineralised, dentine is composed of 70% inorganic hydroxyapatite crystals, 20% organic collagen fibres and 10% of water and a small amount of protein(Chiego, 2014). Due to its lower mineral content, dentine is softer than enamel, which allows mastication without fracturing the crowns. Dentine is divided into primary dentine, the major component of the crown and root, secondary dentine, which deposits internally once a tooth comes into occlusion, and tertiary or reparative dentine, which forms as a response to lesions. Inside the dentine is the tooth's pulp chamber. Pulp is a soft connective tissue which contains thin walled blood vessels, nerves and nerve endings (Torneck, 1994) (Figure 1.1). Finally, cementum forms around the roots, protecting the root dentine and anchors the tooth to the periodontal fibres, which keep the tooth in place (Nanci, 2003) (Figure 1.1).

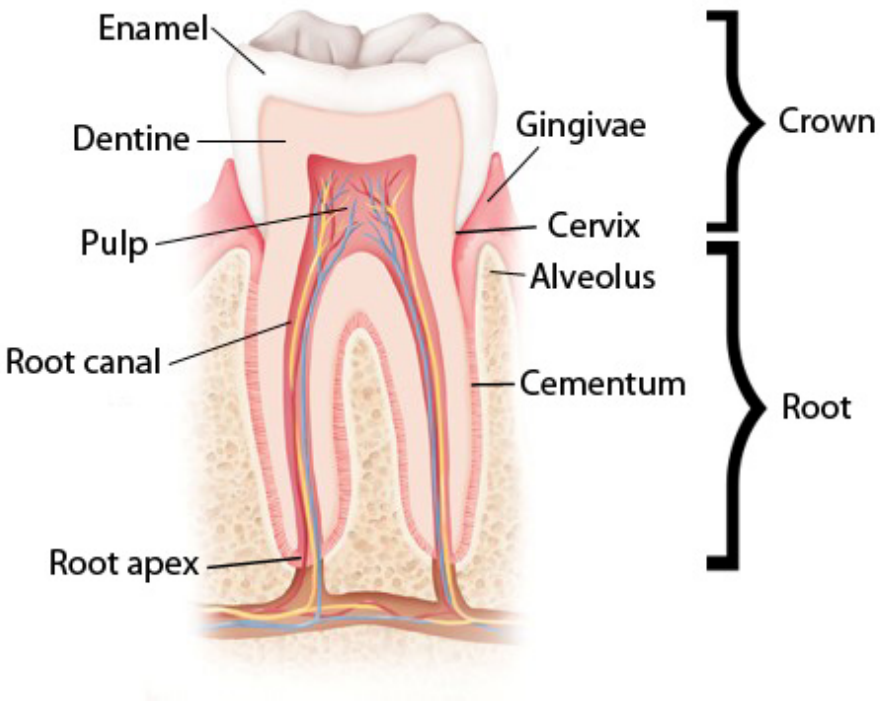

Figure 1.1: General tooth anatomy, indicating the four primary types of dental tissue: enamel, dentine, pulp and cementum. Adapted from Nanci, 2003.

All four types of dental tissue develop from the interaction of two types of cells: the oral ectodermal cells lining the embryonic oral cavity, and the underlying mesenchymal cells, which start from the dental papilla (Berkovitz & Moxham, 1981; Chiego, 2014) (Figure 1.2). Teeth initiate by proliferation of the ectodermal cells overlying specific areas of the oral ectoderm, resulting in the development of the dental lamina. The dental lamina develops into a sheet of epithelial cells that pushes into the

underlying mesenchyme around the perimeter of both the maxillary and mandibular jaws. This dual composition will eventually result in the formation of enamel deriving from the ectoderm and dentine, pulp, and cementum deriving from the mesoderm. Although tooth formation is continuous, early development is characterised by a series of distinguishable stages: the bud, cap, and bell stages (Figure 1.2), defined according to the shape of the ectodermally derived enamel organ, apposition, the phase of hard tissue formation, the maturation stage during which the crown completes and calcifies, and root formation and tooth eruption.

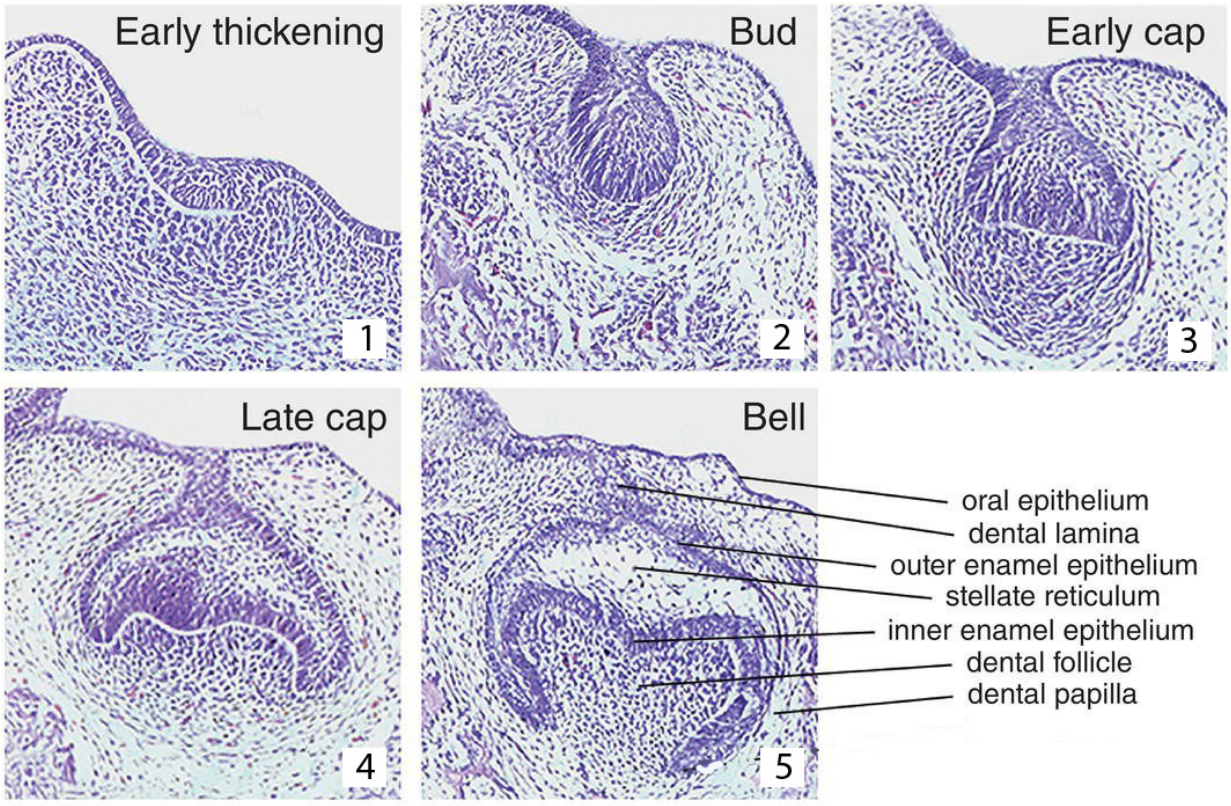

Figure 1.2: Histological view of tooth development: bud, cap and bell stages (adapted from Cobourne & Sharpe, 2003).

Preceded by initial thickening of the oral ectoderm (Figure 1.2, Stage 1), the initial bud stage is characterised by a rounded, localised growth of ectodermal cells surrounded by proliferating mesenchymal cells (Dassule & McMahon, 1998) (Figure 1.2, Stage 2). During the bud stage, tooth buds form at the leading edge of the dental lamina. These will eventually become the deciduous teeth. After the deciduous teeth develop from the buds, the leading edge of the lamina – now called the successive lamina – continues bud formation, which will eventually lead to the formation of the permanent teeth (Chiego, 2014; Nanci, 2003). The successive lamina continues posterior into the elongating jaw. The buds which form the incisors, canines and premolars of the permanent teeth will eventually replace the deciduous teeth. Additional tooth buds develop behind the deciduous dentition, which will become the adult molars, adding to the length of the tooth row instead of

replacing deciduous teeth. In general, the tooth buds form anteroposterior in coordination with the growing jaws. The timing of the development of the deciduous and permanent tooth buds and growth of the jaws and facial bones are therefore closely linked (Sperber, 1989).

As the tooth buds become bigger, the enamel organ develops an indented surface and covers the connective tissue, known as the dental papilla, marking the onset of the cap stage (Simmer et al, 2010) (Figure 1.2, stage 3). An enamel knot becomes visible in the epithelium influencing the future shape of the tooth because of a gene expression series that alternates between the epithelium and the mesenchymal tissue. Enamel epithelial cells on the cap's internal surface become more columnar, while the outer enamel epithelial cells remain cuboid. The mesenchymal cells start to proliferate, completing the dental papilla beneath the internal enamel epithelium and the dental follicle. The ectodermal cells subsequently differentiate to become the enamel organ, remaining attached to the lamina. The mesenchyme now forms the dental papilla, which will later become the dental pulp (Nanci, 2003) (Figure 1.2, Stage 4).

Teeth reach the bell stage after further growth of the dental papilla and the enamel organ, which now has the outline of the tooth they are eventually going to form (Figure 1.2, stage 5). During the cap stage, the enamel organ has four distinct layers overlying the dental papilla: the outer enamel epithelium, the stellate reticulum, the stratum intermedium, and the inner enamel epithelium. The outer enamel epithelium is one-cell layer functioning to keep the shape of the enamel organ (Berkovitz & Moxham, 1981). The stellate reticulum and the stratum intermedium, overlying the inner enamel epithelium, protect the developing tooth and supply it with nutrients. In the later bell stage, the inner enamel epithelium cells become increasingly columnar in shape and differentiate to become pre-ameloblast and then ameloblasts: the cells that will form the enamel of the tooth crowns. Simultaneously, an adjacent layer of cells in the mesenchyme starts to differentiate into pre-odontoblasts and then odontoblasts: the cells that will form the dentine of the tooth crowns and roots (Chiego, 2014; Harris, 2016).

Dentinogenesis, the process of dentine formation, is induced by the pre-ameloblasts differentiating from the inner enamel epithelium to start forming matrix, which turns the pre-ameloblasts into fully functioning ameloblasts that produce enamel matrix. Dentinogenesis therefore always precedes amelogenesis by a few days. With dentinogenesis, the tooth enters the stage of apposition: hard tissue formation. As the odontoblasts enlarge they develop a process at their proximal ends, adjacent to the enamel dentine junction (Chiego, 2014; Nanci, 2003). Simultaneously, the dental papilla differentiates into dental pulp. Gradually the odontoblasts move towards the pulp and their

processes elongate. The odontoblasts now start to deposit a matrix of a meshwork of collagen fibres along the enamel dentine junction, called predentine. The predentine is deposited incrementally, indicating a daily rhythm in tissue formation. During the daily build-up of predentine, the odontoblast processes continue to elongate and form dentinal tubules**,** producing the distinct appearance of the dentine matrix, and extra cellular matrix forms around the tubules.

Matrix formation starts at the cusp tips (Figure 1.3), and as further increments form, more odontoblasts activate along the enamel dentine junction (Figure 1.3). Within 24 hours, the deposited collagenous matrix calcifies by the deposition of calcium phosphate (hydroxyapatite) crystals, turning predentine into dentine. Calcification starts as crystal deposition in small vesicles on the surface and within the collagen fibres. Then, the crystals spread through the matrix, enlarge and merge until the matrix is completely calcified and mineral density increases.

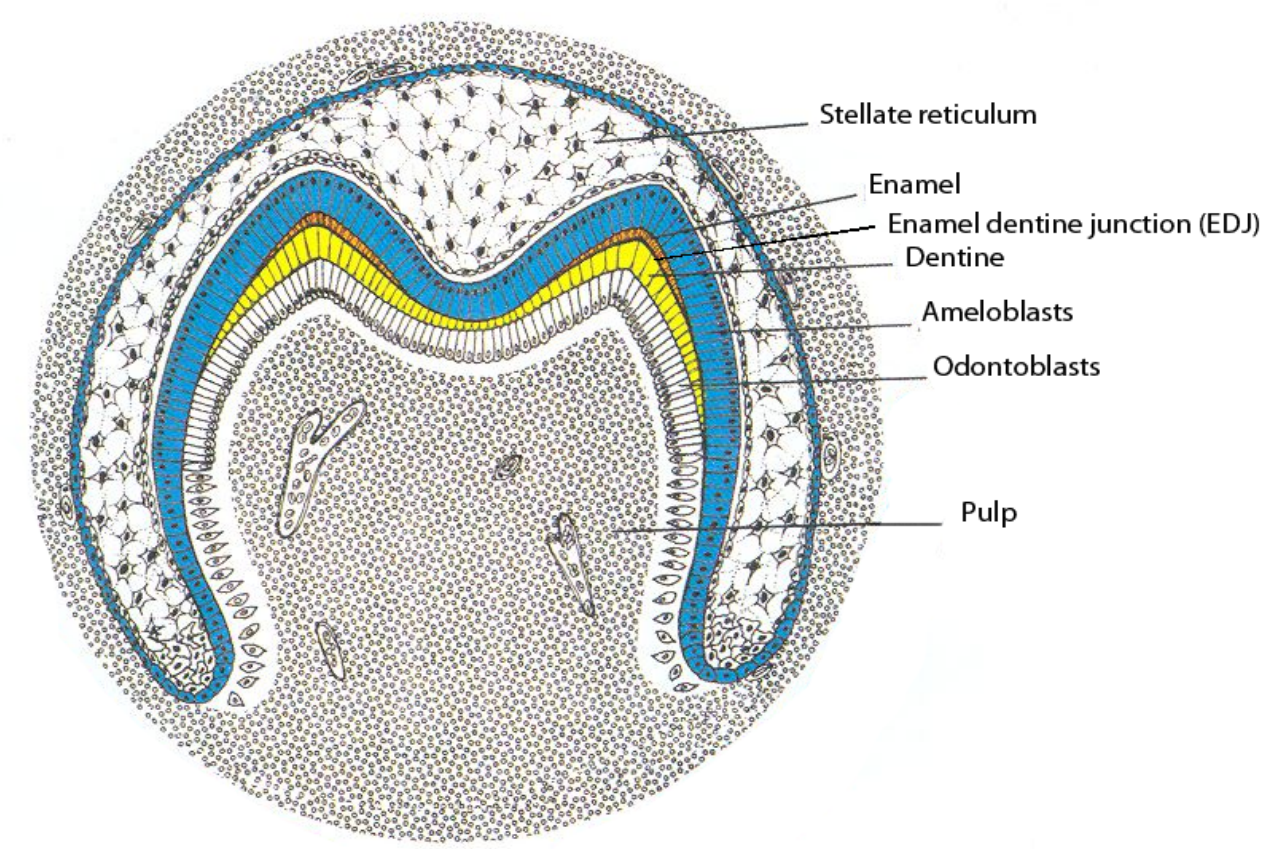

Figure 1.3: Odontogenesis and amelogenesis. Thin layers of dentine and enamel are secreted by the overlying odontoblasts and ameloblasts at the cusp tips, lying close together. The zone where enamel and dentine tissues touch is the enamel dentine junction (EDJ). Image adapted from (Nanci, 2003).

Ameloblasts begin enamel matrix deposition once a few micrometres of dentine have formed, establishing the enamel dentine junction (Figure 1.3). The ameloblasts are positioned in rows with cell-to-cell attachments at their proximal and distal ends, mirroring the row of odontoblasts (Figure 1.3). The attachments keep the cells connected when they move away from the odontoblast line while depositing matrix. Short, cone-shaped processes, known as Tomes' processes, develop at the apical ends of the ameloblasts, which deposit the enamel matrix. The enamel matrix forms in continuous rods, also known as prisms, from the enamel dentine junction. These form in daily increments, at the same time as dentine deposition, until they reach the final surface of the enamel. The rods are the enamel equivalent of the dentine tubules. Enamel rods are keyhole shaped, interlocking with each other. Each rod is formed by four ameloblasts: one forms the head; two form the neck and one forms the tail. Enamel rods form nearly perpendicular to the enamel dentine junction and curve slightly towards the cusp tip. The rods also run almost perpendicular to the enamel's outer surface but are gnarled and tangled near the cusp tips. Throughout the cusp, groups of rods bend at a slightly different angle to adjacent groups when viewed in polarised light. This is seen as light and dark bands of rod groups, termed Hunter-Schreger bands. The bending and gnarling of the enamel is thought to give the enamel strength during mastication and biting (Chiego, 2014; Nanci, 2003).

Initially, a few ameloblasts activate and start matrix deposition. More ameloblasts activate as the process continues until full cusps are formed. Matrix formation starts at the tips of the cusps, forming the cuspal enamel matrix, and then moves laterally to the sides of the crowns (Figure 1.3). Growth of individual cusps by incremental deposition continues until the cusps coalesce in the inter-cuspal region of the crown. Like dentine, enamel matrix mineralisation starts shortly after its deposition, with the first matrix deposited being the first enamel to mineralise. Small mineral crystals enter the enamel matrix accounting for 25% of the total amount of mineral in enamel. After deposition, crystals grow and turn the matrix into mineral, replacing organic material. Mineralisation happens gradually, but it is unknown how much time separates deposition and calcification (Suckling, 1989).

Crown formation completes during the maturation stage. At the cervix (Figure 1.1), the point where enamel deposition ends, an extension of the inner and outer enamel epithelium forms as a double layered root sheath. The lengthening root sheath outlines the shape of the root, whereby the inner cell layer of the root sheath induces odontoblasts of the dental papilla to differentiate and form root dentine. Shortly after this, cells from the dental sac differentiate to cementoblasts, producing cementum matrix, which subsequently calcifies to become cementum that seals the root surface.

Dentinogenesis continues until the complete root length is reached. The root apex then thickens, leaving a narrow opening of 1-3 mm to allow nerves and blood vessels to reach the pulp chamber (Figure 1.1). During root formation, the tooth moves in the jaw to erupt through the alveolar bone and gums. As more teeth develop and erupt, the facial bones remodel to make space for the adult dentition. The exact mechanism of tooth eruption is complex and not yet fully understood (Chiego, 2014; Kjær, 2014; Marks & Schroeder, 1996). The dental follicle, the supply and distribution of nerve fibres to the tooth, bone tissue surrounding the tooth, and the general growth conditions in the body all play a role in eruption (e.g., Kim et al., 2008; Kjær, 2014; Wise & King, 2008; Wise et al., 2011), but none of these factors are decisive by themselves for the initiation of eruption, the following eruptive movements and to end the eruption process (Gowgiel, 1961; Kjær, 2014; Marks & Schroeder, 1996). Root formation continues after eruption until the tooth comes into occlusion and its periodontal ligaments are fully developed.

Eruption is a continuing process, and although this makes it difficult to define clear-cut stages, there are a number of steps in the process which are often distinguished from each other. Alveolar emergence or alveolar eruption is the appearance of a tooth through the crest of the alveolar process. This happens gradually, with a small aperture visible in the jaw bones which subsequently widens until it can accommodate the diameter of a full crown (Hillson, 1996). Alveolar emergence can be observed in dry bone specimen or via radiographs but cannot be assessed by eye on living individuals. We can define alveolar emergence for dry specimens as the first appearance of tooth cusps above the alveolar crest (Hillson, 1996). Gingival emergence, or clinical eruption, is the appearance of teeth through the gingivae. It is used for determining eruption status in living individuals since it can easily be assessed without the use of scanning devices (Hillson, 1996). Again, this is a gradual process where the tips of the cusps appear before the bulk of the occlusal surface. Finally, occlusion is the stage at which teeth come into place and into contact with their opposites (Hillson, 1996). After reaching occlusion, a tooth can still move, which might be related to compensation for wear or external pressure (Chiego, 2014; Hillson, 1996; Nanci, 2003).

Due to the incremental deposition of the matrix of enamel and dentine in the secretory phase of dental development, distinct patterning is visible in both tissues on a microscopic level (e.g., Boyde, 1964; Retzius, 1837). The different markings visible in human and non-human primate enamel and dentine were first described by Retzius (1837), followed by Owen (1845), Andresen (1898) and von Ebner (1902, 1906) and have a long research history establishing their exact spacing, formation, meaning and application. The lines in enamel and dentine are strongly connected to each other. One set of rhythmic lines forming in both tissues relates to a 24-hour cycle (circadian) of tissue secretion

and deposition, which I refer to as daily increments. The second set of rhythmic lines in both tissues consists of regularly spaced lines with a rhythm of multiple days with a complex aetiology. I refer to these as the longer period lines. I refer to a third set of lines of irregularly spaced lines visible in histological sections of teeth and related to physiological stress as accentuated lines. I now review these three different lines, their manifestation, aetiology and relation to life history.

Daily increments are commonly referred to as cross-striations when observed in enamel (Figure 1.4, panel 3). They represent a regular variation in the rate of matrix secretion during a 24 hour rhythm in primates (Boyde, 1989). Slight variation in increment deposition by the ameloblasts' Tomes' processes create alternating angled and horizontal interfaces of the increments which appear as alternating light and dark bands through light transmitted microscopy. The transition from one daily increment to the next has a slightly different mineral composition (Boyde, 1989) and is therefore also observable using micro-radiography and in synchrotron radiation microscopic computed tomography (Micro-CT) (Hillson, 2014). The size of a cross-striation (also referred to as daily secretion rate, (Smith, 2006, 2008) varies with tooth type, tooth size and by region in the cusp. The cross-striations are present throughout the prismatic enamel, but their visibility often varies throughout the tooth. Their visibility is also very dependent on section preparation and thickness. Similar daily increments are present in dentine, most commonly referred to as Von Ebner lines (Figure 1.4, panel 4). The daily secretion along the dentine tubules is related to the functioning of the odontoblast-processes. Von Ebner lines are the equivalent of the enamel cross-striations but are much more difficult to observe via light transmitted microscopy than cross striations and the transition from one daily increment to the next is not as distinct (*Pers obs*, *Pers Comm C. Dean*). Although the exact aetiology of daily increments is still debated (e.g Guatelli-Steinberg, 2016; Hillson, 2014) their formation is related to the circadian clock, an endogenous timekeeping mechanism common in many biological organisms (FitzGerald, 1998). The circadian clock has a stable rhythm of 24 hour which allows organisms to coordinate their behaviour and physiology with environmental changes corresponding with the daily day–night cycle (Kronfeld-Schor et al., 2013). The clock influences circadian hormonal secretion, sleep-wakefulness rhythms, day and night shifts in body temperature, the blood's acid-base balance and influences central and local cell rhythm generators (Boyde, 1989; Dean & Scandrett, 1996; Ohtsuka & Shinoda, 1995; Okada, 1943). The circadian clock has evolved to optimise the economy of biological systems in an organism and allows the body to react predicatively, rather than purely reactively, to regularly occurring stimuli triggered by the 24 hour day and night rhythm (Kronfeld-Schor et al., 2013). Circadian rhythms in hard tissues formation, including teeth, are thought to be under control of this oscillation (Antoine et al., 2009; Bromage, Hogg et al., 2012; Dean, 2006). There is often a faint mark visible within daily increments known as intradian lines, probably resulting from

a 12 hour rhythm (Smith, 2006). However, these marks are rarely consistently visible and may be artefacts of section orientation and plane of focus (Hillson, 2014), and I therefore do not discuss them further in this thesis.

In enamel, the often strongly pronounced longer period lines are called striae of Retzius, Retzius lines or brown striae of Retzius (e.g., Antoine & Hillson, 1986; Hillson, 2014), since they look dark compared to the surrounding enamel when observed via light transmitted microscopy (Asper, 1916; Boyde, 1964; Dean, 1987) (Figure 1.4, panel 1). Retzius lines run parallel to each other, cutting diagonally across the prism boundaries from the enamel dentine junction in an angle up to the crown's surface (Hillson, 2014). On the outside of the tooth, Retzius lines correlate with shallow depressions called perikymata grooves, encircling the outside of a crown (Risnes, 1985a, 1985b).The Retzius lines are continuous through the enamel but clearest directly under the crown surface. The equivalent of the Retzius lines in dentine are commonly referred to as Andresen lines (Andresen, 1898; Dean & Scandrett, 1996). They are often not as distinct as the Retzius lines, but visible in patches as a series of dark lines crossing the dentine tubules (Figure 1.4, panel 2) and visible on the root surface as periradicular bands (Dean, 1995). Longer period lines are thought to represent variations in matrix secretion (Hillson, 2014) and are slightly less mineralised than the rest of the prismatic enamel (Chiego, 2014; Hillson, 2014). Fracture lines in enamel often follow the direction of the Retzius lines (Boyde, 1989). The formation mechanism behind the longer period lines could therefore be like that of the daily increments on a cellular level. They are, however, much more pronounced and their aetiology cannot be explained by the circadian clock since they form according to a longer period rhythm. Two adjacent longer period lines are separated by several daily increments, called the periodicity (Antoine et al., 2009; Bromage, 1991; Reid & Ferrell, 2006; Risnes, 1986). The periodicity is thought to be constant throughout the dentition of an individual, although variation has recently been reported between the periodicity of the deciduous and adult dentition of the same individual (Mahoney et al., 2016; 2017). There is limited intra-specific variation in periodicity, but inter-specific variation can be substantial. The periodicity of an individual's teeth may relate to the Havers-Halberg Oscillation, a biorhythm that regulates growth in mammals and thought to be related to a species' adult body mass and life history traits (Bromage et al., 2009, 2012). The Havers-Halberg Oscillation is also hypothesised to be responsible for the rhythmic formation of concentric lamella in the Haversian systems in bone microstructure. Although the exact aetiology of this biorhythm is not yet fully understood, it is thought to be influenced by an individual's resting metabolic rate (Bromage et al., 2016).

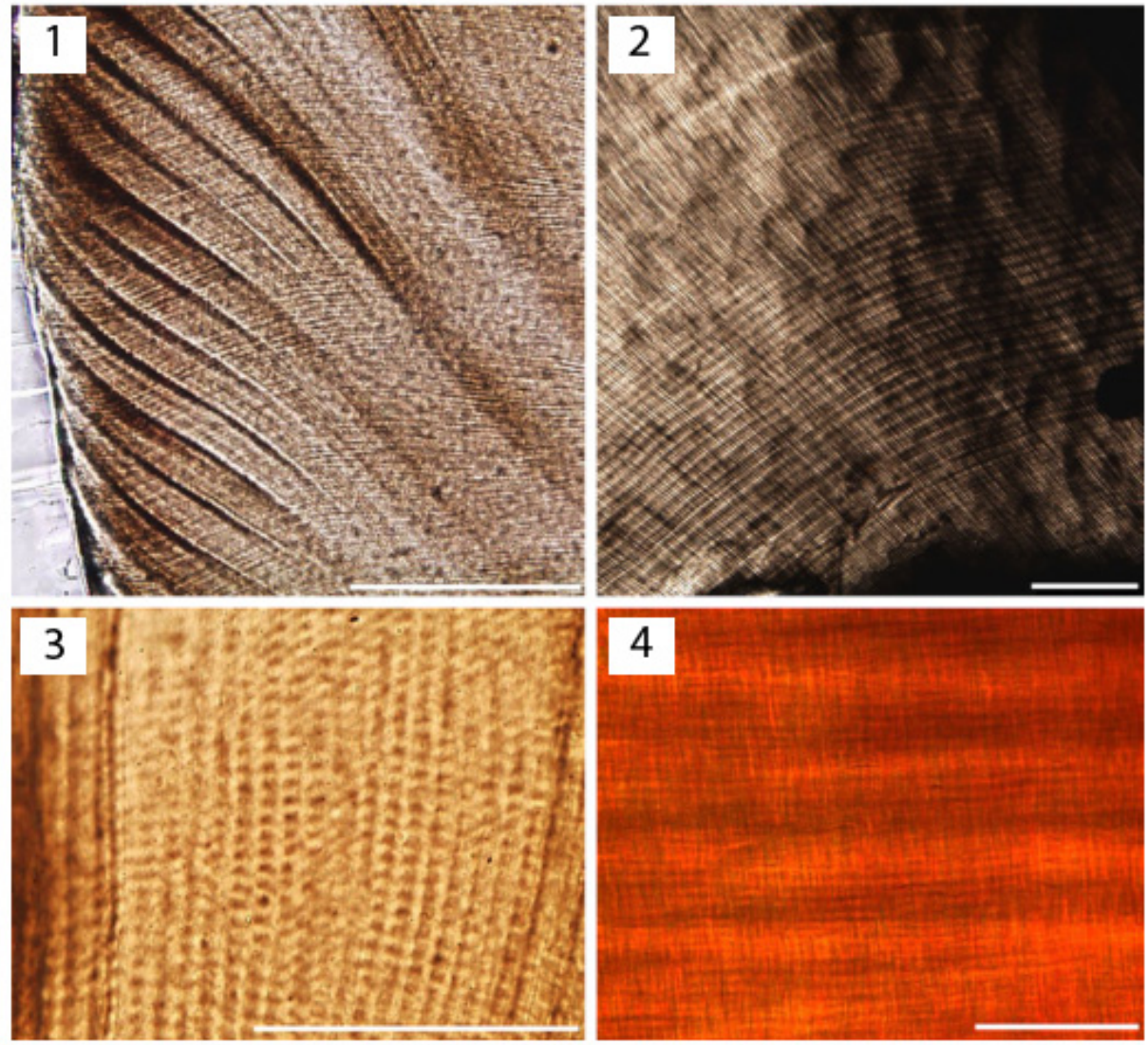

Figure 1.4: Micrographs showing longer period and daily lines in enamel and dentine: (1) Retzius lines, representing a longer period rhythm in enamel (Scale= 0.2 mm). (2) Andresen lines representing a longer period rhythm (Scale = 0.2mm). (3) Cross-striations, representing daily rhythm in enamel (scale = 0.1 mm) (4) Von Ebner lines, representing a daily rhythm in dentine (scale = 0.05mm). Image adapted from Smith, 2006.

Accentuated lines are pronounced, irregularly spaced and superimposed on the daily and longer period lines. They can, but do not always, coincide with the longer period lines. They appear in all teeth forming simultaneously, indicating their linear and chronologic nature (Sarnat & Schour, 1941; Goodman et al., 1984). Although most commonly referred to as accentuated lines, they are also known as accentuated striae of Retzius, Wilson bands or cluster bands (Goodman & Rose, 1990; Rose et al., 1978) when visible in enamel, contour lines of Owen in dentine (Bhaskar, 1991; Nanci, 2008), or hypomineralised bands and calciotraumatic bands (Kierdorf & Kierdorf, 1997; Kierdorf et al., 2000) in both tissues. These last two terms hint at their aetiology. Unlike the rhythmic formation of the daily and longer period increments, accentuated lines are caused by a disruption of ameloblast

and odontoblast activity during the normal process of tooth formation (Rose, 1977; Rose et al., 1978; Rudney & Greene, 1982; Rudney, 1983, Goodman & Rose, 1990) and are often described as regions of hypomineralisation (Amprino & Camanni, 1956; Goodman & Rose, 1990b; Hillson, 1996; Hollander, Applebaum, & Bodecker, 1933; Macho et al., 1996; Molnar & Ward, 1975; Norén, 1984; Rose, 1979; Weber & Eisenmann, 1971; Whittaker & Richards, 1978). Although some studies have reported disturbance during the mineralisation phase (Richards et al., 1986; Suckling et al., 1988; Milhaud et al., 1992; Fejerskov et al., 1994), accentuated lines are generally understood to be brief periods of disruption in enamel and dentine matrix secretion (Guatelli-steinberg, 2001; Hillson, 1996; Schwartz et al., 2006) or a change in prism structure during secretion (Goodman & Rose, 1990; Weber & Eisenmann, 1971; Whittaker & Richards, 1978; Wilson & Shroff, 1970).

Scanning Electron Microscopic (SEM) analyses (Kierdorf et al., 2000) on enamel revealed accentuated lines to be broad, hypomineralised incremental bands with varying types of abnormal structure and zones of aprismatic enamel (Figure 1.5, Kierdorf et al., 2000). These lines can be caused by short delays in the resumption of secretory activity by groups of ameloblasts or periodic constriction of prism diameters. However, they might also represent regions of absence of the prismatic structure and an increase in interprismatic enamel, or, in the most severe cases, abrupt cessation of matrix secretion (Kierdorf et al., 2000). Furthermore, SEM analysis indicated that disturbance happened from the pre-secretory to the secretory stage of amelogenesis, whereby the ameloblasts are obstructed from normal functioning. This happens when the Tomes' processes, the part of the cell that actually deposit the enamel matrix (Chiego, 2014), are not fully formed.

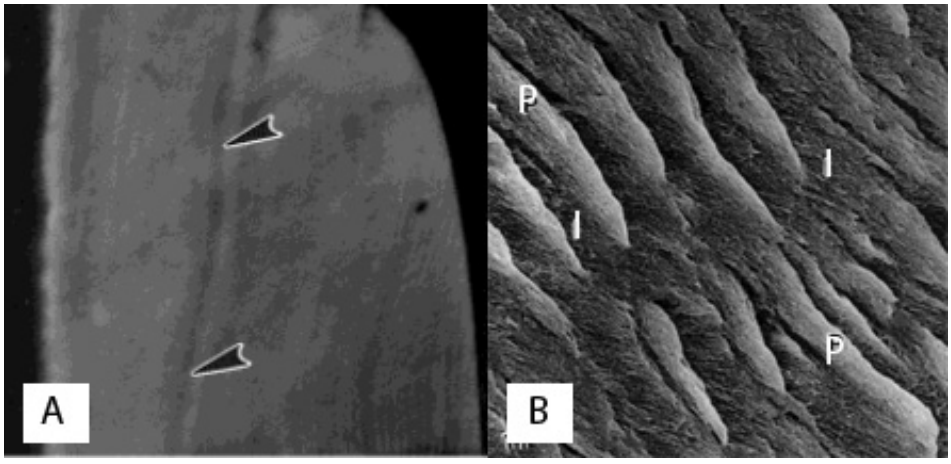

Figure 1.5: Microradiograph of wild boar premolar section. Arrows indicates broad hypomineralised band corresponding to period of fluoride exposure. (B) Scanning electron micrograph a third molar from same study. Accentuated line runs from lower left to upper right corner (P) showing increase in the volume of interprismatic enamel (I). x2,000 magnification. Image adapted from Kierdorf et al., 2000.

Normally, fully functioning ameloblasts have different growth regions for prismatic and interprismatic enamel on their Tomes' processes, laying down crystals (matrix) with their long axes perpendicular to the secretory cell surfaces. However, when the Tomes' processes morphology is impaired, aprismatic enamel can form instead of the normal prismatic structure (Kierdorf & Kierdorf, 1997; Kierdorf et al., 2000; Kierdorf et al., 1993; Woltgens et al., 1995). Aprismatic enamel is softer, more plastic and less mineralised than prismatic enamel (Chiego, 2014), and therefore, an accentuated line composed of mainly aprismatic enamel is hypomineralised in comparison to normal prismatic enamel. The actual mechanism behind accentuated line formation is similar to Risnes' explanation for the normal, periodic longer period rhythm of the Retzius lines (Risnes 1990, 1998). Risnes' SEM studies of normal, healthy human enamel indicated that the rhythmic longer period pattern of Retzius lines is caused by a periodic constriction in prism diameter where the interprism space expands at the expense of prisms themselves (Risnes 1990, 1998). Since the diameter of the prism reflects that of the prism-forming portion of the Tomes' process, Risnes attributed the Retzius lines to a rhythmic constriction of the Tomes' processes near their bases (Risnes 1990, 1998). If this is true, the accentuated lines are formed by the same mechanism as the longer period lines, but instead of reoccurring with a fixed rhythm, the constriction of the Tomes' processes is stimulated by an irregularly timed external 'stressor'. The driving forces behind the impairment of the Tomes' processes functioning, and the reasons for the formation of accentuated lines are diverse, but generally thought to be related to metabolic disturbances. Accentuated lines are therefore often referred to as 'stress lines'. However, to properly understand the nature of the accentuated lines, we need to take a closer look at the concept of metabolic disturbance and stressors and how they affect accentuated line formation.

1.3 Stress and accentuated line formation

Stress is a state of either real or perceived threat to homeostasis, the body's optimum state (Selye, 1973; Silverthorn, 2007; Tsigos & Chrousos, 2002). Homeostasis is maintained by the constant adjustment of biochemical and physiological pathways so that physiological systems function best, controlling the optimum state of blood pH, oxygenation, temperature and blood pressure (Selye, 1973; Silverthorn, 2007; Tsigos & Chrousos, 2002). A stressor can be any environmental perturbation which disrupts homeostasis (Silverthorn, 2007), or can refer specifically to a type of stimulus that requires an emergency energetic response (McEwen & Wingfield, 2003). Stressors can be physical, psychological, or both (Sapolsky, 1994b). Physical stressors could be fights or attacks, which require instant mobilisation of energy, muscle action and increased vigilance (Sapolsky, 1994a). Stressors like

illness, infection, or exposure to toxins can be accompanied by fevers, a rise in body temperature which can prevent the bodily functions from working optimally. Disruption of normal gut function leading to diarrhoea can affect the body's optimal pH due to loss of bicarbonate ions resulting in shifts in the acid-base balance, higher hydrogen ion concentrations and lower pH (acidosis) (Silverthorn, 2007). Similarly, long periods of acid loss from the stomach (e.g., through vomiting) can result in lower concentrations of hydrogen ions relative to bicarbonate ions and rising pH (alkalosis) (Dean & Elamin, 2014) leading to disruption of homeostasis. Stressors can also be psychological or social, such as a novel or unexpected event, requiring alertness and mobilisation of energy to ward off possible threats (Sapolsky, 1994b; Silverthorn, 2007).

The presence of a stressor and a threat to an individuals' homeostasis activates a complex range of behavioural, hormonal and physiological responses involving the endocrine, nervous, and immune systems, collectively known as the stress response (Romero, 2004; Sapolsky, 1987; Smith & Vale, 2006). The stress response is similar across vertebrates and different sources of stress lead to very similar hormonal and neural responses (Romero, 2004). Due to its consistency, this overarching stress response is known as the 'General Adaptation Syndrome' (Selye, 1973; Selye, 1936). The stress response is centrally controlled by 3 major glands: the hypothalamus, pituitary and adrenalin glands, forming the hypothalamic-pituitary-adrenal axis (HPA axis) (Figure 1.6). Together, these glands mediate the effects of stress by activating various behavioural and metabolic processes (Cyr & Romero 2008; McEwen & Stellar 1993; Sapolsky, 1992). The hypothalamus is the prime controller in activating components of the stress-response. It regulates the pituitary gland, which sends signals to the adrenal glands (situated on top of the kidneys) which then secretes glucocorticoids, glucagon, adrenaline and noradrenaline; the key hormones responsible for adaptation to the stressor (Munck et al., 1984; Yates et al., 1980). These hormones are therefore often referred to as 'stress hormones'.

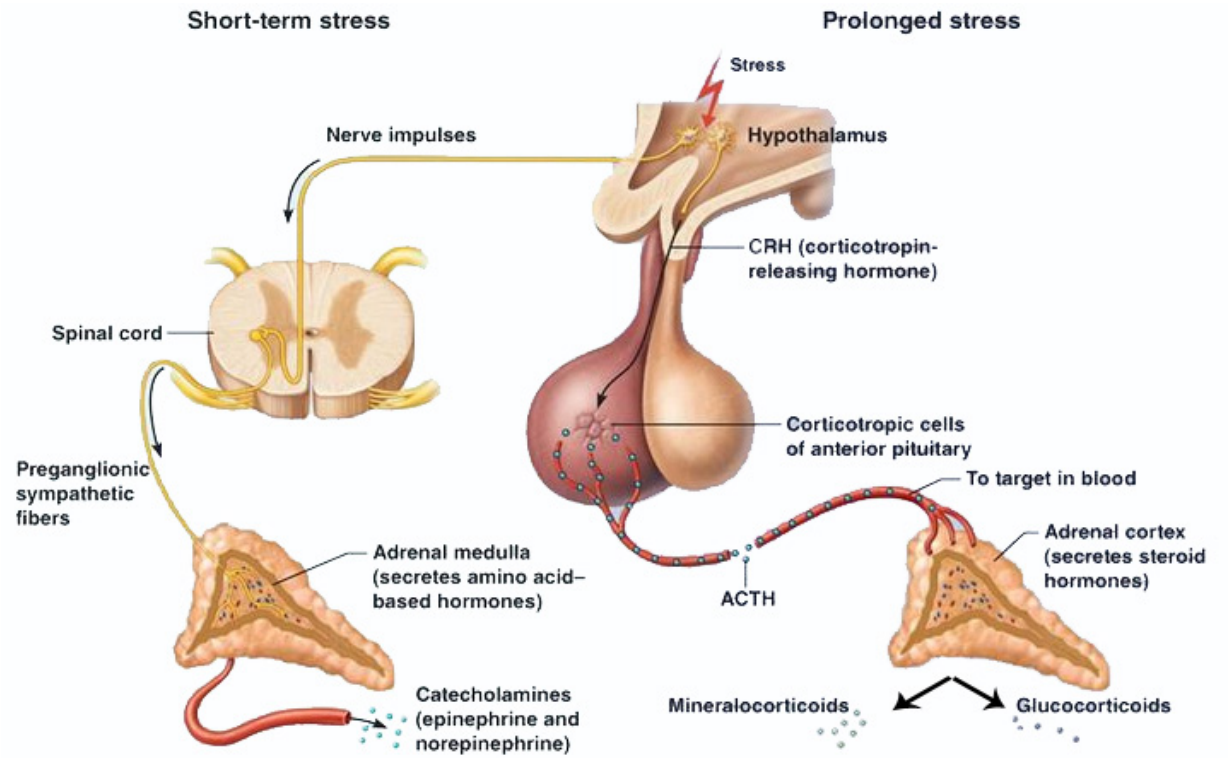

Figure 1.6: The HPA axis with the fast, short term stress responses via the sympathetic nervous system (left) and the delayed, prolonged stress response via the endocrine system (right). Image adapted from Pearson Education Inc., 2013

Stressors that require instant action are mediated by the sympathetic nervous system, which regulates the 'fight-or-flight' response in stressful situations to mediate vigilance and to mobilise energy instantly (Figure 1.6). The brain perceives stress and the hypothalamus sends quick signals to the adrenal glands via the sympathetic nervous system. This increases concentration of adrenaline, excreted by the sympathetic nerve endings in the adrenal glands, and all the other sympathetic nerve endings in the body secrete noradrenaline. This increases cardiac output and ventilation, changes blood pressure, redirects blood flow, increases sweating, mobilises carbohydrates and produces glucose by breaking down fat, converting glycogens into glucose and supplying the bloodstream with glucose for energy (Silverthorn, 2007).

A second, prolonged response to stressors is regulated through the endocrine system (Figure 1.6). This response occurs 30 minutes to several hours after stress exposure (Koolhaas et al., 2011; Smith & Vale, 2006; Tsigos & Chrousos, 2002) and is characterised by hypothalamic release of corticotropin-releasing hormone (CRH), which activates the pituitary gland to release adreno-corticotropic hormone (ACTH). ACTH binds to receptors on the adrenal cortex and stimulates adrenal release of two types of cortisol: mineral corticoids and glucocorticoids. Mineral corticoids are

responsible for the retention of sodium ions and water by the kidneys and increased blood volume and blood pressure. Glucocorticoids break down fat and proteins and convert them to glucose, leading to increased blood glucose. Cortisol in the blood stream mobilises energy by breaking down glycogen and fat and stimulates production of glucose and amino acids by the skeletal muscles, which can help by repairing damaged tissues. At a particular blood concentration of cortisol, the hypothalamus receives feedback to stop the release of CRH and the pituitary release of ACTH. At this point, systemic homeostasis returns (Tsigos & Chrousos, 2002).

The stress response inhibits various hormonal systems and suppresses anabolic processes, since costly and slow building processes can be deferred until the body returns to homeostasis (Sapolsky et al., 2000; Silverthorn, 2007). Among other processes, growth is slowed down by inhibition of growth-hormone release, and insulin release, which normally helps store energy for later use, is obstructed. Vassal constriction leads to suppression of the digestive system and thus suppression of appetite. Reproduction is suppressed due to the inhibition of oestrogen, progesterone and testosterone secretion. Furthermore, inflammation and immune system function is temporary suppressed since the immune response demands a lot of protein syntheses, which is not a priority at a time of stress (Munck et al., 1984). The release of opiates such as beta-endorphin suppresses pain should there be an injury, leading to 'stress-induced analgesia' (Lewis et al, 1984). Activation and suppression of these various hormones and metabolic systems play a critical role in surviving an acute physical stressor; they help the organism restore homeostasis. The stress response is catabolic, costly and inefficient, but necessary to survive an acute emergency. This is in itself not problematic, but if a stressor is prolonged, or chronic, the stress response itself might be destructive (Koolhaas et al., 1999; Sapolsky, 1994b, 2000).

On a cellular level, the effect of stress can be detected in teeth. A rise of body temperature above 37°C for any length of time can affect the quantity and rate of enamel and dentin secretion (Dean & Elamin, 2014) which might happen during prolonged periods of fever. Shifts in acid-base balance can cause changes in structure as well as mineral content during odontogenesis, since many cellular and metabolic processes in the body depend on stable hydrogen ion concentrations in blood (pH 7.35–7.45) and the extra-cellular environment (Dean & Elamin, 2014). Illness and infection often leads to changes in body temperature and pH levels and can therefore disrupt the secretion of enamel and pre-dentine matrix or the mineralisation of the enamel and dentine matrix. Disturbances in calcium metabolism also cause changes in ameloblast metabolism and movement (Rose et al., 1978). Accentuated lines correlate with periods of vomiting (Birch & Dean, 2014), illness and disease such as gastro-intestinal and eye problems (Austin et al., 2016; Birch & Dean, 2014; Smith & Boesch, 2015),

periods of dehydration or diarrhoea (Smith, 2013), sometimes, but not always, with physical trauma (Hupková et al., 2014; Schwartz et al., 2006; Smith & Boesch, 2015), periods of major disruptions in body mass trajectory (Austin et al., 2016; Bowman, 1991), postnatal immunisation (Birch & Dean, 2014) which trigger the formation of antibodies and often result in mild fevers (Kohl et al., 2004), intake or exposure to toxic levels of fluoride (Kierdorf & Kierdorf, 1997; Kierdorf et al., 2000; Kierdorf et al., 1993), administration of antibiotics Tetracycline and Doxycyline (Dean et al., 1993; Owens, 1973), and possibly anaesthetics (Bowman, 1991). Furthermore, events such as veterinary treatment (Schwartz et al., 2006, Smith, 2013); captures (Schwartz et al., 2006; Bowman, 1991) and enclosure transfers (Schwartz et al., 2006, Smith, 2013) are linked with the formation of accentuated lines in teeth. The same holds for periods of malnutrition, although the effect of malnutrition on odontogenesis is mainly studied in the context of more severe hypoplastic defects (Goodman & Rose, 1990a; Hillson, 1996; Guatelli-Steinberg & Benderlioglu 2006). Furthermore, annual reoccurring accentuated lines in the teeth of *Theropithecus oswaldi*, a fossil primate, may reflect stress related to seasonality of food availability (Macho et al., 1996).

1.4 Life history assessment from dental development

How and when primate infants transition to an adult diet is a central part of a species' life history. The age of emergence of deciduous and permanent teeth in the oral cavity is often used as a key marker of life history, since the presence of teeth is closely correlated with the ability to process an adult diet (Godfrey et al., 2001; Smith, 1991, 1992). Schultz compared dental development with life history stages in primates, based on five developmental periods: prenatal, infantile, juvenile, reproductive and adult (Schultz, 1960). He marked the transition between the infantile and juvenile phases with the eruption of the first adult molar (the first adult tooth to erupt) and the transition between the juvenile and adult phases with the eruption of the third molar (the last tooth to erupt). Smith explored this finding further, examining a large data set of living primate species, finding that first molar eruption ages were highly correlated with birth mass, age at weaning, female age at first birth and neonatal and adult brain mass (Smith, 1991a; Smith, 1991b). Thus, patterns of dental development can serve as a proxy for life history variables. These large scale comparative studies of dental eruption led to the formulation of "Schultz's rule" (Schultz, 1935; Smith, 2000), an explanation of the way in which the deciduous teeth are replaced by the adult dentition in primates with fast and slow life histories and growth trajectories. In primates with fast life histories, the first and second molars of the permanent dentition are the first to erupt into the oral cavity after the full deciduous

dentition has erupted, completing the full dental arch. When these permanent molars are in place, the deciduous incisors, canines and premolars are replaced by their adult successors. In contrast, in slower growing species the successor teeth erupt relatively early in comparison to the permanent molars, lengthening the period of the functional use of the dentition, to serve a longer life span (Schultz, 1935; Smith, 2000). Weaning age, brain size, body size, age at sexual maturity and overall lifespan also correlate strongly with the time it takes for the first permanent molar crowns to form across a broad taxonomic range of primates (Macho, 2001). Deciduous teeth erupt during infancy, although there is significant variation in the timing of the eruption of dental elements among primate species. Within the cercopithecines, the first dental elements generally erupt within two weeks after birth, but there is variation; e.g., yellow baboon (*Papio cynocephalus*), are rather late when compared to other cercopithecines, with the eruption of their first deciduous elements about 3.5 weeks after birth. In contrast, hamadryas baboons (*Papio hamadryas*), are commonly born with already erupted teeth (Smith et al., 1994). It is hypothesised that the state of the dentition around birth can serve as an index of precociality (Smith et al., 1994).

Due to the connections between dental development and life history, paleoanthropologists have taken an interest in the application of dental development to life history reconstruction from the fossil record. They are interested in questions such as how rapidly or slowly extinct taxa grew, if they show similarities to extant species, and if knowledge about the pace of growth and development could help us to understand their phylogenetic affinities. When focusing on one species, we could ask, in terms of life history, how stages of life in an extinct taxon can be determined, such as the period of infancy, when weaning took place, and at what age they were likely to start reproduction. Combining the state of dental development with the state of skeletal growth in fossil remains can give us an indication of skeletal maturity at a given stage of dental development when an individual is recovered with a dentition that is developing. Using extant primates as a model is not a guarantee of the right fit for an extinct species (Smith et al., 2015b), specifically when taking the existing variability in dental development compared to skeletal maturation among extant primates into account (Dean & Lucas, 2009; Smith, 1989; 1992; 2016). Aging the remains of juveniles from the fossil record employing extant populations therefore leads to circular reasoning when comparing fossil to modern taxa. However, growth increments visible in the microstructure of teeth can be linked to absolute time and may be accurate to a few days or weeks (Antoine et al., 2009; Schwartz et al., 2006; Smith, 2013; Smith & Tafforeau, 2008; Smith et al., 2006). That means when fossil remains are found of an individual with developing teeth, we can correlate the state of that individuals biological development (skeletal growth and dental development) to an exact age, rather than having to rely on estimations. Histological assessment of fossilised immature remains is therefore fundamental to the

study of life history from the fossil record and has transformed the field of palaeoanthropology forward (Dean, 2006, 2010; Smith, 2008, 2013), specifically where cranial and post-cranial remains can be associated as partial skeletons. This has enabled proper comparisons among dental development, skeletal development, stature and body mass attainment in extinct species with that of extant primate data (Antón et al., 2014; Dean, M., Smith, 2009; Dean et al., 2014; Graves et al., 2010; Ruff & Burgess, 2015). Dental histology has grown into a standard tool to be included for the examination of newly found fossil remains.

Humans are unique among extant primates since they have a period of childhood. We wean offspring comparatively early for our body size, and so create a period of post-weaning dependency that is unique to our species (Bogin, 1997; Bogin & Smith, 1996). Paleoanthropologists are interested how the human life history strategy evolved and how the prolonged juvenile growth period of childhood in humans came about. In this context, much research has focused on the australopiths (Dart, 1948; Dean, M., Smith, 2009; Kuykendall, 2003; 2009; Lacruz & Ramirez Rozzi, 2010) and the first fossil hominins attributed to early *Homo* (De Castro et al., 2015; Dean, 2010; Dean & Lucas, 2009; Dean et al., 2001; Zanolli et al., 2016), to determine whether there was a slow period of growth between the end of weaning and the beginning of puberty, as in modern humans (Bogin, 2006; De Castro et al., 2015; Jones, 2011; Key, 2013). Before employing dental histology, the heavily worn deciduous teeth of juvenile australopiths were regarded as evidence of a delay in the eruption of the first permanent molars, and with that, a prolonged period of childhood similar to modern humans (Dart, 1948). If the australopiths had a long period of childhood dependency, that would make them seem more like modern humans than great apes. However, from the 1980s onwards, the idea that early hominins had human-like childhoods changed dramatically. As discussed previously, the work of Smith (1989) demonstrated that molar emergence ages were correlated with aspects of life history, or the overall pace of growth and reproduction, in living primates. This work was used as a comparative context for fossil remains, and ages of first molar emergence in a small number of early hominins showed seemed similar to those of living great apes (Bromage & Dean, 1985; Dean et al., 1993), supporting the notion that life history trajectories of early hominins were more rapid than those of extant humans. Since then, numerous scholars have cited these studies to suggest that early hominin life history was 'great ape-like' (Anemone, 2002; Dean, 2010; Dean & Lucas, 2009; Dean et al., 2001; Hawkes & Paine, 2006; Skinner & Wood, 2006) although Dean & Lucas (2009) also noted the considerable variation in extant great apes life histories. Other scholars emphasized a more mosaic-like or unique pattern of life history in australopiths (Kuykendall, 2003; Macho & Wood, 1995), while some suggested the possibility of a more rapid life history in early hominins than in the great apes (Beynon, 1987; Smith, 1989).

The circular reasoning of interpreting dental development from fossil in context of life history using comparative data from extant primate models, which may not be a good fit for fossils, still existed. Therefore, research on dental development increasingly focused on histologically observable dental microstructure representing absolute time, rather than merely eruption and wear patterns. An initial study on dental microstructure and incremental dental development in Pliocene and early Pleistocene hominins reporting ages at death for six juvenile hominins from counts of perikymata and estimates of Retzius line periodicity and crown formation times (Bromage & Dean, 1985). This yielded ages which were markedly younger than those predicted from extant human growth standards, but similar to those of great apes. The suggestion that the duration of early hominin dental development was more ape-like than human-like was subsequently interpreted as evidence that these hominins had an abbreviated period of dental growth and a less prolonged infancy than extant humans (Beynon, 1992; Beynon & Dean, 1988). The debate on dental development in relation to hominin life history also included on later *Homo* species, specifically how Neanderthals and *Homo sapiens* differed in term of life history pace and dental development. Neanderthal tooth crowns appeared to grow more rapidly than fossil or modern *Homo sapiens* teeth for a given chronological age, resulting in significantly faster dental maturation (Bayle et al., 2010; Shackelford et al., 2012; Smith et al., 2012; Smith et al., 2010; Thompson & Nelson, 2011) and appeared more comparable to values of *Homo erectus* (Dean & Smith, 2009; Dean et al., 2001). When compared with earlier hominin taxa, both Neanderthals and *Homo sapiens* showed extended duration of their dental development. This period of dental immaturity was however particularly prolonged in modern humans, and Middle Palaeolithic *Homo sapiens* juveniles showed greater similarity to recent humans. Recently, a study presented precise calculations of dental development and age at death in Pliocene and Pleistocene hominins on a scale not previously performed using non-destructive synchrotron virtual histology (Smith et al., 2015b). It established the nature of similarities and differences in dental development among early hominins, extant humans, and African apes to a sample of East and South African fossil juvenile individuals. Values for crown formation times of the molars and premolars of the australopiths and early *Homo* from the sample were lower or at the lower end of extant human values, while *Paranthropus robustus* dentitions had the shortest formation times. The main outcome was that Pliocene and early Pleistocene hominins showed a high amount of variation, much more so than in any previously performed study. From this ongoing hominin life history debate, we can so far conclude that trying to determine whether hominins were “ape-like” or “human-like” is overly simplistic, since each fossil taxon seems to have evolved its own unique life history strategy, as well as its own and pace of dental development (Dirks, 2018).

The application of dental microstructure to the fossil record in the framework of hominin life histories is of obvious interest to paleoanthropologist in relation to human life history. However, dental histology is also employed to study other lineages, in pursuit of knowledge on understanding current primate life history variability. Research including that of primitive hominoids and catarrhines provide a crucial comparative framework for understanding the evolution of extant Old World monkeys. A study on what was known as *Proconsul heseloni* (Beynon et al., 1998), now referred to the genus *Ekembo*, the best represented Early Miocene fossil primate, and widely regarded as the earliest known hominoid, employed dental histology to study its complete dental development, in addition to a previous histological study on its enamel thickness to make body size estimates (Gantt, 1983; 1986). The sequence and timing of dental development in *Ekembo* was reconstructed using ground sections allowing for longer period and daily increment measurements, accentuated lines matching between teeth, thereby establishing a chronological time schedule for dental development. Life history predictions based on this study were speculative but compatible with the predictions of Kelley (1997) based on 23 species of primates, whereby he states that age for first permanent molar emergence falls at the upper end of the range of means for all extant nonhominoid catarrhines, many of which are considerably larger on average than *Ekembo* (*Proconsul) heseloni*. On this evidence Kelley (1997) has cautiously suggested these results indicate a more prolonged life history for *Ekembo* (*Proconsul) heseloni*. Beynon and co-authors' study recommended that other fossil species, including *Victoriapithecus*, should be analysed to put Proconsul in a better context. Indeed, the fossilised teeth of *Victoriapithecus macinnes* have since then been analysed. However, in this case, unlike *Ekembo* in which the whole dentition was studied, *Vicoriapithecus macinnes,* one of the first known Old World monkeys (Benefit, 1994; Dean et al., 2004) was analysed merely using isolated fossil teeth. Results demonstrated a fast enamel growth trajectory, indicative of a primitive character expected for the last common ancestor of the ceropithecids and hominoids (Dean et al., 2004), but the obtained results could not be placed in the context of life history as with complete dentitions. Recently the dental microstructure of *Anapithecus hernyaki*, part of an extinct group of catarrhines known as the pliopithecoids, was reanalysed using synchrotron visual histology (Le Cabec et al., 2017). Those results indicated that *Anapithecus* grew its dentition faster and initiated its teeth earlier than suggested previously by a study based merely on perikymata counts (Nargolwalla et al., 2005). However, the results were interpreted in the context of great apes and Miocene hominoids' dental development and life history, rather than the more appropriate comparison of *Ekembo*, comparably sized Old World monkeys and hylobatids (Beynon et al., 1998; Dirks, 1998; Dirks & Bowman, 2007). The last two studies on *Anapithecus* and *Victoriapithecus* highlight the problematic approach of trying to interpret a species' life history from variables measureable from single teeth, rather complete dentition, as well as the need to place obtained results in the correct context.

In contrast to *Anapithecus* and *Victoriapithecus*, a holistic approach to dental development and life history was taken when studying the remains of subfossil lemurs (Godfrey et al., 2001a; Hogg et al., 2015; Schwartz et al., 2002, 2005). Subfossil lemurs are known to be different from extant lemurs on multiple levels, such as in their anatomy, most notably in their body size, but also regarding their ecology and behaviour (Jungers et al., 2002). The histological study of the subfossil lemur *Palaeopropithecus ingens*, a palaeopropithecid, the sister group to extant indriids, showed it had an advanced state of molar crown formation at birth, and could therefore be classified as dentally precocious. This finding indicated a pattern characteristic of *Propithecus* and other indriids; regardless of a relative prolonged gestation length, which in *Palaeopropithecus ingens* was likely greater than 9 months, they still seem to have rapid dental development. Their results demonstrated that large body size in a primate does not determine their rate of dental development or their pace of life history. Correlation of body size and life history should be done with caution from fossil remains.

The research on these subfossil lemurs stressed the importance of integrating complete dentitions when trying to interpret life history variables from fossil remains, in contrast with variables measurable from single teeth such as extension rates (Guatelli-Steinberg et al., 2012), periodicities (Antoine et al., 2009; Bromage et al., 2012), single tooth crown formation times (Dean et al., 2004), or striae angles (Hogg & Walker, 2011). As shown, truly meaningful interpretations only come from completely analysing dental development, preferably through a combination of complete dental histology, matching teeth using accentuated lines combined with x-ray analysis of multiple individuals of the same species (Dirks, 2018). Since availability and access to fossil teeth is generally extremely limited, it is understandable that scholars try to deduce life history information from single teeth. One of the reasons that the sub-fossil lemurs are so well studied, analysed and reported is that they are phylogenetically very remote from *Homo sapiens,* which makes it easier to obtain access to fossils for destructive research. Teeth from fossil hominins are much more difficult to obtain for destructive research, which hinders rigorous statistical comparison between fossil taxa (Dean, 2016). Destructive analysis as in traditional histology is progressively being replaced by non-destructive virtual histology, such as of synchrotron virtual histology, which so far has proven to often be successful in visualising microstructure (Smith et al., 2010, 2015a; Tafforeau et al., 2006; Tafforeau & Smith, 2008). Getting access to beamlines at synchrotron facilities is however difficult, since these are extremely expensive procedures limited to a few locations in the world. The synchrotron facility of the ESRF in France is the primary facility for visualising dental microstructure as the techniques were developed there (Smith et al., 2010, 2015a; Tafforeau et al., 2006; Tafforeau & Smith, 2008).

Aside from gaining access to the inner microstructure of fossil teeth, there are limitations in interpretation. Although dental development has proven to have clear links to life history, it has also proven to not be in direct lock-step correlation with skeletal development or other maturation processes (Schwartz et al., 2002, Dirks, 2003, Dean & Liversidge, 2015). Inferences about life-history variables derived from dental maturation, although insightful, should therefore still be made cautiously (Dirks & Bowman, 2007, Smith et al., 2015b). If comparing dental development with skeletal growth from fossil remains fails to resolve questions on life history evolution, we might turn to proxies for specific life history events from teeth instead. Age at first reproduction for example is a better biological definition of adulthood than the end of tooth and/or bone development (Dean, 2016). Therefore, a more reliable avenue for future research on life history development and maturation from fossil teeth could be to obtain information about the timing of specific life history events, such as nursing history, age at menarche and age at first reproduction (Dean, 2016; Dean & Elamin, 2014; Dean & Liversidge, 2015; Dirks et al., 2002; Humphrey et al., 2008). We can aim to bring aspects of reproductive biology into context with the timing of skeletal as well as dental maturation stages (Dean & Elamin, 2014; Dirks & Bowman, 2007). Superimposing aspects of reproductive biology onto the chronological record of skeletal and dental development would throw new light on the question of how, when and where currently existing life history trajectories came to be (Dean, 2016; Dirks et al., 2002)

1.5 Life history stress and accentuated line formation

Life history events mark key points of physiological change and development in an individual's life and since individuals need to adapt, physically, psychologically, or both, to novel situations, these events are often considered to be 'stressful' (Dirks et al., 2010; Setchell & Lee, 2004). Since accentuated lines form in teeth during some events that can be considered stressful, due to their disruptive effect on homeostasis, we can hypothesise that stressful life history events might correlate with accentuated lines too (Dirks et al., 2002). Birth is considered to be stressful due to the rapid change from inter to extra uterine environment and the systemic physiological disruption that happens at birth correlates with accentuated line formation (Eli et al., 1989; Kurek et al., 2016; Norén, 1984; Schour, 1936; Witzel, 2014; Zanolli et al., 2011). The presence of this neonatal line is so well established that it forms an anchor point for dental developmental studies, correlating dental development sequences to the chronological age of an individual (Antoine et al., 2009; Birch & Dean, 2014; Dirks et al., 2002). However, it is not yet established if physiological or psychological stress related to other life history events and phases such as weaning, sibling birth, and sexual cycles and

parturition in female primates are similarly correlated with the formation of accentuated lines in dentitions, although there are indications this could be the case.

Weaning is the life phase or process in which the dependency on breast milk in the diet of an infant is reduced until final cessation of mother milk takes place (Martin, 1984). Although gradual, weaning is the withdrawal of a stable source of nutriment for an infant and loss of immunological support (Humphrey, 2010). During weaning the mother also changes her distribution of resources from current to future offspring, meaning a decrease of attention for the weanling (Lee et al., 1991). It therefore represents an evolutionary conflict of interest between mother and offspring (Dettwyler & Fishman, 1992; Katzenberg, 1996; Lee, 1996; P. S. Martin, 1984). Additional to possible psychological stress related to decrease in attention from the mother, a weanling's behaviour such as temper tantrums, distress calls and an increase in attempts to maintain proximity with its mother might also be an honest signal of nutritional need (e.g., Dirks et al., 2010a; Godfray, 1995; Kilner & Johnstone, 1997; Lee, 1996; Trivers, 1974). The relation between stress and weaning has been indicated by multiple studies (e.g., Maestripieri, 2002; Mandalaywala et al., 2014; Weary et al., 2008), and weanling distress is observed in a wide variety of primates, including yellow baboons (*Papio cynocephalus*) (Altmann & Samuels, 1992) and rhesus macaques (*Macaca mulatta*) (Hinde, 1977; Hinde & Atkinson, 1970; Mandalaywala et al., 2014). Resumption of the mother's sexual cycling is a key event in the weaning process, whereby the mother shifts her attention away from her infant towards mating (Lee, 1996). It includes a peak in maternal rejection to the infant, and an increase in the infant's stress response to this decrease in attention and access to nutrition (Berman et al., 1994; Maestripieri, 2002). Maternal rejection and specifically aggression may lead to an infant's increase in cortisol levels (Mandalaywala et al., 2014). Therefore, weaning stress might also correlate with the formation of accentuated lines (Dirks et al., 2002, 2010). The teeth of four wild hybrid anubis-hamadryas baboons showed accentuated lines when they were just over 12 months old, and hypothesised to represent the nutritional or psychological stress of weaning (Dirks et al., 2002). Furthermore, accentuated lines coincided with times of dietary transitions during weaning in anubis baboons from another population (Dirks et al., 2010). Given the positioning of the lines in relation to baboon life history trajectories, these lines may correlate with the stress experienced by infants during resumption of the mother's menstrual cycle (Dirks et al., 2002).

The first birth of a new sibling is also a novel event in a juvenile primate's life. Most primates grow up in the company of their siblings and this can influence their behaviour and development (Lamb & Sutton-Smith, 1982). According to parent-offspring conflict theory, the birth of a subsequent sibling is a shift in the distribution of a mother's investment away from the older sibling towards the new-born, predicting an increase in behavioural conflict between the mother and the older offspring

(Trivers, 1974). This conflict triggers a stress response in the older sibling (Altmann, 1980; Devinney et al., 2001, 2003; Hudson & Trillmich, 2008).

The onset of menarche occurs when females experience their first sexual cycle, sexual swellings in some species, and their first engagement in mating activity. During both their first and subsequent cycles, females experience an increase in male attention and mate-guarding, whereby a male closely follows a cycling female and prevents other males from gaining access to her (Alberts et al., 1996; Girard-Buttoz et al., 2014; Palombit, 2014; Setchell et al., 2005a) Furthermore, risk in aggressive approaches by males increases at this time, such as in a captive colony of hamadryas baboons, whereby the number of injured females from male bites increased at the time of cycling (Zinner et al., 1994). In species in which females display sexual swellings, the additional weight of the sexual swelling may also increase energetic costs of locomotion, particularly in young females who have not yet reached full adult size (Zinner et al., 1994). Hybrid baboons revealed a distinct cyclical pattern of accentuated lines beginning at about the age of 4 years, hypothesised to correspond to the age at which females undergo their first menstrual cycles (Dirks et al., 2002).

First reproduction is also a life history event with an abrupt change. At the time of parturition, changes take place in a females' blood chemistry, particularly mineral homeostasis in both the mother and her foetus (Dean & Elamin, 2014; Kovacs, 2011) and a female must adopt novel behaviours of infant care and lactation after parturition. Furthermore, in vervets (*Chlorocebus pygerythrus*), female core temperature drops dramatically at the time of parturition (Barrett et al, unpublished), which disrupts homeostasis. Teeth may therefore also record parturition events as accentuated lines (Dean & Elamin, 2014). Mammals such as the spotted dolphin (*Stenella attenuata*) showed markers in its teeth corresponding to some of their calving episodes (Klevezal & Myrick, 1984), as did the teeth of spotted souslik (*Spermophilus suslicus*) (Trunova et al., 1999). Rabbit dentine changed in appearance around the time of parturition (Okada, 1943; cited in Dean & Elamin, 2014) and a female macaque (*Macaca mulatta*) had one accentuated line in her teeth forming at the time of a stillbirth, although she was also ill at the time of the parturition (Bowman, 1991). Human third molars also showed clear accentuated lines in their roots that may correlate with parturition (Dean & Elamin, 2014). However, for all these examples, no exact correlation could yet be made between life history events and accentuated line formation due to the absence of life history data (Dirks et al., 2002) or since age of dental development was not exactly known (Dean & Elamin, 2014).

Males and females of the same species might experience stress related to life history events and phases at different times or in different ways. Weaning distress (Altmann & Samuels, 1992; Hinde, 1977; Hinde & Atkinson, 1970; Mandalaywala et al., 2014) as well as distress related to sibling birth

(Altmann, 1980; Devinney et al., 2001, 2003; Hudson & Trillmich, 2008) are reported for infants regardless of their sex, although differences in responses between the sexes exist (Devinney et al., 2001; DiGregorio et al., 1987; Dunn & Kendrick, 1980; Nadelman & Begun, 1982). However, once primates go through puberty, ending in sexual maturity, male and female developmental paths can diverge markedly. Females reach sexual maturity once they are able to bear an infant to term (Setchell & Lee, 2004). This process is accompanied by hormonal, psychological and behavioural changes, and individuals must cope with novel, sometimes stressful situations related to sexual interaction with males, pregnancy, parturition and infant care. Males reach sexual maturity once they can impregnate a female (Setchell & Lee, 2004) and their psychological, behavioural and social interactions change, predominantly in relation to inter-male aggression and competition for rank and access to receptive females (Barrett et al., 2002; Schiml et al., 1996; Strier et al., 1999). Accentuated lines related to life history events might therefore show at different times and in different ways among the sexes of the same species.

1.6 Stress, life history and dental development in *Mandrillus sphinx*

If accentuated lines in teeth correlate with stress related to life history events, the presence of accentuated lines in primate teeth might serve as proxy to reconstruct life history. This would allow us to reconstruct the life history of an individual without observational data for living animals. Testing if teeth indeed form accentuated lines correlated with life history related stress requires the study of dental development of individuals for whom full life history data are available (Dirks et al., 2002), which has so far not been possible, since it is difficult to obtaining a combination of such datasets. In this thesis, I fill this gap by studying the histological sections of the teeth of well documented, naturally deceased mandrills (*Mandrillus sphinx*, Cercopithecinae) from a semi free-ranging colony of mandrills, housed at the Centre Internationale de Recherches Médicales, Franceville (CIRMF), Gabon for whom full life history data are available.

Mandrills (*Mandrillus sphinx)* are social semi-terrestrial primates, the largest cercopithecoid and known for their colourful appearance (e.g., Dixson, 2015; Setchell, 2009, 2016). They are indigenous to the dense equatorial forest of Cameroon, Equatorial Guinea, Gabon and Congo (Grubb, 1973), an area of the world where primate species are rapidly declining (Estrada et al., 2017). Due to increased destruction of habitat and bush meat hunt, mandrills are currently listed as 'vulnerable' (IUCN, 2017). Mandrills have an eclectic but generally tough diet; they eat fruits and pith, seeds (often with hard shells), leaves and flowers, but also small invertebrates and vertebrates (Rogers et al., 1996). Their molars are bilophodont, a key adaptation in cercopithecoids (Napier & Napier, 1970; Swindler, 2002),

with cusps aligned into two high bucco-lingual ridges. These ridges interlock maxillary and mandibular teeth in an opposing saw-tooth pattern which creates strong shearing action ideal for reducing leaves and fibrous plant matter. The tough diet of mandrills has a marked effect on their teeth, which wear down fast (Galbany et al., 2014). They have the same dental formula as all catarrhine primates of two incisors, one canine, two premolars and three molars per quadrant (Swindler, 2002).

Both sexes of mandrill, and particularly males, have a coloured face with a red nose and blue paranasal ridges and a red stripe on their muzzles. They have brightly coloured genitals and males have colourful skin on the rump (Osman Hill, 1970; Setchell & Dixson, 2001). The intensity and expression of the colours of face and genitals varies greatly between individuals and between the sexes (Setchell et al., 2006). Additional to colour, mandrills are extreme in their sexual size dimorphism; an adult male being 3.4 times the mass of an adult female, making them the most sexually dimorphic of all primates (Setchell et al., 2001).

Together with the little studied drill (*Mandrillus leucophaeus,* Gadsby et al., 1994; Grubb, 1973; Terdal, 1996)*,* mandrills make up the genus *Mandrillus*. In the past *Mandrillus* was thought to be closely related to *Papio* (e.g., Szalay & Delson, 1979; Wolfheim, 1983), but we now know they are genetically as well as anatomically much closer related to *Cercocebus,* the terrestrial mangabey (Disotell, 2000; Fleagle & McGraw, 1999, 2002; Groves, 2000). The split between mandrills and the *Cercocebus* probably lies around 4 and 5 million years ago (mya) (Goodman et al., 1998; Page et al., 1999; Telfer et al., 2003), when equatorial Africa saw a wetter climate and rainforest expanded during the late Pliocene (4.6 to 2.43 mya). The more recent split between mandrills and drills occurred probably around 3.17 mya (Tefler, 2006), again influenced by climatic and habitat changes. From 2.43 mya until approximately 1.0 mya there was a period of regular cyclical changes in climate leading to rainforest expansion and contraction. During this time, the (ancestral) mandrills and drills might have become separated from each other; the (ancestral) drills to the north of the Sananga River in Cameroon, the (ancestral) mandrill to south (Grubb, 1973). This natural barrier could have played an important role in restriction of gene flow (Grubb, 1973). Although all mandrills after this split are *Mandrillus sphinx*, one more phylogenetic divergence took place around 800,000 years ago. Around this time, mandrills north and south of the Ogooué River running through Gabon became separated, resulting in two groups with different mitochondrial haplotypes (Telfer et al., 2003). The two haplotypes are not considered different enough for taxonomic and nomenclatural changes (Dixson, 2015).

Wild mandrills live in large groups (up to 845 individuals, Abernethy et al., 2002), mainly consisting of adult females, infants and adolescents. Adult males are often solitary (Harrison, 1988; Hongo, 2014; Rogers et al., 1996), mainly join the group for mating purposes (Abernethy et al., 2002). The density of the rainforests and their large home ranges (up to 182 km^2 range, White et al., 2010) obstruct long-term systematic studies on wild mandrills (Harrison, 1988). Therefore, a lot of our understanding of mandrill biology comes from captive (e.g., Bettinger et al., 1995; Pansini, 2006; Phillips & Wheaton, 2008) or semi-free ranging conditions (e.g., Feistner et al., 1992; Setchell, 2016). The mandrill colony housed at CIRMF has played a crucial role in expanding our knowledge of mandrills, due to the large size of the colony, and the possibilities of systematic observations of known individuals (Setchell, 2016).

Studies at CIRMF indicated that mating happens (moderately) seasonally: at CIRMF 63% of females have sexual swellings between July and September (Setchell & Wickings, 2004), leading to a birth season between January and March (Setchell et al., 2002). Wild mandrills have similar mating seasonality, from June to November (Abernethy et al., 2002). When kept in enclosure settings with groups consisting of adults, adolescents, juveniles and infants, one male gains top-rank (Dixson et al., 1993). Other males over 10 years of age vary in their association with the group (Setchell & Dixson, 2001; Wickings & Dixson, 1992b). Data on wild mandrills, although scarce, do not refute this (Abernethy et al., 2002; Hoshino et al., 1984). Males compete heavily for rank since the alpha male has a large advantage in siring offspring, resulting in extreme reproductive skew (the alpha sired 76% of all offspring between 1983 and 2002 at CIRMF, Charpentier et al., 2005). Alphas manage this reproductive advantage by controlling access to peri-ovulatory females though extensive mate-guarding (Setchell et al., 2006). In contrast to males, females do not compete for rank but inherit dominance from their mothers (Setchell, 1999) resulting in stable ranks and distinct matrilines (Wickings & Dixson, 1992a).

CIRMF mandrills have a stable gestation period of 175 days (mean, SE =±1day, Setchell et al., 2002) and have a mean birth weight of 640g, males only being slightly larger than females at birth. Mothers' variables, including age, rank and parity have marked effect on an infant growth and development (Bernstein et al., 2012; Setchell et al., 2001; Setchell et al., 2006). Infants born to higher-ranking or older females are heavier than those born to lower-ranking or younger females (Setchell et al., 2001). Both sexes are weaned at a median age of 7.7 months (range 6.1-8.6 months, Setchell et al., 2002), but dominant females wean their young earlier than subordinates (Setchell et al., 2002a), giving them a reproductive advantage. Male infants of dominant females mature more

rapidly than those born to subordinates (Setchell et al., 2006) and have a higher chance of surviving into adulthood (Setchell and Dixson, 2002; Setchell et al., 2006).

Pre-weaning differences in growth and development between the sexes are small, but shortly after, their paths start to diverge markedly as a result of differences in growth rate and duration (Wickings and Dixson, 1992; Setchell et al., 2001) (Table 1.1). By the age of 2 years, males are already much heavier than females (Wickings & Dixson 1992). Both males and females have an adolescent growth spurt, but females have an earlier and less marked growth spurt than males. The female growth spurt starts around 18 months of age and peaks around when they are 3 years (Setchell et al 2001). Females have an adult body mass of 10-12kg and their adult body size is not related to their rank (Setchell, 1999). Females have their first swelling cycle at a median age of 3.6 years (range 3.2–4.6 years (Setchell & Wickings, 2004). First cycles are often irregular and do not always result in conception. The median age at first birth in the CIRMF population is 4.7 years (range 3.3-6.1 years) (Setchell et al., 2002). Therefore, females start reproducing multiple years before reaching full body mass. Females have one infant at a time with a mean inter-birth interval of 405 days (Setchell et al., 2002, 2005). They keep on cycling and conceiving throughout most of their lives and reproductive output only decreases after the age of 22 years, but reproductive output varies with age and rank. Dominant females have their first sexual cycle on average 6 months earlier than subordinates. Furthermore, dominant or multiparous females are more likely to conceive than nulliparous or lower-ranking females. Dominant females have their first infant 1.3 years (mean) earlier than lower ranking females (Setchell et al., 2002). Since dominant females need fewer cycles to conceive than subordinates, they have shorter inter-birth intervals, leading to a reproductive advantage (Setchell & Wickings, 2004). It is not yet known if there is rank difference in the ovulatory nature of cycles itself among high and low-ranking females (Setchell, 2016). Females continue to grow for multiple years after they have their first cycles, not attaining full adult body mass until they are 7 years (Setchell et al., 2001). At CIRMF, female mandrills have a mean lifespan <22 years, with only females becoming older than this having a post-reproductive period.

The male growth spurt starts later than for females, around the age of 4 years, but continues until the age of 8 or 9, resulting in adult body mass of 30 to 35 kg. Male stature growth ceases at 9 to 10 years, while mass peaks at 10 to 12 years, and declines markedly in males aged 18 years and older. Male testes descend at a median age of 3.8 years (Setchell & Dixson, 2002). Although males are technically capable of siring offspring at this time, they continue to invest in growth instead of reproduction for an additional 6 years, resulting in the mandrill's extreme sexual dimorphism (Setchell et al., 2001). Testes volume increases from 5.5 years onwards, reaching a maximum size at

13 to 15 years (Setchell et al., 2006). Variation in testes size among males is substantial, correlating their dominance rank and other sexual traits (Setchell et al., 2006) although generally mandrill testes are relatively large for their body size compared to other primates (Dixson, 2012). Male secondary sexual traits began to develop at the age of 6 years, and testosterone levels begin to increase markedly at 7 years. Male physical development is accompanied by changes in their behaviour: After the age of 5 years, males start to peripheralise from their group or become solitary (Setchell & Dixson, 2002; Setchell et al., 2006). Once they've reached full size, some males rejoin their group, others stay solitary (Setchell & Dixson, 2002; Setchell et al., 2006). Males compete with each other for dominance, and their rank increases with age from 6 to 11 years, peaks from 11 to 16 years, and falls again from 16 to 20 years (Setchell et al., 2006). Related to rank competition, rate of male injury increases from age 5 years and peaks at 11 to 12 years. Most male injuries occur during the mating season (Setchell et al., 2006) when males compete over access to females.

Table 1.1: Life history variables and events for semi-free-ranging mandrills living at the CIRMF.

Life history variable	Females	Males	Source
Gestation length	175 days (mean SE =±1day)		Setchell et al., 2002
Weaning[1]	7.7 months (median, range 6.1-38.6)		Setchell et al., 2002
Age at first cycle[2]	3.6 years (median, range 3.2–4.6 years		Setchell & Wickings, 2004b
Testes descend[3]		3.8 years (mean)	Setchell & Dixson, 2002
First reproduction[4]	4.2 year (mean ±0.1, range 4.0–4.4	11.4 years (mean ±1.0)	Setchell et al., 2005
Adult body mass attained	7 years (mean)	10 years (mean)	Setchell et al., 2001, 2006
Adult crown rump length attained	6 years (mean)	11 years (mean)	Setchell et al., 2001, 2006)

[1]Median weaning age estimated as median interbirth interval (405 days (Setchell et al.,2002) minus the median gestation length (175 days, Setchell et al., 2002); after Lee et al. (1991). Weaning age is strongly correlated with rank of the mother, whereby high ranking females wean their young earlier than lower ranking females (Setchell et al., 2002). [2]Age at first cycle is a proxy for menarche. [3]Testes volume increase from 5.5 years, maximum at 13–15 years. (Setchell et al., 2006). [4]First reproduction is first birth for females, first sire for males**.**

Males' mean age at first reproduction is 11.4 years (±1.0 year, Setchell et al., 2005) but only one out of three individuals (32%) sires (Setchell et al., 2005). Of these males, 52% sire at least one offspring by the age of 10 years (Setchell et al., 2001; 2006) and all of these males have sired by the age of 18 years. Male reproductive output ends by the (mean) age of 19 years. Siring is not restricted to

dominant males but is highly skewed in their favour (Dixson et al., 1993; Charpentier et al., 2005). Low ranking males sire through sneaky copulations (Setchell et al., 2005). Development is highly variable among individuals, ranging from large, brightly coloured, highly social males to peripheral or solitary, and less coloured appearances, and anything in between (Setchell & Dixson, 2001). Males have two-thirds the life span of females (14 years in males compared to >22 years in females) (Setchell et al., 2005). If they pass the age of 19 years, males can have a long post reproductive period (Setchell & Dixson, 2002).

1.7 Thesis structure

In this thesis, I test the hypothesis that the relationships among dental development, accentuated line formation and life history events are reflected at the level of the individual. If this is the case then I will be able to use accentuated lines in teeth to infer age of weaning, menarche and age at first reproduction. This will set the frame for studies on individuals for whom life history information is not known (e.g., wild populations and fossil taxa). To be able to do so, I collated life history data correlated to the life events of naturally deceased, semi-free ranging mandrills from the colony at CIRMF. These data include dates of birth and death, ages at mother's cycle resumption (a key event in the weaning process), and first and subsequent menstrual cycles and first parturition in females. I also obtained the age at which stressful events occurred for both sexes, including veterinary interventions (captures) and major changes in the social environment. I combined this collated life history and additional stressful events with histological assessment of mandrill dentitions, by first establishing the dental development sequence of individual mandrills, and next assessing accentuated line formation in the individuals' dentition by plotting stress indicators against known life history events to establish which events are recorded in the teeth and which are not.

The aims of this thesis are therefore as follows:

1) To examine the chronology of dental development in individual male and female mandrills, providing the first histological information on dental development and tooth formation in mandrills including crown initiation, completion, and intervening growth processes as crown extension rate, Retzius periodicity and daily secretion rate.

2) To determine sex-specific dental development chronologies for mandrills and compare mandrill dental development and chronology with other, known, aspects of mandrill life history, including the

sequences and timing of dental eruption (Setchell & Wickings 2004a) and the age at first cycle and reproduction in females (Setchell & Wickings 2004b), and placing mandrill dental development in the context of what we know about other African papionins.

3) To determine the ages at formation of accentuated lines in the teeth of male and female mandrills. This allows me to test the hypotheses that stress associated with life history events, as well as changes in alpha male status and captures, affects tooth formation and is therefore correlated with the formation of accentuated lines in tooth sections

To address these aims, I divided my thesis into 6 chapters. After having reviewed the background literature in this first chapter, Chapter 2 outlines the general methods that I used throughout this thesis. The following 3 chapters are data chapters. In Chapter 3, I report my results on the chronology of dental development in male and female mandrills. This allows me to construct a general sex-specific dental chronology for mandrills and determine what, if any, developmental differences exist between the sexes. In Chapter 4, I use the chronology of dental development in female mandrill to determine the ages at formation of accentuated lines in their teeth. This allows me to test the hypotheses that stress associated with life history events, changes in alpha male and captures, affects tooth formation and is therefore correlated with the formation of accentuated lines in tooth sections. In Chapter 5, I do the same for male mandrills. In Chapter 6**,** I provide an overarching discussion of the results, my thesis conclusion and future directions.

Chapter 2: General Methods

In this chapter I outline all the methods I used to address the aims set out in Chapter 1. As well as generating an original dataset of dental histology, I collated data from Setchell's long-term records and the files held at The Centre International de Recherches Médicales de Franceville (CIRMF). Here I present the material I used for my thesis, the material's provenance, the histological methods I used to analyse the material, the type of life history data I collated and how I combined these two data sets for my analysis.

2.1 Study population

CIRMF is located in Franceville, Haut Ogooué, Gabon, in Central Africa (Figure 2.1). It houses by far the largest colony of mandrills in the world. CIRMF maintains and provisions the mandrill colony as a breeding colony under semi-natural conditions. The mandrill colony was established in 1983 when 15 founder animals (7 males aged 2–4 years and 8 females aged 1–6 years) were released into a naturally rain-forested enclosure (Feistner et al., 1992). CIRMF obtained these founder animals when they were confiscated from hunters. Since the founder animals were wild individuals, their exact chronological ages were unknown. The CIRMF veterinarians estimated the animals' ages based on dental development and body mass (Wickings & Dixson, 1992). Expansion of the colony has since occurred through breeding, and occasionally by the addition of further mandrills rescued from hunters (Figure 2.2). CIRMF regulates the size of the colony by removing some mandrills and by the use of contraceptive implants (Wickings & Dixson, 1992).

The founder individuals had ID codes of a single number, for example 1. First generation offspring have the mothers' number and an additional letter as their ID: 1A, 1B, etc. The second generation has another number in addition: 1A1, 1A2, etc. The third generation has another letter: 1A1A, 1A1B, and so on. When an infant is born, it is usually captured when still carried ventro-ventrally by the mother to ensure correct identification. Individuals are tattooed on the inner leg or chest to ensure correct identification throughout their lives. At a later stage an ear-tag is added to identify animals during daily observation (e.g., Setchell et al., 2005). Where infants are not captured, maternity is assigned using genetic analysis (Charpentier et al., 2005).

Figure 2.1: Location of CIRMF in Franceville, Gabon. Image adapted from mapsof.net

Most of the mandrills live in two large and one smaller naturally rain-forested enclosures covering 12 hectares. Over time, some have been housed in individual cages in the primate centre, and others have lived in outdoor group cages, housing up to ten individuals. Enclosure 1 consists of 6.5 ha. Enclosure 2 was added in 1994 (3.5 ha) when 17 mandrills (including 6 adult females and 4 adult males) were transferred from the first enclosure. Enclosure 3 was added in 2002 (2 ha), containing animals that had previously been housed in the outdoor group cages (Setchell et al., 2008). From the foundation of the colony in 1983 to 2006, the year in which life history data collection used in this thesis ended, 307 animals were born into the colony, belonging to five maternal generations. 162 animals were removed, escaped or died in this period (Setchell, 2016). Group sizes ranged from the original 15 to a maximum of 104 in enclosure 1 in 2002, a size comparable to some of the smaller groups of mandrills observed in the wild (e.g., Rogers et al., 1996). All identified individuals used in this study lived in Enclosure 1 and 2. The enclosures are surrounded by a low cement wall and a double-wired fence about 2 meters high, topped with electrified and ground wires angled inwards. The areas of the enclosures close to the fence are kept clear of vegetation, allowing observation of the animals around feeding time, which happens twice a day. The enclosures have small, fenced, concreted areas for provisioning and capturing the animals. The feeding areas have sliding doors

used by the animal technicians to control access to daily provisioning of monkey chow and seasonal fruits (mostly bananas). Water is available from dispensers and a stream which runs through the enclosures. An observation tower between the feeding areas allows observers to view Enclosure 1 and 2 (Figure 2.3).

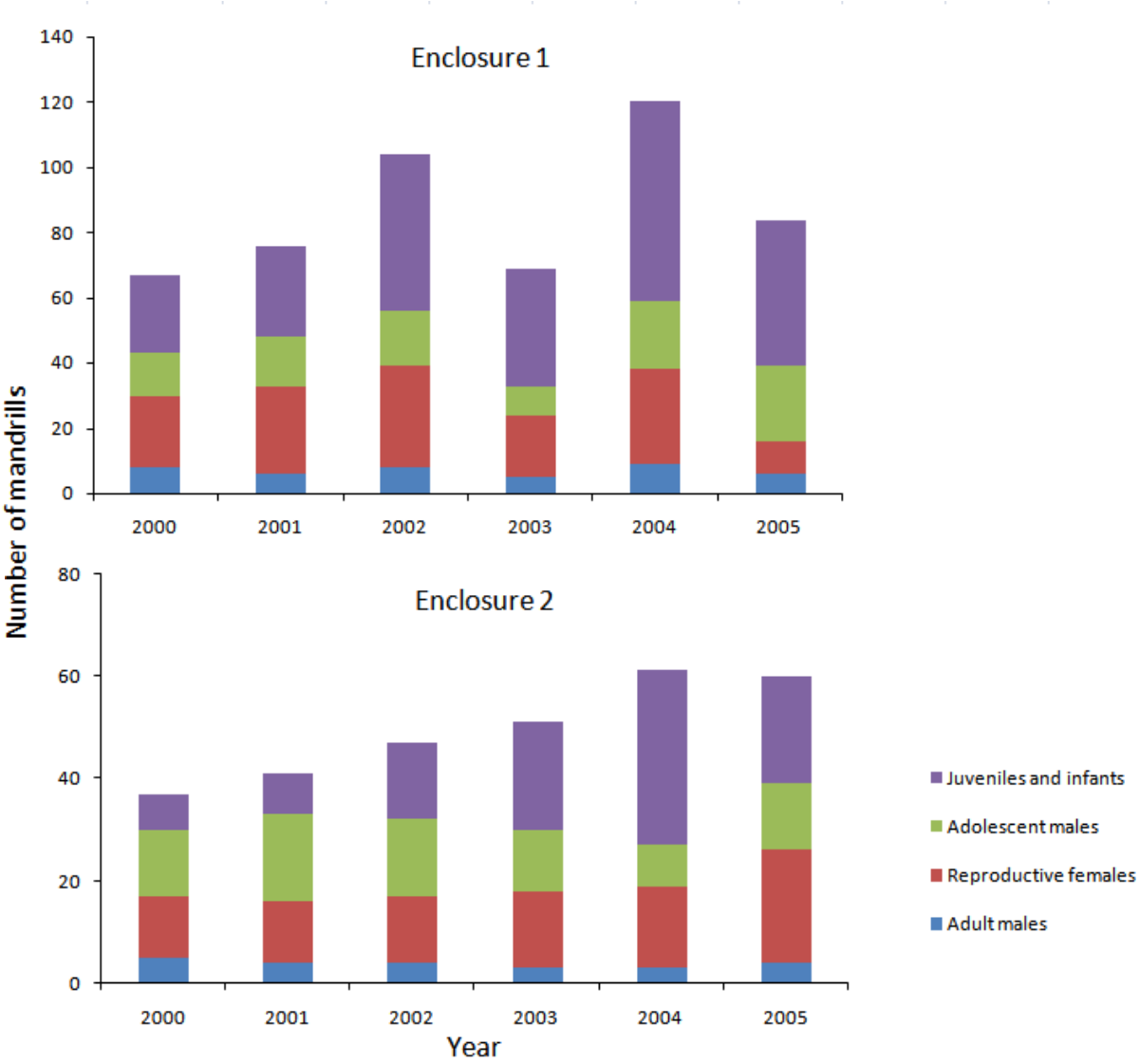

Figure 2.2: Overview of CIRMF mandrill colony size, including Enclosures E1 and E2. Group composition as in January of each year. Reproductive females are females old enough to show sexual swellings during the year, adolescent males are aged 4–9 years, adult males are aged 9+ years (Setchell et al. 2006).

Figure 2.3: Enclosure 1 as viewed from the observation tower, showing mandrills in open space in the foreground, the natural rainforest vegetation, and the fence between Enclosures 1 and 2 on the left. Photo by S. Lemmers, 2014.

Researchers or staff perform daily observations at feeding time, noting the presence or absence of individuals, presence of new infants, injuries and pelage condition, and female sexual swellings. If they do not see an individual for more than 3 days in a row during the daily census, animal technicians search the enclosure for the missing animal. This is except for solitary males, as solitary males are often absent during the daily observation sessions. If the missing animal is found dead, this is noted in the colony records. If it is not found, the individual is recorded as 'missing'. If an individual is found in state of decomposition, the date of death is estimated based on state of decomposition and the date on which the animal was last observed at feeding time (*pers. comm*. Setchell & CIRMF staff). Deaths during veterinary treatment are also noted in the colony records. If an autopsy is conducted, the results are noted in the records.

2.2 Crania and mandibles

As a result of a long-term collaboration with between Setchell and CIRMF, I obtained the crania and mandibles of 7 naturally deceased mandrills from the CIRMF colony: 4 males and 3 females, ranging 6.1 - 12.9 years at death (Table 2.1). All except one male (HT12_15) had known ID's. The identified animals were born between 1980 and 2003 and died between 2001 and 2011.

Table 2.1: Overview of the 7 mandrills used in this thesis with ID, sex, date of birth and death and reason for death taken from the CIRMF colony records. Mandrill HT12_15 was of unknown ID, with age at death based on the results from Chapter 3 (indicated with *).

ID	Sex	Date of birth	Date of death	Age at death (years)	Reason for death
5D3A	Female	23/02/2001	09/09/2011	10.6	Human accident
PB	Female	26/04/2002	09/09/2011	9.4	Human accident
16L	Female	08/04/2003	16/11/2011	8.6	Unknown. Found dead in feeding area of the enclosure
2D8	Male	24/10/2000	5/10/2013	12.9	Illness, died at primate centre
5i2	Male	27/09/2002	09/11/2011	9.1	Unknown. Found in state of decomposition in enclosure
17E2	Male	17/02/2002	24/06/2010	8.4	Fell from a tree. Found in state of decomposition in the enclosure.
HT12_15	Male	Unknown	Unknown	6.1*	Unknown

CIRMF staff collected the mandrill crania and mandibles I use in this thesis from animals that died in the enclosures or at the research centre. When animals die while being in the enclosures, carcasses are often difficult to retrieve; the dense forest and fast decomposition of remains because of the tropical climate often obstruct retrieval (*pers. comm*. CIRMF staff). Decomposition is much faster for females than males, and particularly fast in infants (Pinheiro & Cunha, 2006), explaining why my sample does not contain infants. When animals die at the primate centre (after being captured for medical attention), these problems do not arise. This is however more often the case for the older individuals than for the younger ones.

2.3 Life history data and stressful events

For 4 out of 7 individuals there was detailed life history information available (Table 2.2), two males, two females, one of each sex from a low-ranking mother, the other from a high-ranking mother. Setchell determined female rank from the outcome of approach-avoidance interactions during daily observation periods. Female rank order shows minimal change over the years other than those due to maturation or death (Setchell & Wickings, 2004). Female mandrills of 3 years and older are estimated to have attained their adult rank (Setchell et al., 2002). Female rank is in percentage of females dominated, to account for demographic changes over time (Setchell et al., 2002).

Table 2.1: Background information on the female mandrills 5D3A and PB, used for the analysis performed in Chapter 4.

ID	**5D3A**	**PB (6B2C)**	**17E2**	**2D8**
Sex	**Female**	**Female**	**Male**	**Male**
Matriline	5	6	17	2
Mother's ID	5D3	P 6B2	17E	2D
Enclosure	E1 (6.5 ha)	E1 (6.5 ha)	E2 (3.5 ha)	E1 (6.5 ha)
Mother rank at birth*	8 of 21 (68%)	28 of 28 (0%)	13 of 13 (0%)	1 of 21 (100%)
Own rank from age 3.5 years	11 of 30 (66%)	36 of 36 (0%)	Not determined	Not determined

I collated the following life history data from Setchell and CIRMF files for the 4 mandrills:

1) *Dates of birth*

   These dates are accurate to the day when taking place during the period of data collection by Setchell (till 2006). When births took place outside of Setchell's data collection period, date of birth is the 'first date seen' by the CIRMF staff.

2) *Age of death and causes of death.*

   When animals are found in a state of decomposition, CIRMF staff estimates how long ago the animal died based on the state of decomposition of the remains.

3) *Data of female sexual swellings*

   I used daily records of the prominent cyclical sexual swellings exhibited by female mandrills (Setchell & Wickings, 2004a) to establish the female reproductive cycle for the two female study subjects and the mothers of all four individuals. Daily records of female cycles (1991-2005) are based on the prominent cyclical sexual swellings exhibited by female mandrills (Setchell & Wickings, 2004) (Table 2.3). Studies of yellow baboons (*Papio cynocephalus*), olive baboons (*Papio anubis*) (Shaikh et al., 1982; Wildt et al., 1977) and zoo mandrills (Phillips & Wheaton, 2008) show that the sexual swelling correlates with increased oestrogen levels during the follicular phase, and that ovulation occurs during the last few days of maximal swelling. Setchell assigned pregnancy *post hoc* from the birth of an infant, based on the mean gestation period of 175 days (SE =±1day, Setchell et al., 2002) and sexual swelling records (Table 2.3). From these sexual swelling data, I collated the ages of the individuals when their mothers resumed their sexual cycling. Resumption of cycling and

associated mating behaviour represents a period of mother-infant conflict in primates and the end of the period of high maternal investment (Lee, 1996), and therefore represent a key event in the weaning phase. Furthermore, I collated the ages at which the female mandrills had their first and subsequent cycles.

Table 2.3: Scoring system for sexual swellings in female mandrills at CIRMF (after Setchell 1999).

Score	Description
0	Flat, no swelling. Sexual skin is pale-coloured
+1	Small swelling, increasing in size but not maximal. Sexual skin is pinkish
+2	Medium swelling, increasing in size, but not maximal. Sexual skin is pinkish
+3	Maximum swelling, sexual skin is turgid and bright pink/reddish
BD	Day of sexual skin breakdown, clear decrease in swelling turgidity and size from previous days
–3	Large, post–breakdown swelling, decrease in swelling and loss of coloration
–2	Medium swelling, decreasing in size
-1	Small swelling, decreasing in size
P	Pregnant, small swelling. Colour is redder and skin is more wrinkled than during the early follicular-phase swelling

4) *Dates and duration of mate-guarding*

Additional to sexual swelling data, Setchell and colleagues also kept daily records of the occurrence of mate-guarding, with the identity of the male and female involved, and the reproductive status of the female. Mate-guarding is an unambiguous behaviour whereby a male closely and persistently follows a female, interacts with her sexually (often specifically during her peri-ovulatory period), and attempts to prevent other males from gaining access to her (Setchell et al., 2005). These data consist of the dates on which the mothers of the four individuals were mate-guarded during their first resumed cycle as well the dates on which the females themselves were mate-guarded during their first and subsequent cycles.

5) *Dates of parturitions*

I collated the dates of birth of subsequent infants that were born to the mothers of the two females and the dates on which the females themselves gave birth to offspring. I could assign dates to parturitions that took place outside Setchell's observation period with certainty of a week based on the first observation of the new infant by CIRMF staff, the

known stable gestation period of mandrills (Setchell et al., 2002) and the collated cycling data.

6) *Timing of the mating season*

I defined the mating season as June to October for each year, based on published information (Setchell 2009, Wickings & Dixson 1992). However, many females living in Enclosure 2 had contraceptive implants during the data collection period (Melengestrol acetate, provided by Contraception Advisory Group of the American Zoological Association). Females with contraceptive implants do not show sexual swellings (Setchell et al., 2008, 2010).

7) *Dates of alpha male take-overs*

Male mandrill at CIRMF contest heavily for top rank and alpha take-overs and alpha status is gained through aggressive challenge or via succession (Setchell, 2003; Setchell et al., 2005, Setchell et al., 2006). I collated the dates at which the event took place, or if no date was present, the week during which the take-over took place.

8) *Dates of veterinary captures by CIRMF staff*

Captures for full veterinary controls occur once per year, normally in March. The captures take place by closing animals in the feeding pen at around 10 am (morning feeding time), and delivering anesthetized intramuscular injections of ketamine using a Telinject blowpipe containing the anaesthetic Imalgene1000 (10 mg/kg of body weight; Rhone-Mérieux, Lyon, France, (Wickings & Dixson, 1992). Once anesthetized, animals are transported to the primate centre for veterinary examination. Samples and measurements are taken and identification tattoos and ear tags of all individuals are checked (e.g. Setchell, 2016; Setchell et al., 2001) Afterwards, the mandrills are placed back in the covered feeding pen to recover from anaesthesia, and released into the enclosure when fully awake, usually the same day of the capture. On occasion, the veterinarians keep the animals in cages at the primate centre for treatment or protocols. Additional captures are kept to a minimum for animal welfare reasons but take place for various reasons including treatment of illnesses and traumas or as part of research projects. The dates and reasons for all captures, procedures and results of veterinary checks are noted in the colony records.

2.4 Considerations regarding semi-free ranging conditions

Living circumstances have an inevitable effect on an animal's growth, development, physiology as well as psychology (e.g. Blank et al., 1983; Leigh, S. R. 1994; Novak & Suomi, 1988; Novak, 2013; Wielebnowski, 2003). The choice of studying primates from a semi-free ranging colony such as CIRMF therefore undoubtedly effect on my subject animals' growth, development and social interactions, influencing the results of my thesis. It can therefore be debated what the advantages and disadvantages are for my research questions to study animals from such a semi-free ranging setting. One of the main advantage of studying animals from a semi-free ranging setting at CIRMF, in contrast to wild mandrills, is the possibility of obtaining long term demographic and observational data. Although primates can also be monitored in the wild (e.g. Altmann et al., 1981; Nash, 1978; Palombit,1995; Smith & Boesch, 2015), this is still extremely difficult for mandrills due to their dense natural habitat (Hongo, 2016). Furthermore, the detailed life history data which I need for investigating the correlation between life history stress and accentuated line formation is difficult to obtain from wild primates. A study on three wild juvenile chimpanzees (Smith & Boesch, 2015) investigated the correlation between observational data and accentuated line formation, but the amount detail and number of events that could be included was limited. Specifically, the information on female cycling and male-female interaction during the mating season is extremely difficult to obtain in the wild, whereas the CIRMF circumstances facilitated such observations and long-term documentation(Setchell, 2016; Setchell & Wickings, 2004b; Setchell et al., 2002, 2010). Furthermore, it could be argued that the mandrills at CIRMF, due to their semi-free ranging living conditions will show different behaviour, interactions and therefore experience different stressors in comparison to wild conspecifics. Although this may be true, it does not affect the hypotheses of this thesis, whereby I want to test if which event can be associated with accentuated line formation.
Circumstances at CIRMF allow for the collection of skeletal remains rapidly after an individual has died, resulting in the access to the crania of the animals included in this study. Obtaining the number of crania as included in this thesis from wild primates, and specifically for primates as mandrills will be much more challenging. The study of mandrill dental development would specifically improve from the addition of juvenile individuals with developing teeth. Obtaining such material from a semi-free ranging setting as CIRMF proved already to be highly challenging, and only one individual with developing crowns was available to include in this study, who's ID was unknown (HT12_15, Table 2.1). To find such material in the wild will be even more challenging, since remains of infants and juveniles tend to compose faster than remains of adult individuals (Pinheiro, 2006).
Finally, daily provisioning of the mandrills may accelerated dental development and eruption

compared to wild conspecifics (Machanda et al., 2015; Phillips-Conroy and Jolly, 1988; Smith and Boesch, 2011; Zihlman et al., 2004). However, a later study showed that the effect might be small (Smith and Boesch, 2011). Therefore, the developmental data obtained in this thesis can considered as useful for the analysis as mandrills as a species.

2.5 Collection of research material

2.5.1 Cleaning the crania and dentitions

CIRMF staff collected remains from deceased animals and placed them in plastic bags for controlled decomposition in a designated area. They left the material outside on the soil in a punctured plastic bag adding the mandrill's ear-tag or a plastic card with their ID numbers for later reference. Staff checked the state of decomposition occasionally and collected the material once all the soft tissue was gone. Staff also aimed to collect all teeth that fell out during the decomposition process (Figure 2.4) but regularly could not retrieve all teeth. Next, staff cleaned the material with water with bleach, or water with salt. Bleach was used only briefly and mainly for the post-cranial skeleton since bleach has a negative effect on the conservation of the dentition. Staff cleaned the material using a soft brush. After this first stage of cleaning and washing, they placed the material in a bath of water with alcohol for 2-3 months (Figure 2.5). They checked the baths at irregular intervals from once a week to once a month. They refreshed the water once the alcohol turned yellow. Multiple crania and mandibles go into alcohol baths at the same time, accompanied by the corresponding ID labels or tags (Figure 2.5). The staff then left the material to dry and stored it until sending it to the United Kingdom. As a result of this procedure, some teeth are missing from the crania and teeth show taphonomic damage to the enamel, possibly from the bleach. Based on CIRMF circumstances and newly gained knowledge on handling of animal remains, I wrote a protocol in English and French to facilitate in future hard tissue collection and treatment for the CIRMF staff (Appendix A.1: English & Appendix A.2: French).

Figure 2.4: A male mandrill cranium during the process of decomposition. Cranium is ready for cleaning, since all the soft tissue has degraded. The I^2 got lost during decomposition. Photo: S. Lemmers, 2014.

Figure 2.5: Example of mandrill skulls in a bath of water and alcohol as part of the cleaning process. Photo: S. Lemmers, 2014.

2.5.2 Shipping and sample preparation

We shipped the material from Gabon to the hard tissue laboratory in the School of Dental Science, Newcastle University. After we received the specimens, we placed them in a -80ºC freezer for 24 hours, to kill any invertebrates present. Next, we sent the crania and mandibles to Prof Michael Fagan, Hull University, to scan the material using computerised topography, for future reference. I checked the dentitions, noting the presence, absence, and ante- or post-mortem loss of teeth and state of wear which allowed me to prioritise individuals for analysis, since the success of histological analysis is highly dependent on the condition of the teeth. Next, I chose one quadrant of the permanent dentition per individual for extraction. Preferably I chose the teeth from the mandible since the data from other species for comparison is also often from the mandible. This therefore will facilitate inter species comparison. Also, mandibular teeth are easier to extract from the jaw than the maxillary teeth in which molars generally have more roots. The C_1 is also more suitable for sectioning than the C^1 due to its smaller size and lesser curvature. Where possible, we took teeth from the same quadrant, but in cases where teeth were missing or damaged, we extracted matching teeth from another quadrant. Where mandibular teeth were absent or damaged however I chose maxillary teeth. We extracted the selected teeth carefully to avoid breaking the teeth or cracking the enamel. Where root morphology hindered direct extraction, we used a small saw to cut away a piece of the jawbone to free the root and glued the piece of bone back in place once the tooth was extracted.

2.5.3 Sampling

For the analysis performed in Chapter 3, I sampled teeth from three female and four male mandrills (Table 2.4). I concentrated on the mandibular dentition and used maxillary teeth when mandibular teeth were missing or badly damaged. Dental development is very similar in primate maxillary and mandibular molars (Swindler, 2002), although initiation and formation times for individual cusps and tooth eruption vary slightly (Dirks, 1998; Dirks & Bowman, 2007; Dirks et al., 2002; Reid et al., 1998). I sampled the best preserved teeth from either the left or right quadrant of the jaws, since the left and right sides generally develop similarly, more so than mandibular and maxillary teeth (Swindler, 2002).

Table 2.4: Sample used for the analysis of mandrill dental development in Chapter 3. L and R indicate left and right, (m) and (d) indicate mesial or distal cusps, (i) indicates incomplete crown, (med) indicates metaconid, (hyd) indicates hypoconid, (end) indicates entoconid, * indicates age at death determined histologically

Specimen ID	Sex	Date of birth	Date of Death	Age at Death (years)	Teeth Sampled	Incomplete Roots
5D3A	Female	23.02.2001	09.09.2011	10.5	RI_1, RI_2, RC_1, LP_3, RP_4, LM_1(m), LM_2(m), LM_3(m)	None
PB	Female	26.04.2002	09.09.2011	9.4	LI_1, LI_2, LC_1, LP_3, LP_4, RM^1(d), RM^2(d), RM^3(d)	RM^3
16L	Female	08.04.2003	16.11.2011	8.6	RI_1, RI_2, RC_1, RP_3, RP_4, RM_1(end), RM_2(m), RM_3(d)	RM_3
2D8	Male	24.10.2000	05.10.2013	12.9	RI_1, RI_2, RC_1, RP_3, RP_4, RM_1(end), RM_2(m), RM_3(d)	None
17E2	Male	17.02.2002	24.6.2010	8.4	RI_1, RI_2, LC^1, LP^3, LM_1(d) LM^2(d), LM^3(m)	LC^1
5I2	Male	27.09.2002	09.11.2011	9.1	LI_1, LI_2, LC_1(i), LP_3, LP_4, LM_1(med, hyd), RM_2(m), LM_3(m, d)	LM_3
HT12_15	Male	Unknown	Unknown	6.1*	RI_1, RI_2, RC_1, RP_3, RP_4(i), RM_1(d), RM_2(d), RM_3(m, d)	RC_1, RP_3, RM_3

For Chapter 4, I assessed the formation of accentuated lines in the teeth of the two adult female mandrills, PB and 5D3A (Table 2.5). Both females had fully erupted adult dentitions when they died, and their teeth were worn. The incisors and the functional cusps of the molars were the most worn. Because 5D3A was older than PB, her teeth were more worn. Tooth wear differences among the different teeth was comparable with predictions based on the eruption sequence and the duration of functional use of teeth in both individuals (Galbany et al., 2014; Scheid, 2012; Setchell & Wickings, 2004), with the M_1 showing most wear and M_3 the least. Matching teeth (details in 2.6.9) becomes more challenging when teeth are worn and missing the occlusal surface of M1 can lead to the absence of the neonatal line. However, wear of the other teeth than the M1 does not prohibit the construction of accentuated line sequences drastically. The amount of wear per tooth, other than of the M1, is therefore not necessary to discuss here. Teeth from the two females were however taphonomically damaged, which made accentuated line observation more difficult. PB's enamel was in fairly good condition with only a few areas in the enamel showing taphonomic damage. 5D3A's enamel showed multiple areas of taphonomic damage. The canine was in very poor condition with the enamel almost completely deteriorated. The P_3 section was well preserved but was slightly

obliquely cut due to the tooth's curved morphology which made parts of the enamel unsuitable for analysis.

Table 2.5: Sample used in the analysis performed in Chapter 4. L and R indicate left and right side of the mandible or maxilla. All molars had a medial and distal section.

Specimen ID	Teeth Sampled	Incomplete Roots	Total number of thin sections
PB	LI_1, LI_2, LC_1, LP_3, LP_4, LM_1, LM_2, LM_3, RM^1, RM^2, RM^3	RM^3	17
5D3A	RI_1, RI_2, RC_1, LP_3, RP_4, LM_1, LM_2, LM_3	None	11

I sampled the left quadrant of PB's mandible. Due to the high amount of wear, poor quality of the enamel of the molars and the upper M^3 having an open apex, I also sampled M^1, M^2 and M^3 from the right quadrant of the maxilla (Table 2.5). 5D3A's teeth were complete with full apical closure. I sampled the anterior teeth and the P_3 from the right quadrant of her mandible, the P_4 and molars from the left quadrant due to teeth being lost taphonomically, sampling 8 teeth in total. For both females, I used one section for each incisor, canine and premolar and a mesial and a distal section of the cusps of the bilophodont molars, resulting in 17 thin sections for PB and 11 sections for 5D3A (Table 2.5).

For Chapter 5, I assessed the formation of accentuated lines in the teeth of the two male mandrills 17E2 and 2D8 (Table 2.6). The two males lived in separate enclosures and were from two different matrilines (Table 2.2). 17E2 was 3.9 years and 2D8 was 5.2 years when life history data collection ended in January 2006. Both males had erupted and worn adult dentitions when they died. 17E2's C^1 root however was still developing and his C^1 crown was therefore still erupting when he died. 2D8's dentition was complete 3.2 years before he died (Table 2.6). The incisors and the functional cusps (the hypoconids and protoconids of the mandibular molars and the protocones and hypocones of the maxillary molars) of both males showed most wear. Of all teeth, the M1 showed the most wear and the M3 the least. These tooth wear differences reflect the eruption sequence and thus the duration of functional tooth use (Galbany et al., 2014; Scheid, 2012; Setchell & Wickings, 2004). Because 2D8 was older than 17E2, his teeth were much more worn. For 2D8 I sampled the right mandibular quadrant and for 17E2 I sampled a mix of the mandibular and maxillary teeth, because multiple mandibular teeth were taphonomically lost. This led to 12 thin sections for 17E2 and 10 for 2D8 (Table 2.6).

Table 2.6: Sample used in the analysis performed in Chapter 5. section per incisor, canine and premolar, two sections per molar. L and R indicate left and right side of the mandible or maxilla.

Specimen ID	Teeth Sampled	Incomplete Roots	Total number of thin sections
17E2	RI_1, RI_2, LC^1, LP^3, (P4 missing), LM_1, LM^1, LM^2, LM^3	LC^1	12
2D8	RI_1, RI_2, RC_1, RP_4, RM_1, RM_2, RM_3	none	10

2.6 Sample preparation

2.6.1 Thin section preparation

We replaced extracted teeth with casts made using President Fast Soft Putty ©. We used President Light Body ©, where there was a specific need for a higher resolution replica (Protocol in Appendix A.3). Once extracted, we chose one half of each tooth, leaving the other half untouched. We prepared one thin section of about 70-100 µm in thickness from each anterior tooth and two sections (mesial and distal) from each molar (Figure 2.6). We made the sections according to a protocol designed by D. J. Reid and adapted by P. Walton, Hard Tissue Laboratory, School of Dental Science, Newcastle University:

We cleaned every tooth using a weak soap solution and a cotton swab and let the tooth air dry. We coated them in a light layer of cyanoacrylate to prevent chipping and breakage and marked the teeth at the correct orientation with a red solvent-proof pen before sectioning, so that solvents would not dissolve the markings. The desired plane of sectioning is the midline axial plane for canines and incisors and the mesio-distal plane through buccal and lingual cusps for premolars and molars (Figure 2.6). On molars we marked the distal surface with a dot and the preferred mesial or distal cusps with a line indicating the desired plane of cut. Using dental sticky wax, we attached the marked tooth securely to a cutting chuck, with the cutting line aligned with the saw blade. We secured the cutting chuck to the arm of the annular saw, so that the plane of section was exactly parallel to the saw blade.

For cutting, we used a Micro Slice II with a diamond edge blade. We lowered the arm of the annular saw carefully until the blade began to cut into the tooth block along the marked plane of section. We made the cut slowly and steadily to keep the section smooth and undamaged. Having made the first cut, we adjusted the arm of the saw using a micrometre dial, taking the width of the saw blade (220-280 µm) into consideration, to cut a section approximately 700 µm thick. This thickness allowed us to polish both sides of the section until the section was at the desired thickness of 100 microns. We

assessed the quality of the section under a dissecting microscope to see which side came closest to the tips of the dentine horns (the ideal plane of section). We marked this side with a dot. We stuck the unmarked side to a glass microscopy slide using the smallest amount of dental sticky wax possible. We marked the exposed surface with diagonal lines using a permanent marker. We polished the marked side of the slide to obtain the desired thickness using a Logitech PM2 lapping machine. Due to the large size and curvature of the male canines, we sawed these teeth into three before sectioning, and mounted the parts on separate histological slides.

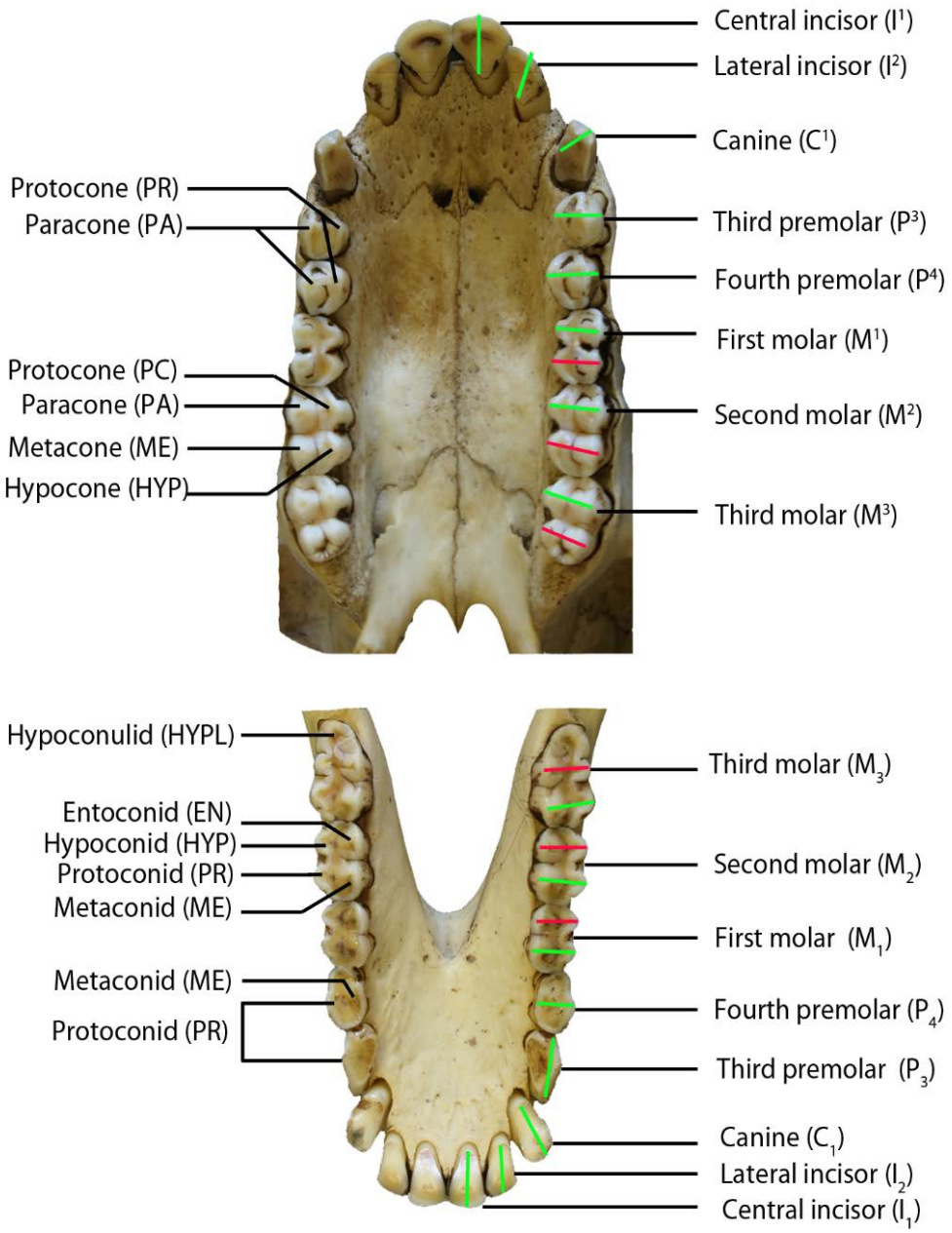

Figure 2.6: Maxilla and mandible of a female mandrill with tooth terminology and planes of sectioning. For molars, green lines indicate mesial and red indicates distal sectioning planes. Cusp terminology for the specific cusps on the left.

Next, we attached the microscope slide with the tooth section to a micrometre slide holder. The slide holder kept the slide in place via air pressure during polishing on the glass polishing wheel. The lapping machine indicated the combined thickness of the slide and tooth section, which we kept at >100 µm so as not to lose material. We polished the section with 9-micron aluminium oxide powder in a water suspension until all the permanent marker lines on the section were removed. This ensured that the surface of the tooth section was smooth and would lay flat against the permanent mounting slide. Once polishing was finished, we cleaned the slide and attached tooth section in an ultrasonic bath. We held the slide over a flame to melt the sticky wax and release the tooth section. We dipped the section in graded baths of xylene to remove any remaining wax and debris. We did this under a fume hood as xylene is extremely toxic. Once the slide was clean, we etched a new slide for 2-3 seconds in hydrofluoric acid to facilitate a good bond between the slide and the bonding material. We used Diamond Solution Zero Bond to bond the tooth section to the etched slide and cured it for 24 hours under a spring-loaded compression and UV light. When ready, we removed the slide from the spring-loaded compression, and placed it against the UV light for several more hours. When the section was completely bonded to the glass slide, we polished the exposed section surface gently with slightly wet felt, and then dipped it into Xylene to clean off any debris. We used a digital micrometre calliper to measure the thickness of the slide and section together, in several areas, to determine how much of the tooth should be polished down to achieve a final section thickness of around 100 microns. We put the slide back in the slide holder of the polishing device and polished it further using 3-micron alumina polishing compound until we reached a final thickness of 100 microns. We cleaned the section ultrasonically to remove the polishing compound, and rinsed it in distilled water, graded alcohol baths, and xylene. We let it dry overnight.

We carried out final lapping using 3-micron alumina, followed by a brief lapping with 1micron diamond polish. We cleaned the finished section thoroughly in an ultrasonic bath to remove surface lapping compound. We examined it under low power magnification, washed it in distilled water, dehydrated in graded alcohol and cleaned it in Histoclear® under a fume hood. While still wet, we mounted the slide in Histomount®, and left it to cure for several days. Although sections are ready to use at this stage, we kept them flat as the Histomount® remains partly liquid for at least another month.

2.6.2 Equipment and software

I performed all histological analysis of the thin sections at the School of Dental Sciences at Newcastle University and at the Bioinformatics lab in the Anthropology Department, Durham University. I used an Olympus BX51 microscope mounted with a Q-Imaging Micropublisher 3.3 RTV camera and Improvision Openlab 5.0.2 image analysis software. I used polarized light and neutral density filters available on the Olympus BX51 microscope depending on the quality and thickness of the sections and the micro-structures I wished to view (Figure 2.7). Polarising filters configure the movement of light waves and force their vibration in a specific direction, enhancing the contrast (e.g. Risnes, 1986).

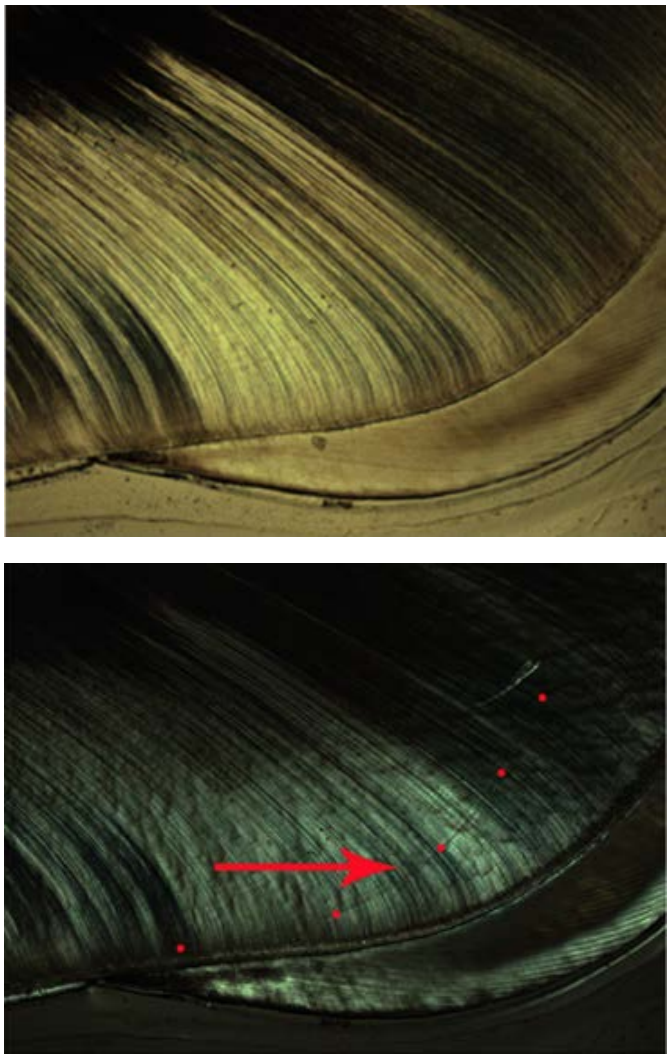

Figure 2.7: Effect of polarisation filter on visibility accentuated lines in thin sections. Micrographs of a premolar (mandrill PB), 4x objective. (A) Normal light, no clear accentuated lines visible. (B) full polarisation, enhancing visibility of highly accentuated line (red arrow).

I made a photomontage of each tooth by transferring images made with Improvision Openlab 5.0.2 image analysis software to Adobe Photoshop CS5. I made a low-resolution montage with the 4x objective to get an overall view of the whole section (Figure 2.8). I kept the light, focus and filter settings the same throughout the acquisition of digital images for a photomontage, to allow image recognition in the Photoshop repositioning application. Once I had merged all images, I adjusted the brightness field, contrast levels and light curves to make the histological structures more visible. I only used the photomontages as an overview function, since images got slightly distorted when merging, obstructing accurate measurements. I made higher resolution micrographs with the 10x, 20x and 40x objectives, focussing on the structures enamel and outer dentine stretching from the crown dentine junction towards the root apex, on which I performed the actual measurements (Figure 2.8).

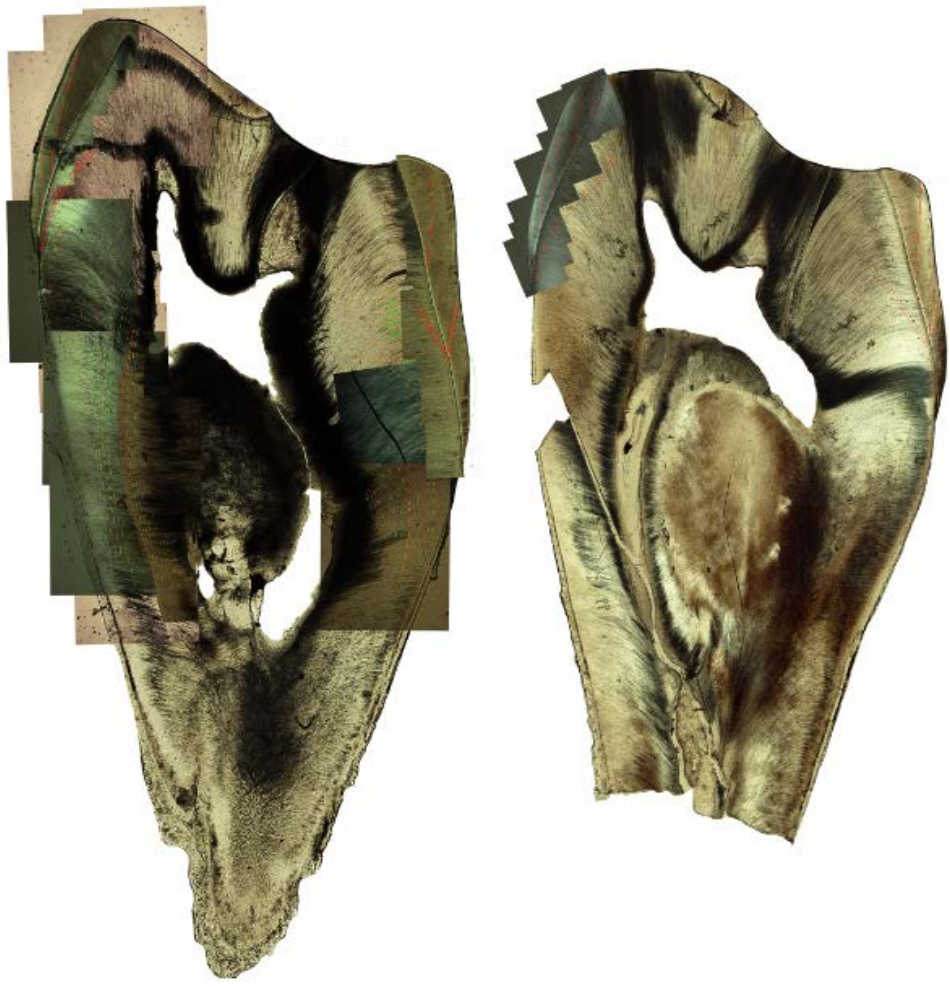

Figure 2.8: Example of photomontages. M_1 of mandrill 5D3A, distal section left, mesial section right. low power magnification overview sections (4x objective, background) and high-resolution images for details (10, 20, or 40 x objective, foreground).

2.7 Dental histology

My histological data collection and analysis has two main components:

1) Reconstructing the dental development of individual mandrills. I do this by:
   - Calculating crown formation times of each tooth per quadrant of an individual using a simplified version of a method originally formulated by Risnes (Risnes, 1986).
   - Correlating all teeth per jaw quadrant of an individual to each other by using clear accentuated lines as anchor points, thereby creating a dental development sequence.
   - Calibrating the dental development sequence to calendar time using the neonatal line in the first molars as age 0 (birth) or the last formed increment in open roots of developing teeth as age of death. This forms the focus of the analysis performed in Chapter 3, using all 7 mandrills.
2) Calculating the accentuated line sequence for individual mandrills in order to obtain a record of timing of physiological disturbances. I do this by:
   - Marking and calculating the position of accentuated lines visible in all tooth sections of an individual.
   - Matching the pattern of accentuated lines in the teeth of an individual to each other, to obtain a continuous record of accentuated line sequence from birth (neonatal line) until the end of dental development or until death, whichever comes first. This forms the focus of the analysis performed in Chapter 4 (female mandrills 5D3A and PB) and Chapter and 5 (male mandrills 2D8 and 17E2).

The two components of the analysis are intertwined: to calculate dental development sequences of individuals, I need to correlate the teeth of one individual to each other, using accentuated lines as anchor points, and to obtain a complete accentuated line sequence per individual, I need to calculate an individual's dental development sequence and correlate it to calendar time. Although dental development sequences and accentuated line sequences are two different components, the data collection itself did not take place in these two separate steps. I will now explain the several steps of my histological measurements. I will describe the overarching methods that I used, as well as additions where I had to make adaptions to my standard methods due to the state of the material (worn or absent teeth).

2.7.1 Crown formation time calculation

To construct dental development chronologies for individual mandrills, I first calculated the crown formation time of each sampled tooth per individual before matching all sampled teeth per individual to each other using clear accentuated lines then correlated the sequence of dental development with calendar time. There are many ways to determine the crown formation time of a tooth (Dean, 1998; Hillson, 2014; Reid et al., 1998). I used a simplified version of a method originally formulated by Risnes (Risnes, 1986), using cumulative prism lengths, stepping down along the enamel dentine junction (Dean, 1998; Hillson, 2014) (Figure 2.9). I marked accentuated lines throughout the crowns at their intersection with the enamel dentine junction (Risnes, 1986, Dean & Beynon 1991). I then measured along the prisms (blue lines, Figure 2.9), from these points at the enamel dentine junction to the next accentuated line in the series as it approached the enamel dentine junction and continued this procedure until I reached the cervix of the crown. Every prism length I divided by the daily secretion rate for that area, calculated by measuring at least 10 sets of daily increments (cross striations) in the area of the prism, and taking the mean of these measurements. This yields the number of days it took to form the enamel from one accentuated line to the next. This total number of days from all measured prism lengths gave me the total crown formation time of a tooth. I could not include all the cusps of every molar in the dental development analysis due to taphonomic damage and wear of the teeth.

For teeth with open roots, I also calculated the root formation time using a similar method, measuring from the cervix towards the root apex, using accentuated lines in the dentine (Figure 2.9). Instead of following prisms I followed the tubule lengths between adjacent accentuated lines (Figure 2.9), starting at the crown cervix and ending at the last increment at the apex of the root, which coincided with the death of the individual. Some teeth had damaged enamel. This was particularly the case for canines, which have extremely thin enamel, rendering them highly susceptible to taphonomic damage. In these cases, I used the coronal dentine to calculate crown formation time, in the same way as I analysed root formation time.

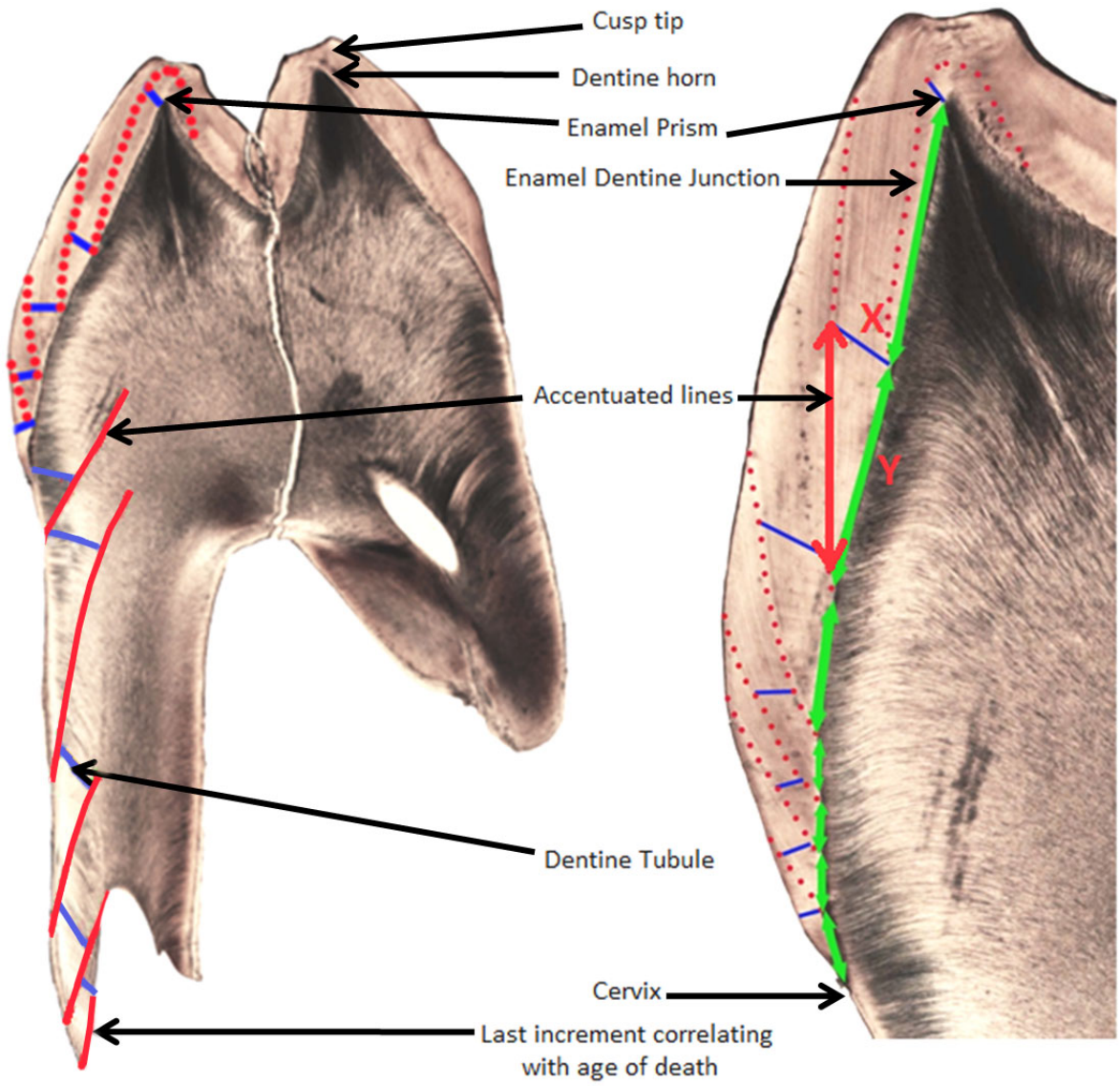

Figure 2.9: Calculation of crown and root formation times. prism lengths (in blue) between adjacent accentuated lines (red). On the left a molar with well-preserved cusps and an open root, allowing calculation of full crown formation time and calibration to calendar time by matching last increment of the root to age of death. On right a detail of crown extension rate calculation: dividing the length of the enamel dentine junction between two accentuated lines (Y) by the number of days measured along the prism lengths (X). Scale: 4x objective (left), 10x objective (right).

2.7.2 Matching teeth for dental development

I used the pattern of accentuated lines visible in enamel to determine the developmental position of each tooth in relation to the others in an individual (Figure 2.10). If the enamel was damaged, I used accentuated lines in dentine instead. I used the published sequence of development and relative positioning of the teeth of baboons and geladas (Swindler & Beynon, 1993; Dirks et al., 2002), to understand the likely positions of teeth relative to each other, and where accentuated lines were

likely to match. I then compared the pattern of accentuated lines in M_1 with that in I_1, then compared the pattern in the I_1 with those in I_2 and C_1. Next, I compared the patterns for P_3, P_4 and M_2. Finally, I placed the M_3 in the sequence (Figure 2.10).

Once I had matched the teeth in an individual, I calibrated the sequence of dental development to calendar time by matching the neonatal line in the M1 (if present) to the known date of birth noted in the CIRMF records. For individuals where no neonatal lines were present or where the neonatal line was obliterated by poor preservation or wear, I correlated the last formed increments of open roots of developing teeth to the known date of death from the CIRMF records. I then used the dates of birth and death to determine the age at crown initiation and completion for each tooth. I could not calculate the exact age at initiation for worn teeth since the first formed increments were worn away. The calculations I present in this chapter from worn teeth are therefore inevitably older than the true age of initiation.

One individual, 2D8, had extremely worn M1s, with no neonatal lines preserved and complete dentition at death, with no open roots. I matched 2D8's teeth to each other but could not match the dental sequence to calendar time. To address this problem, I used the results of the calculation of dental sequences of the other males (17E2, HT12_15 and 5I2, Chapter 3) as a guide for positioning 2D8's dental development sequence (Figure 2.11). I did this as follows: 2D8 is older than the other three males in my sample and has more tooth wear, so his estimated ages of tooth initiation will be later than those of other males. The age at completion of a tooth is not affected by wear and 2D8's teeth are likely to complete at similar ages to those of the other males. The dental emergence pattern of the younger males shows that incisors emerge with very little or no root development, and C_1 and P_3 emerge when the crowns are still developing (Chapter 3). Combining the constraints that 2D8's teeth should be completed around the same time as for the other males, that his C_1 and P_3 should emerge while crowns are still forming, and his incisors should erupt with very little or no root development, produces the most likely positioning of 2D8's dental development sequence with respect to calendar time. With this positioning, all teeth except the I_2 and M_3 initiate after the mean age at initiation based on the three younger males. Since the top of 2D8's I_2 is damaged and M_3 initiation varies, this is acceptable. Furthermore, in this positioning, 2D8's incisors erupt with little root and the C_1 and P_3 erupt when crowns are still forming, similar as the three younger males (Figure 2.11).

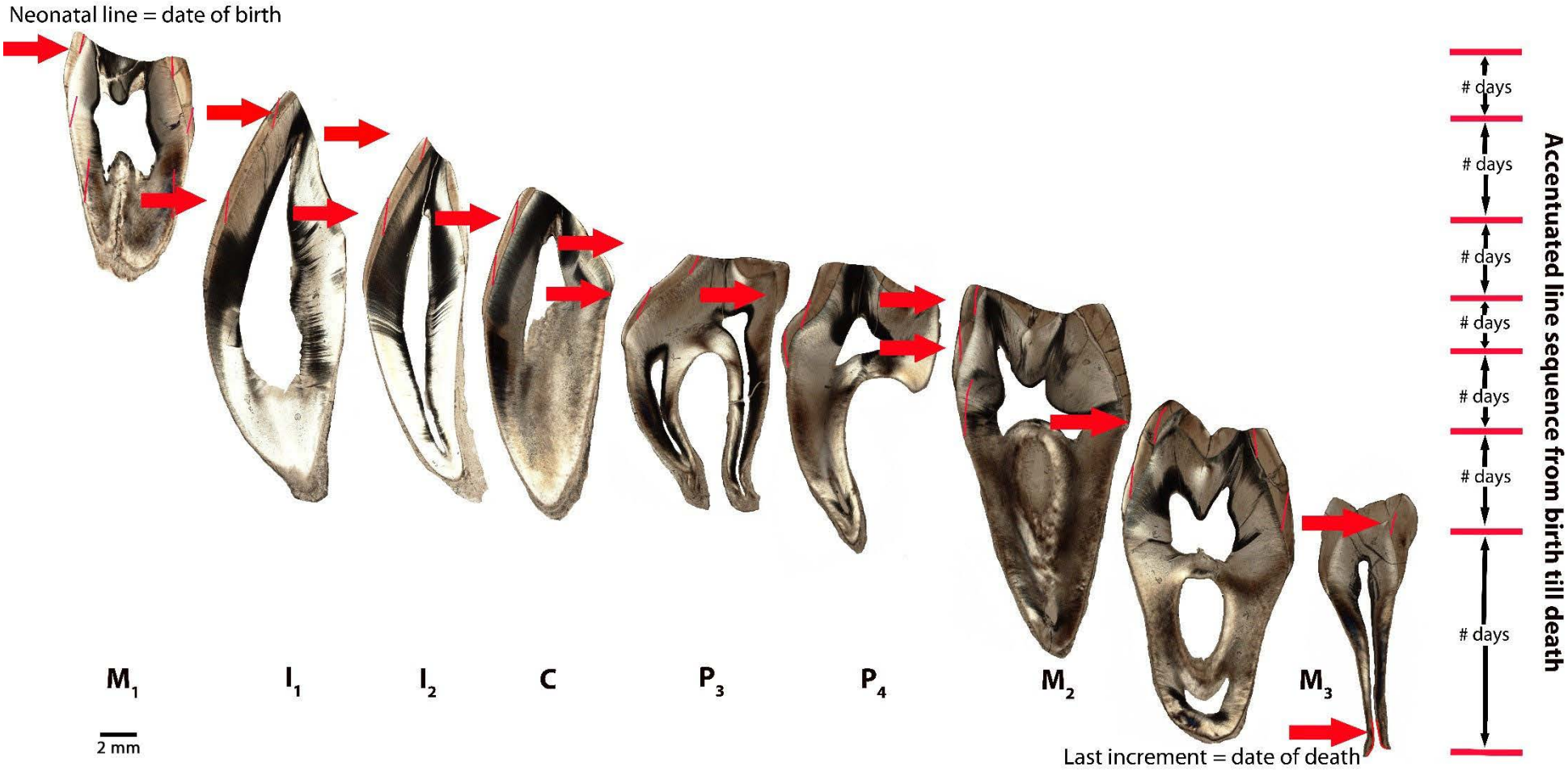

Figure 2.10: Schematic representation of accentuated line matching procedure. The neonatal line (top left) in the first molar links the whole sequence to calendar time. If teeth are still developing, the sequence can be linked to age at death using the last formed increment (bottom right). Micrographs made with 4x objective.

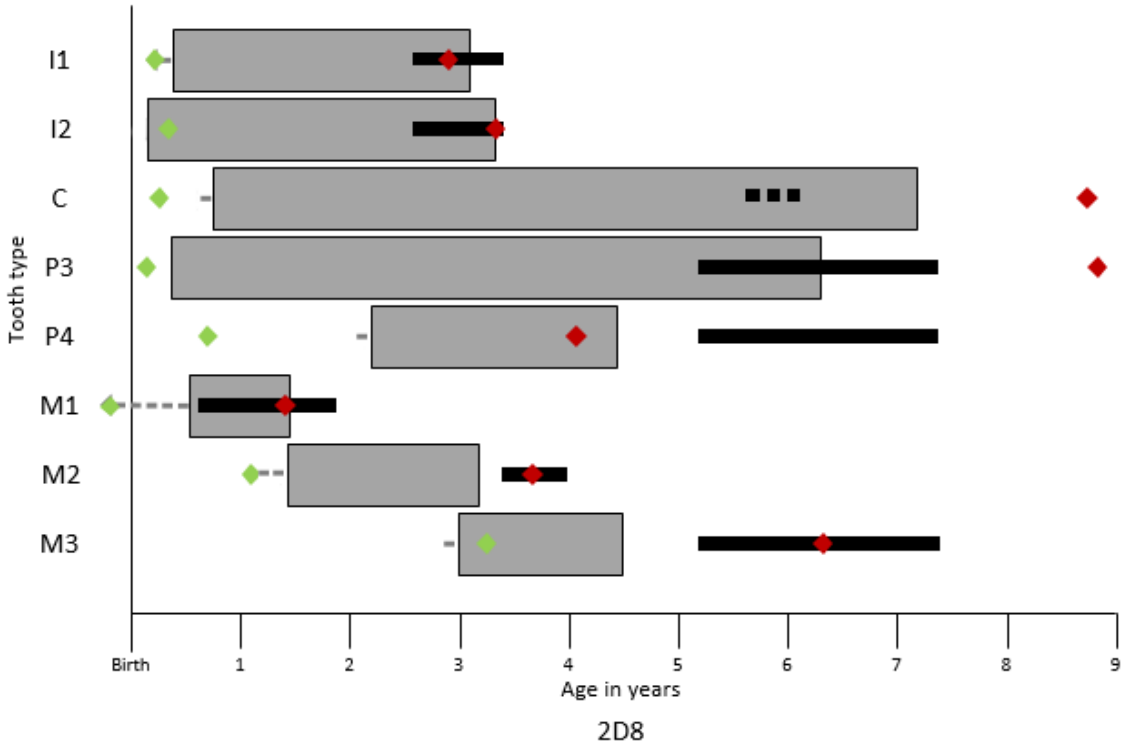

Figure 2.11: 2D8's dental development sequence positioning based on the results of Chapter 3. Grey bars are crown formation times, black bars the range of dental emergence. Green indicates the mean male crown initiation, red indicates the mean male age at crown completion.

I combined the obtained dental development data of all individuals with data on ages at gingival emergence to determine the state of dental development at dental emergence. I collated dental emergence data from the CIRMF colony records. The CIRMF staff record the state of each mandrill's tooth by noting absence (no tooth visible), 'point' (when a first tip of a tooth cusp is visible through the gingiva), or presence (tooth emerge through the gingiva). These records are usually made annually, so I took the period between the absence and the presence of a tooth as the emergence period, as in Setchell & Wickings (2004). There was some ambiguity in the CIRMF records, due to writing errors, missing records or data only recorded for one side of the dentition. The left and right sides of the mandrill dentition emerge with little variation (Setchell & Wickings, 2004), so I estimated missing data from the state of the other side of the dentition during the same veterinary examinations, and corrected apparent errors in the records based on published data for mandrills (Setchell & Wickings, 2004). For the male of unknown identity (HT12_15), I used the state of the dentition at death and the published male mandrill emergence data by Setchell & Wickings 2004 to determine dental emergence ages of his teeth.

2.7.3 General sex-specific sequence of dental development

I used the dental chronology for each individual to calculate overall male and female dental development chronologies for mandrills. To do this, I used the initiation ages of the least worn teeth and the mean age at completion for each tooth type per sex. I excluded teeth with developing crowns for mean age at completion calculation and I excluded the data of 2D8, since his dental development could not be calibrated to calendar time with the presence of neonatal lines or open roots. Combining the age at initiation of the least worn teeth with the mean age at completion of all completed crowns yielded the crown formation time. I used data from an earlier study of the same mandrill colony for the range and mid-point of gingival emergence for comparison with the sequence of dental development (Setchell & Wickings, 2004).

2.7.4 Retzius line periodicity and daily secretion rate

The Retzius line periodicity is the number of daily increments between two adjacent longer period lines. Periodicities differ to a small extent among individuals of the same species (e.g., Reid & Dean, 2006) but are thought to be constant in all the permanent teeth of one individual (FitzGerald, 1998). I determined the periodicity in each tooth by measuring the distances between adjacent longer period lines, and the distance between adjacent daily increments in the same area, and dividing the distance between longer period lines by the mean distance between daily increments. I cross-checked my measurements with two independent observers (Dirks & Adhara) and repeated the measurements in at least five different areas per crown to ensure measurement reliability. This I did for all sampled teeth for all individuals, establishing a mean periodicity for each individual, each sex and for mandrills as a species.

2.7.5 Enamel extension rates

Enamel extension rate is the rate at which the crowns grow in height, an indirect measure of the numbers of ameloblasts differentiating along the inner enamel epithelium during tooth development (Dean, 2009; Risnes, 1986). I calculated the enamel extension rate by measuring along the enamel dentine junction between the accentuated lines that I used for the crown formation analysis and matching process (Chapter 2). I divided the length of the enamel dentine junction by the number of days that it took to form the part of the tooth between the two accentuated lines (Figure 2.9,

dividing line length Y by number of days along X). I calculated these enamel extension rates from the cusp tip of each tooth to the cervix, to obtain the range in extension rates during tooth growth. I excluded teeth that were too damaged along the enamel dentine junction. I collected these data when calculating crown formation, and used accentuated lines, which are unevenly distributed, so my measurements of enamel extension rate are not regularly spaced. Other researchers have measured enamel extension rates in a more systematic manner by measuring extension rates at specific distances down the enamel dentine junction (e.g., Dean, 2009; Guatelli-Steinberg et al., 2012; Kierdorf et al., 2014). However, this was not my primary aim.

2.6.6 Measuring the position of accentuated lines

Since accentuated lines mark brief periods of disruption, they are recorded in all teeth of an individual which are developing at the same time. Therefore, each accentuated line provides a temporal anchor point to match teeth developing simultaneously (Dean et al., 1993; Dirks et al., 2002; Schwartz et al., 2006). I matched accentuated lines in each tooth with the overlapping sections of the other teeth of that individual (Figure 2.10). For the other mandrills in Chapter 3, I focussed on the most clearly visible accentuated lines, since for them I only used the positioning of the accentuated lines as anchor points to match teeth to each other in order to obtain a developmental chronology. For the mandrills I additionally used for matching accentuated lines to life history data (mandrills 5D3A, PB, Chapter 4, 2D8 and 17E2, Chapter 5), I measured all accentuated lines visible in teeth, yielding a continuous record of accentuated lines from birth to the end of dental development or to the time of death. I scored lines as accentuated if they were visible for at least 75% of the distance from the enamel dentine junction to the surface of the tooth (Antoine et al., 2009a; FitzGerald & Saunders, 2005; Goodman & Rose, 1990). I marked and measured the position of each accentuated line on the digital montages. I determined the number of days between each accentuated line by dividing the prism length between two adjacent lines by the mean daily secretion rate (DSR), obtained by measuring at least 10 sets of daily increments in the area where I measured the prism length. I took measurements with a precision of 0.1 µm. Dental development has a daily rate of tissue deposition in primates and therefore, I rounded all my measurements of the age of formation of a line to a single day. Some accentuated lines do not have this resolution, however, and can appear to cover more than one day. In those cases, I measured the midpoint of an accentuated line for its position. If a line covered more than one longer period line (7 days, Chapter 3), I measured both the position where the accentuated line started and the position where it ended. I kept measurement error to a minimum by repeating multiple of my measurements and I kept observer bias to a minimum by having two independent specialists replicating a selection of my markings and measurements throughout the period of data collection (Dirks & Adhara). This resulted in obtaining a

pattern of marked accentuated lines and a set of corresponding measurements indicating the number of days between all marked lines for each tooth (Figure 2.10).

I focused my accentuated line assessment, measurements and matching on the enamel, since I found the lines generally to be clearer in the enamel than in the dentine, allowing for more precision in my measurements. I used accentuated lines in the dentine for areas to improve confidence in measurements where few or no crowns were developing simultaneously and when enamel quality was poor or absent. This was particularly necessary when measuring and matching the M3 to the other teeth, since most crowns are complete by the time the M3 initiates.

2.7.7 Accentuated line classification

The teeth contained a dense pattern of accentuated lines, and it was clear that some accentuated lines in a tooth were more distinct than others. Although this is a known phenomenon, it is not yet understood what causes this difference (e.g. Goodman & Rose, 1990; Rose, 1977). Apart from some lines being more distinct than others, the visibility and intensity of accentuated lines corresponding to the same point in time was not uniform among overlapping teeth either. For example, accentuated lines in the incisors and canine look different from the accentuated lines in the molars. This is partly related to the differences in morphology and therefore microstructure between the teeth, differences between cuspal and lateral enamel, and therefore the position of the accentuated line within the tooth, and also to the thickness and quality of the section and preservation of the teeth. This results in some lines being very distinct in one tooth and only just visible in another tooth, even though they relate to the same point in time, and therefore relate to the same disturbance of ameloblast and odontoblast function.

To overcome this non-consistency of accentuated line expression among the teeth of one individual, I decided to apply a classification system. I thereby decided per tooth if a line was accentuated or highly accentuated. I did this as follows: within one tooth, I marked every visible accentuated line, but divided them in two categories: accentuated or highly accentuated, based on how distinct they appeared within that section. For the final combined accentuated line sequence per individual, I classified lines only as highly accentuated if they were marked as highly accentuated in at least two sections from two different teeth that overlapped in development (Figure 2.12). I could not apply this rule to the lines in the top of the M1 and the root of the M3, as they develop earlier (M1) and later (M3) than the other teeth and have no other teeth for correlation. Therefore, in the final

accentuated line sequence, I included all accentuated lines visible in these M1 and M3 parts in the final sequence, but only mark them as highly accentuated if they were similar in appearance to the lines in the rest of that specific tooth that I had marked as highly accentuated in the final sequence.

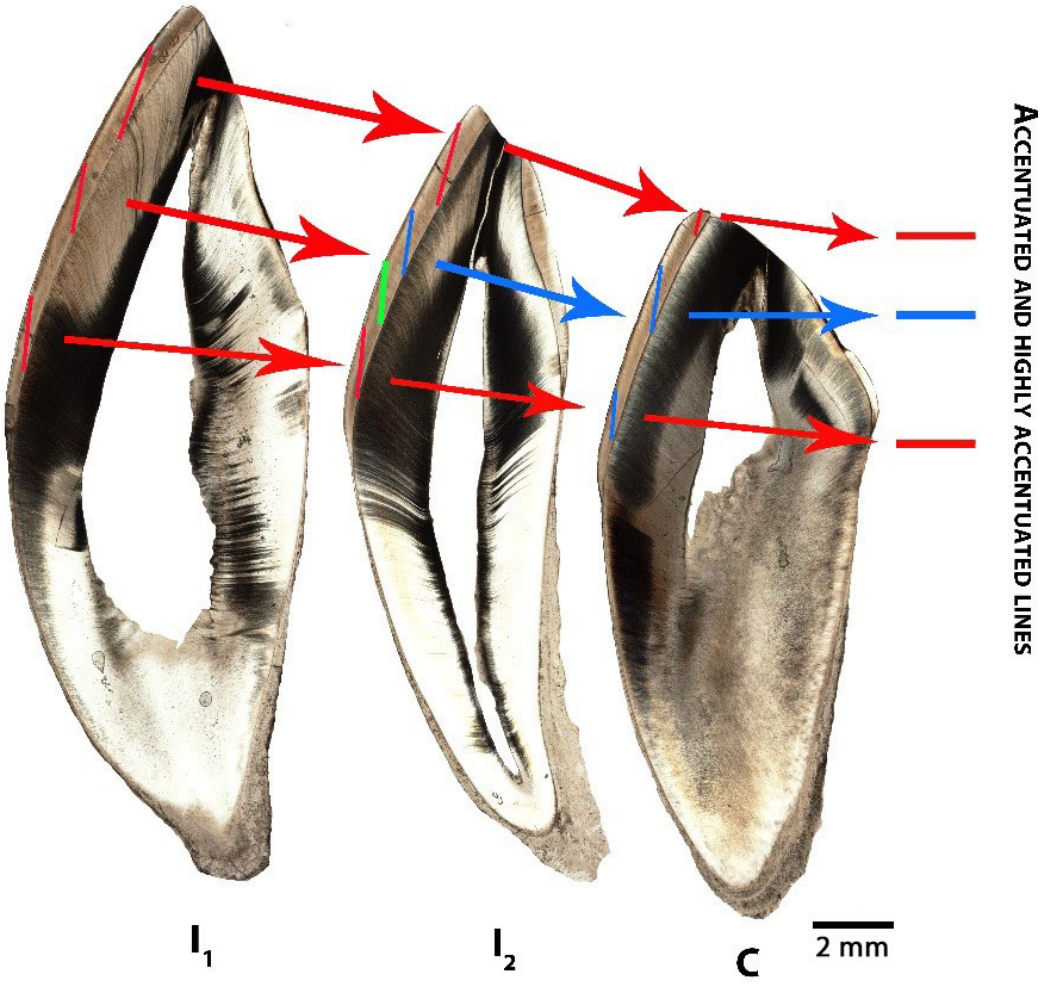

Figure 2.12: Accentuated line classifications for final accentuated line sequence. Blue = accentuated lines, red= highly accentuated lines. Green line = accentuated line that is only visible in one tooth, does not have any corresponding lines in other overlapping teeth, and therefore not included in the final accentuated line sequence. Micrographs taken with 4x objective.

2.7.8 Correlating accentuated line sequences to calendar time

To correlate the obtained highly accentuated line sequences to calendar time, I used two different strategies: I used the neonatal line visible in first molars to match dental development to known date of birth. From there onwards I could assign an age to every following highly accentuated line. For individuals who died before the end of dental development, I could correlate the developing crowns or roots to known age at death. For 5D3A I used the neonatal line visible in the LM_1 distal section to

match dental development to her known date of birth. I could not identify a neonatal line in PB's first molars due to wear, but I could correlate the developing root of the RM^3 to her known age at death, and thus accurately correlate the sequence of highly accentuated lines to calendar time.

17E2 had a neonatal line in his M_1, allowing calibration of his dental development sequence to calendar time. His C^1 root was still open at his death too but using this as a calibration point was likely to introduce error since the longer period lines and accentuated lines in his canine were not clear. Moreover, since the canine is very large, multiple smaller measurement errors will result in a larger error in the timing of the end of crown formation, and therefore not a good reliance for calibration. I therefore calibrated his sequence based on the neonatal line. 2D8's first molars were extremely worn with no neonatal lines preserved and his dentition was complete when he died. Without a neonatal line or open roots, it was difficult to calibrate the dental sequence to calendar time. To overcome this problem, I used the positioning of the dental sequences based on the three younger males discussed in Chapter 3 as a guide, yielding the most likely positioning of his dental development sequence (Figure 2.11).

2.7.9 Matching accentuated lines to life history information

Although it is not yet fully understood what causes the difference in accentuated line severity, it is thought that the duration and severity of the stressor affect the line appearance (e.g. Goodman & Rose, 1990; Rose, 1977). Therefore, for testing the hypothesis that the accentuated lines correlate with life history data, I only focussed on the highly accentuated lines, instead of taking every minor perturbation into account. After first having determined the age at formation of the highly accentuated lines, I then matched the observational data to these highly accentuated lines, which I had collated as a second data set, blindly from the histological data. Previous research has demonstrated that although dental development has a daily rate of tissue deposition, daily precision is not realistic when measuring and matching multiple teeth, due to inevitable measurement error at that level of precision. To overcome this measurement error in the matching of accentuated lines to life history events, I decided to give a margin to my matching. I chose seven days as the range of my matching, because this equals the mean periodicity for mandrills (Chapter 3), and accentuated lines often appear to overlie striae of Retzius (Hillson, 2014). Therefore, for an event predicted to be correlated with an accentuated line, it had to occur within a seven-day range of the formation of a highly accentuated line (3 days before, 3 days after or on the day of the line formation itself). If the

life history event and highly accentuated line did not coincide within this seven days range of each other, I would consider it not to be a match.

Since the calibration of 2D8's dental development sequence to calendar time was estimated, his accentuated line sequence was likely not to match life history events within the margin of seven days as for the other mandrills. I chose a range of six weeks instead, since 2D8's teeth cannot initiate at a later age than the current positioning due to their state of wear, but could in theory initiate up to six weeks earlier, whereby all his teeth (except for the damaged I_2) would still initiate at a later age than the teeth of the three younger males combined (green marks, Figure 2.11), an essential criteria for 2D8's calibration of dental development sequence to calendar time (Chapter 3).

2.7.10 Dental wear

Due to the ages of the individuals and their tough diet, all (erupted) teeth in my sample show wear, in varying degrees. The amount of enamel wear of teeth is age-related, with young individuals having less wear than older individuals. The incisors and the functional cusps of each individual's molars are worn most, being the hypoconids and protoconids of the molars in the mandible and the protocones and hypocones of the molars in the maxilla. Since teeth of an individuals' dentition do not emerge simultaneously but in a sequence, wear also differs between teeth; with the first molar (the first to emerge) being further worn than the third molar (the last to emerge). When teeth are worn, I could not acquire all accentuated lines from initiation till completion of the tooth, and tooth initiations are therefore all minimal crown formation times and age at initiation of each tooth is the latest age at initiation: the tooth will have initiated earlier but the calculated age is the closest age possible to get from the sample (Figure 2.13).

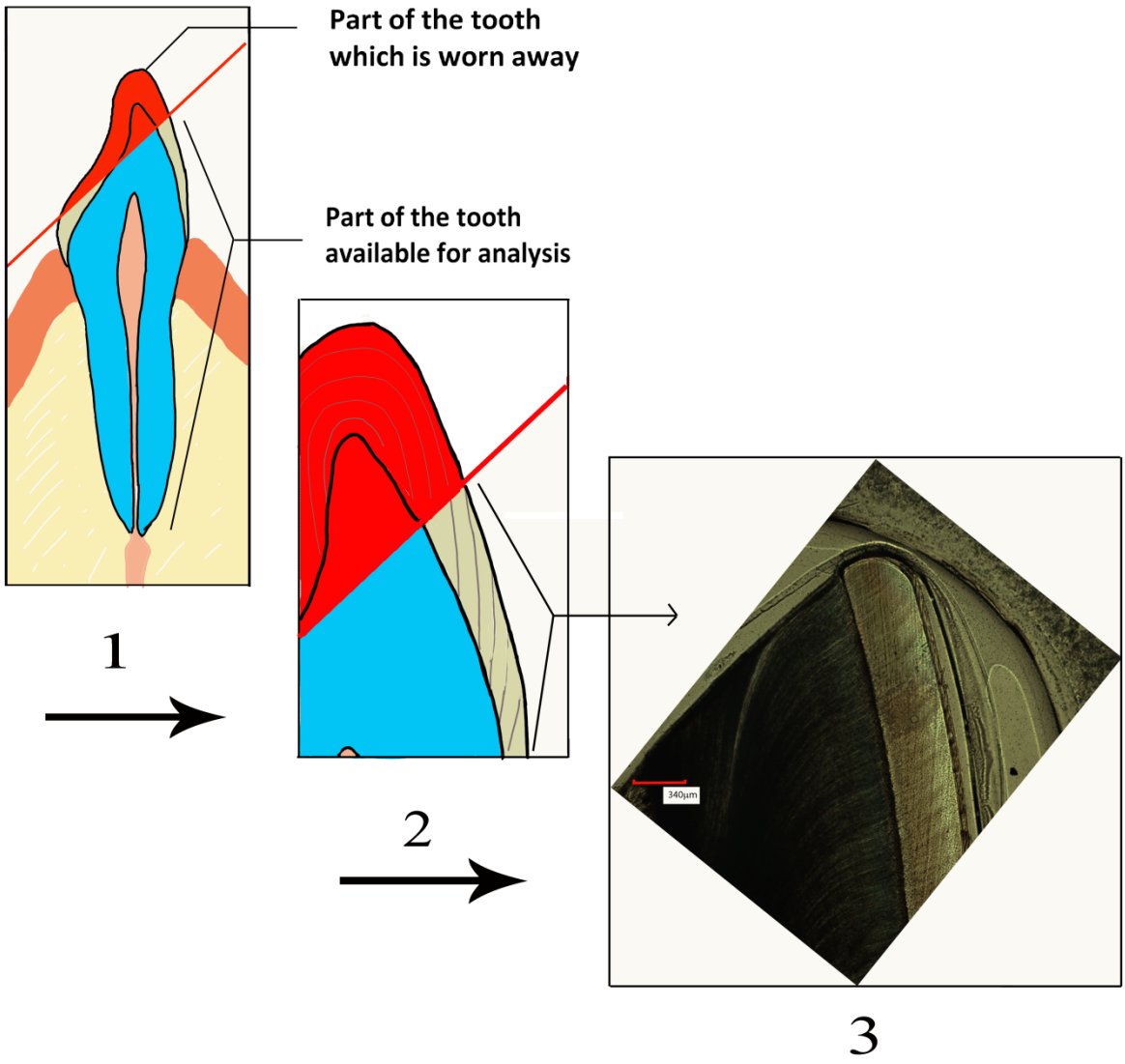

Figure 2.13: Tooth wear in relation to a complete tooth, demonstrating how all calculated initiation ages of worn teeth are bound to be estimates. 1: Cross section of a tooth in the jaw. Red = area lost by wear. 2 = crown tip, including longer period lines. 3 = Micrograph of the same region of the tooth in of I_2 (mandrill 5D3A).

Chapter 3: The sequence and chronology of dental development in mandrills

3.1 Chapter aims

In this chapter, I combine histological analysis of the dentitions of naturally deceased male and female mandrills (*Mandrillus sphinx*, Cercopithecinae) housed at CIRMF, Gabon, with their life history data to:

1) Examine the chronology of dental development in individual male and female mandrills which I will use in the following chapters (4 & 5) to examine the timing of accentuated line formation in the teeth of individuals

Additionally, by examining individual mandrill dental development sequences I collect data to:

2) Construct a general sex-specific dental chronology for mandrills and investigate sex differences in dental developmental

3.2 Results

3.2.1 Sequence of dental development in females

5D3A's M_1 initiated before birth with neonatal lines visible after 22 days of tissue formation (Figure 3.1). The other females probably also initiated their M_1 before birth, but 16L's M_1 and PB's M^1 cusp tips were lost due to extensive wear (Figure 3.2). Anterior teeth initiated stepwise for all females, with I_1 first, followed by I_2 and then C_1. I could not calculate the initiation of 5D3A's C_1 as it was extremely worn. Premolars initiated stepwise with P_3 followed by P_4. M_2 showed little wear and initiated at a similar age to P_4. The last tooth to initiate was M_3 which initiated at a similar age across the females. 5D3A's and PB's M3s initiated before the end of their M2 crown formation, but 16L's M_3 initiated after M_2 root formation had begun, with no overlap between the crowns

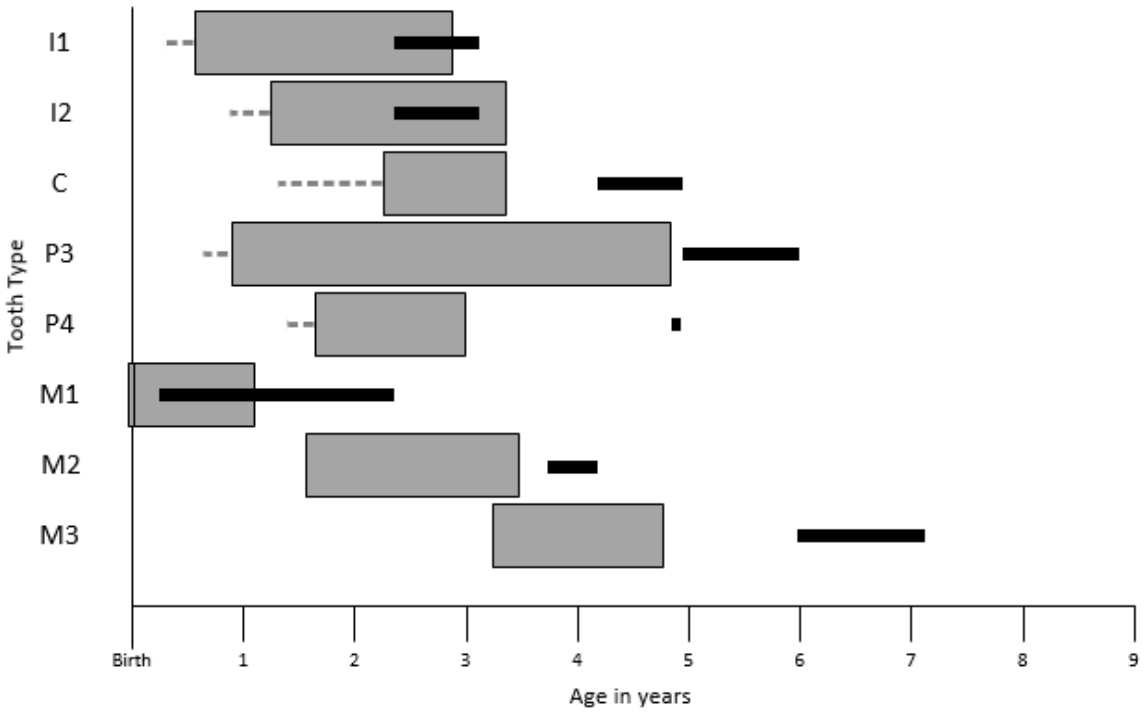

Figure 3.1 (A) Female 5D3A

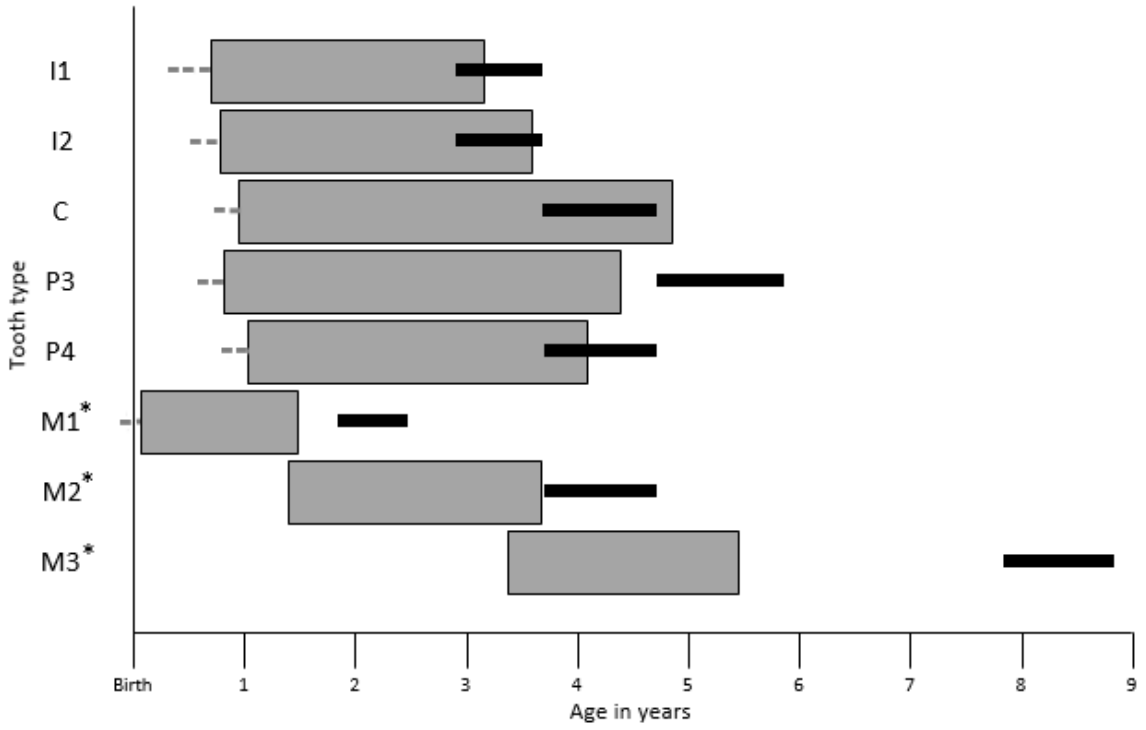

Figure 3.1 (B) Female PB

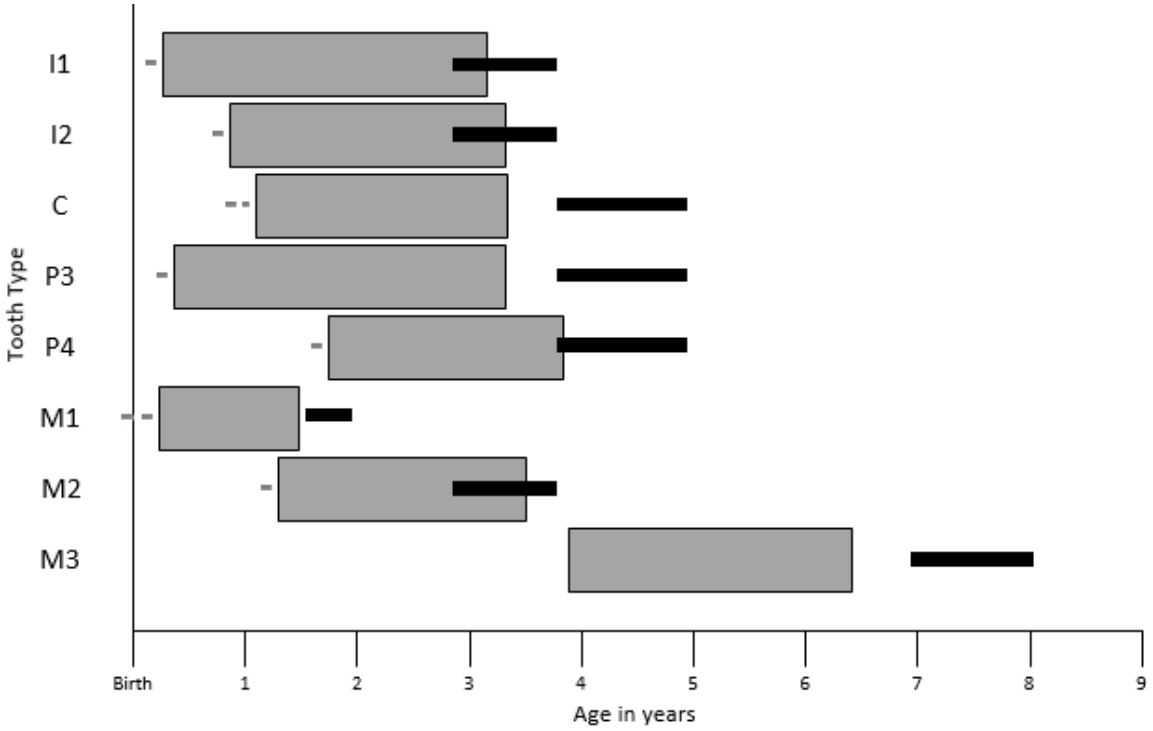

Figure 3.1 (C) Female 16L

Figure 3.1 (A-C): Sequences of dental development in three female mandrills (5D3A, PB and 16L). Mandibular teeth, unless marked with * for maxillary. Grey bars indicate crown formation time, black bars indicate gingival emergence (range). Short black bars indicate the tooth was observed to be emerging through the gingiva at the time of a CIRMF control. Dotted line indicates estimation of tooth wear.

Crown formation time of the M1 was similar among females (Figure 3.1). 5D3A, the oldest female, had the most tooth wear on her molars and therefore the most underestimated M_1 crown formation time. The crown formation time of incisors was similar across the females as well. Canine crown formation time was more variable than that of M1 and the incisors. PB's C_1 had a large crown and two roots (Figure 3.2) and grew for an additional year and a half compared to the other females. Females had different P_3 and P_4 crown formation times and age at completion, but this could be related to slight differences in the sectioning plane (Figure 3.3). Crown initiation and crown formation time of the M2 were very similar among the females. The formation and completion time of the M3 varied across the females but this difference is probably partly due to the cusps available for measurement (Chapter 2, Table 2.4).

Anterior teeth showed little or no time between the end of crown formation and gingival emergence, and some teeth emerged when the crowns were still forming (Figure 3.1). In particular, the incisors had little or no time between the end of crown formation and emergence. In 5D3A and 16L, C_1 emerged later relative to crown formation than the incisors. PB's large C_1 emerged while the

crown was still developing. The premolars and molars emerged with some of the root already developed.

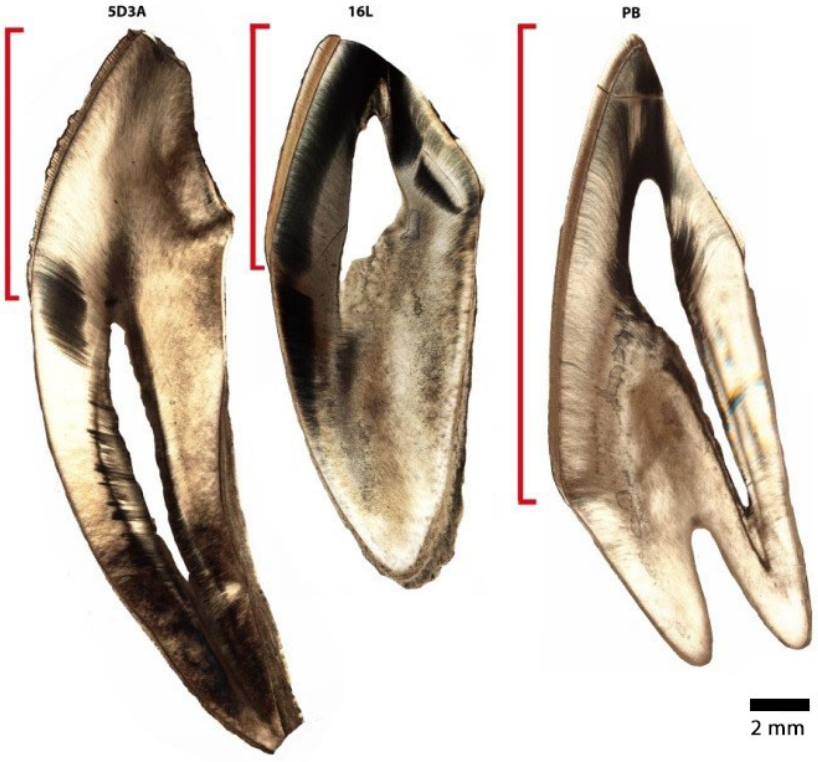

Figure 3.2: Thin sections of the female canines. PB has a larger canine crown than the others an and two roots.

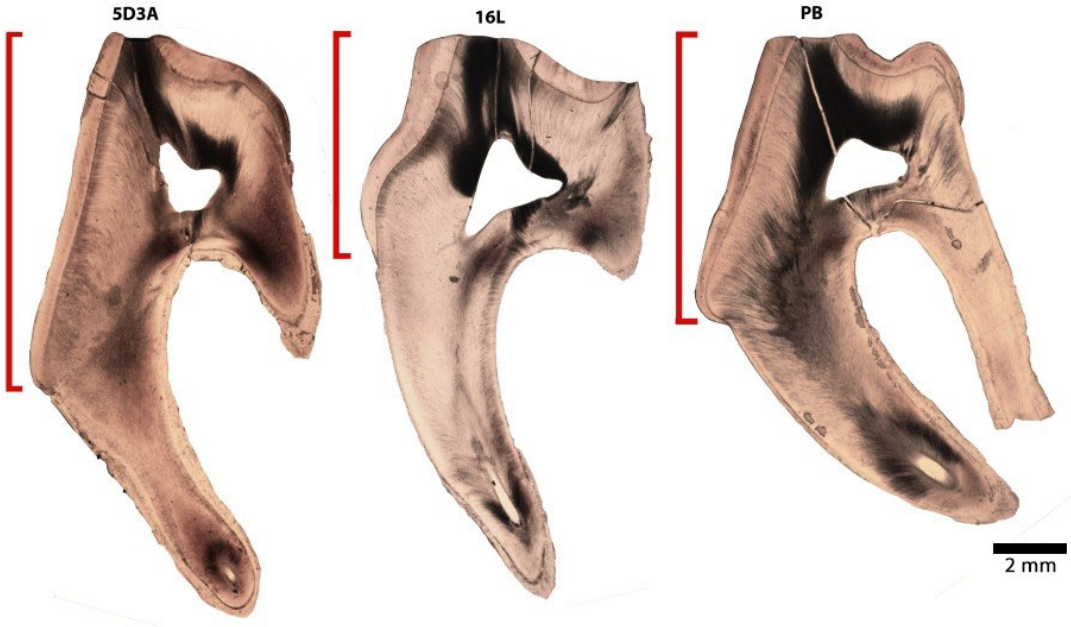

Figure 3.3: Thin sections of female P_3. 5D3A and PB have an elongated honing-like anterior, much more so than 16L, probably due to different section planes.

3.3.2 Sequence of dental development in males

Neonatal lines were visible after 62-76 days in male M1s, apart from in 2D8 whose M_1 was extremely worn. All male incisors initiated shortly after birth. The anterior teeth initiated within a short period of each other, but the order differed across individuals. In 17E2 and HT12_15 the I_1 initiated before I_2, while in 2D8 and 5I2 the I_2 initiated first. Canine initiation varied: 2D8 and 5I2 both initiated their C_1 after the incisors. HT12_15's unworn C_1 initiated before his incisors. 17E2's C^1 initiated before birth. In all males, P_3 initiated before P_4. Molars initiated stepwise: M2's initiated as the M1 crowns completed. M3s initiated just before or at the time of M2 crown completion, except for HT12_15 who initiated M_3 after M_2 root formation had begun, with no overlap between the crowns (Figure 3.4).

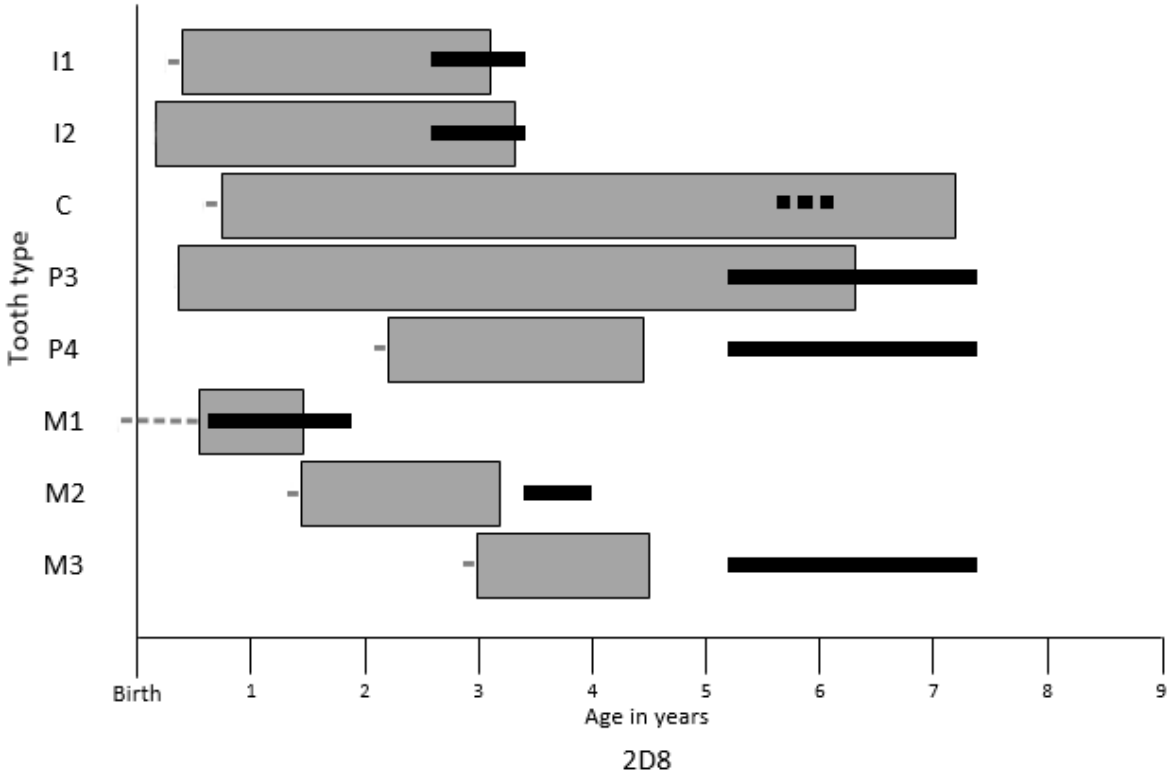

Figure 3.4 (A) Male 2D8

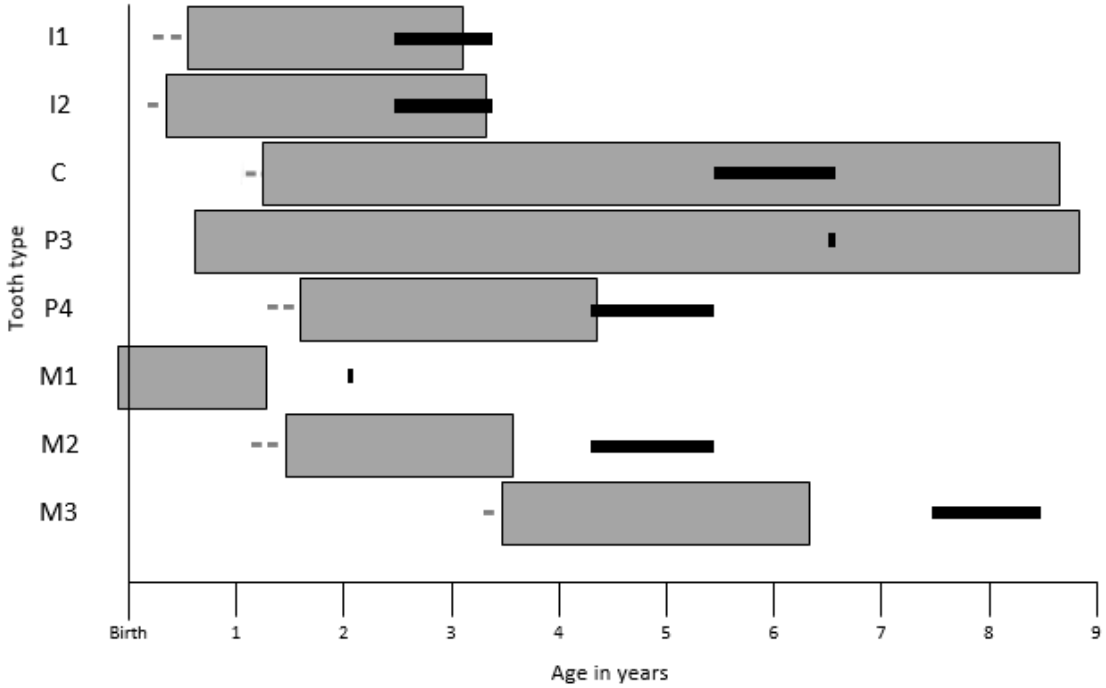

Figure 3.4 (B) Male 5I2

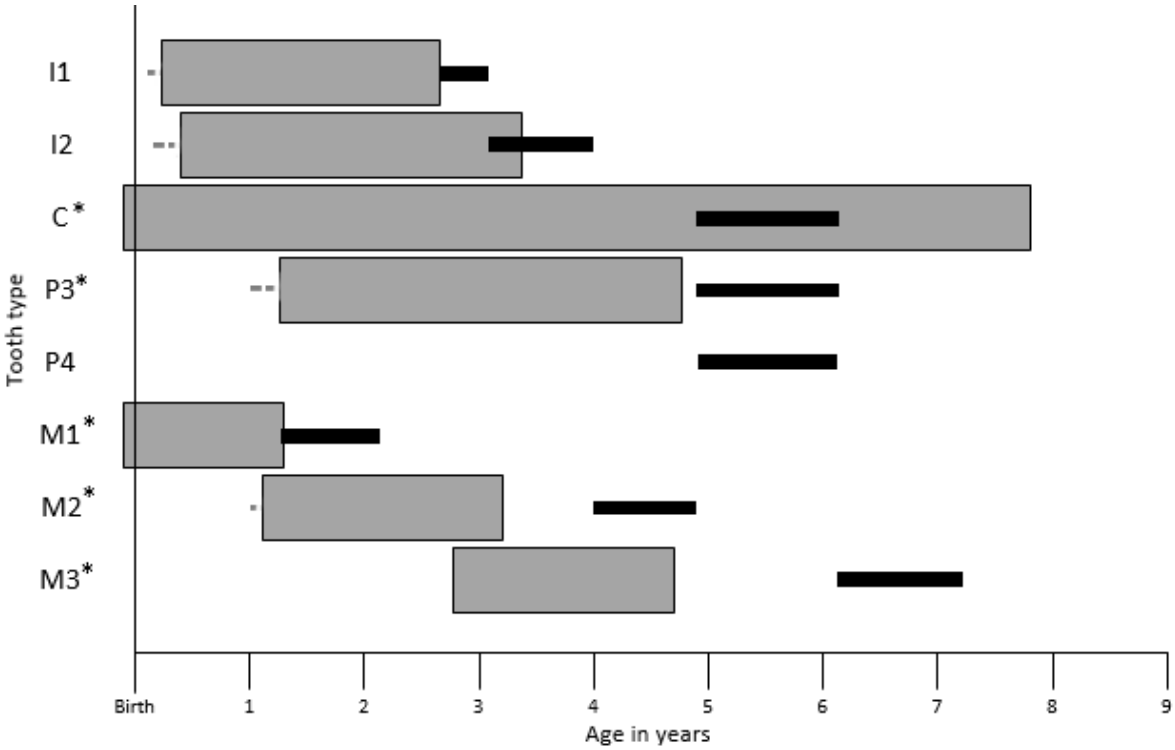

Figure 3.4 (C) Male 17E2

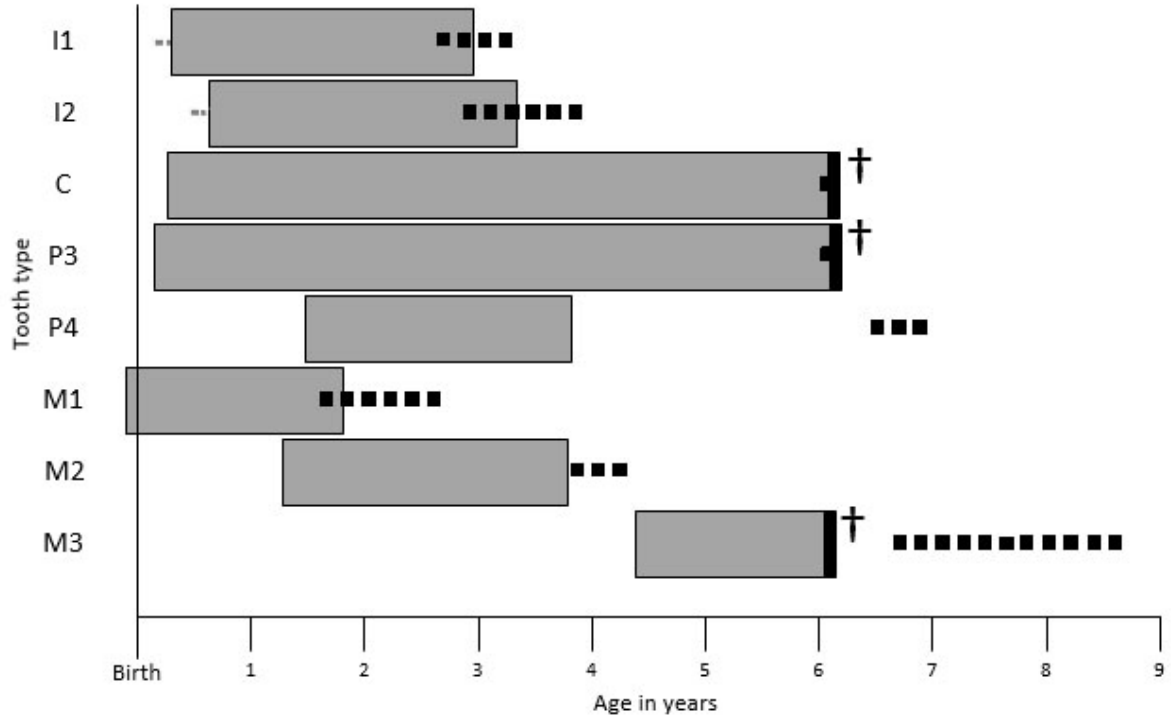

Figure 3.4 (D) Male HT12_15

Figure 3.4 (A-D): Sequences of dental development in four male mandrills (2D8, 5I2, 17E2, and HT12_15). Mandibular teeth, unless marked with * for maxillary. Grey bars indicate crown formation time, black bars indicate gingival emergence (range, dotted in case of ambiguity from CIRMF files). Short black bars indicate the tooth was observed to be emerging through the gingiva at the time of a CIRMF control. Dotted grey line indicates estimation of tooth wear. HT12_15 died before crown development completed (†).

Canines had the longest crown formation times of all teeth (Figure 3.4). 17E2's C^1 took longer to form than C_1 in the other males. Male P_3 had very elongated honing facets with gnarled enamel and only slightly shorter formation times than C_1. However, P_3 and C_1 crown formation time varied among individuals and 5I2's P_3 and C_1 took much longer to form than those of 2D8. HT12_15's C_1 was still developing when he died. Only a P^3 was available for 17E2, which is a much smaller tooth than P_3 with no honing facet. Its formation time was therefore also much shorter than P_3 in the other males. M1 had very similar formation and completion times across individuals, except for 2D8 whose M_1 was very worn. M3 crown formation time varied, but this was related to the cusps available for measurement (Chapter 2, Table 2.4).

As in females, several of the male teeth emerged through the gingiva before the end of their crown formation. This was particularly the case for the C_1 and P_3 which emerged when crowns were still developing, but also the incisors emerge with little or no root formation. 2D8's C_1 emergence was unclear from the CIRMF records but was probably similar to that of the other males (See Appendix B). The male P4 and molars emerged much later after the end of crown formation than the incisors, C_1 and P_3. I had no data for gingival emergence in HT12_15, but the C_1 and P_3 were erupting through the alveolus at the time of death, the stage prior to gingival emergence, and the crowns were still developing (Figure 3.5).

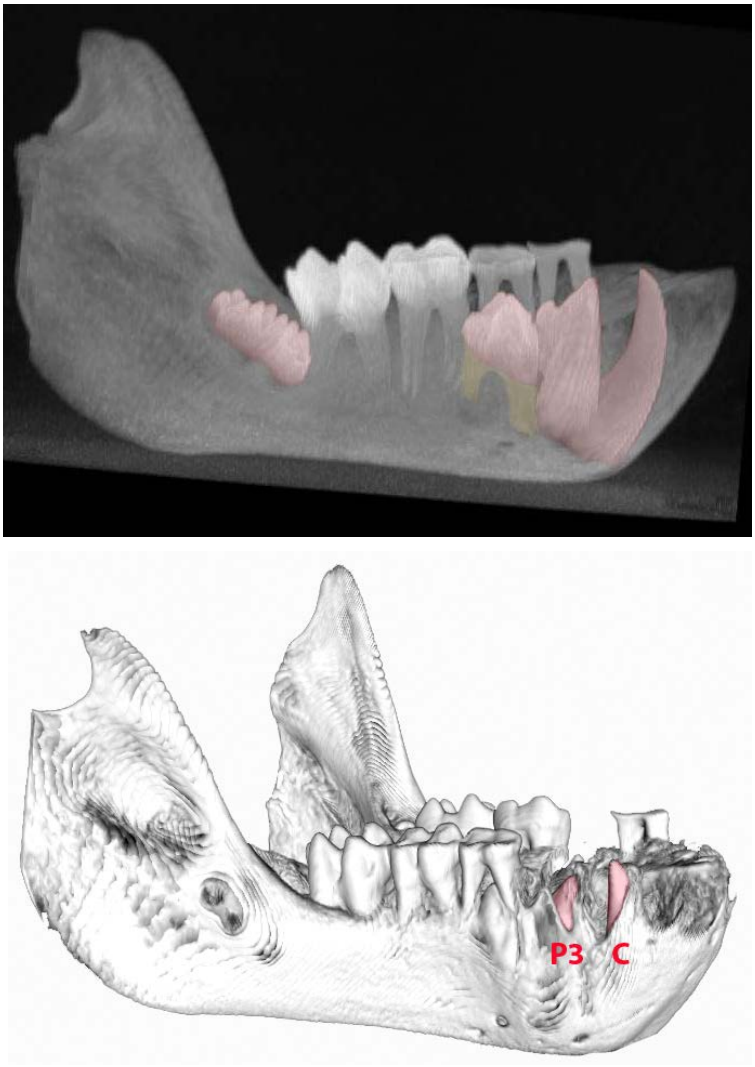

Figure 3.5: Mandible of male HT12_15, showing state of dental development at death. C_1 and P_3 are erupting through the alveolus. P_4 is close to eruption, and M_3 is still fully within the crypt. Permanent incisors were fully erupted but did not stay in position during scanning. The dp_3 and dp_4 remained in occlusion but are worn down to their roots with no enamel left. Scan imaging courtesy of Tony Owens, Superintendent Radiologist, Dental Hospital. Newcastle upon Tyne. Image editing by S. Lemmers

3.3.3 Sex-specific sequence of dental development

Males appear to initiate dental development earlier than females with more prenatal enamel formation in their M_1. (Figure 3.6 & 3.7). All other teeth except the P_4 also appear to initiate earlier in males than in females, although tooth wear makes this difficult to assess with certainty. Male crowns took longer to form than female crowns except for I_1 which took longer in females. Crown formation time differed most between the sexes for C_1 and P_3. Female incisors appear to emerge at the end of or soon after crown completion. Males may emerge their incisors later than females in comparison to the end of their crown formation. The molars initiated stepwise in both sexes. In both sexes, M_2 initiated after M_1 is complete, but M_3 initiated during M_2 crown formation. Female M_3 took longer to emerge after crown completion than those of males, although the timing of M_3 emergence has a very wide range in both sexes (Setchell & Wickings, 2004). Females finished crown development earlier than males did. When including root formation, females also completed their dental development earlier than males do. The last tooth to finish developing is the male C^1 (Figure 3.6 & 3.7)

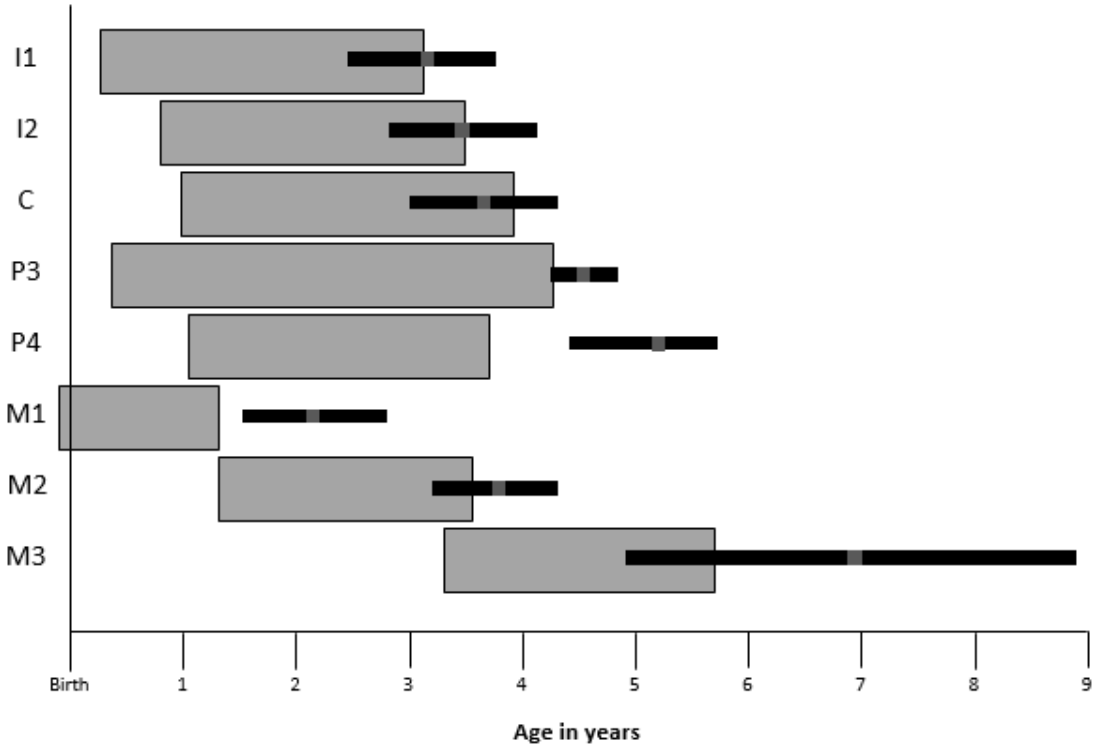

Figure 3.6: Sequence of dental development in female mandrills. The chart is a composite of data from three female mandrills with initiation based on the least worn tooth, and age at crown completion based on the mean age at crown completion from all individuals. Grey bars indicate crown formation time, black bars indicate age at gingival emergence (range) with mid-points in grey boxes, based on published data (Setchell, 2004).

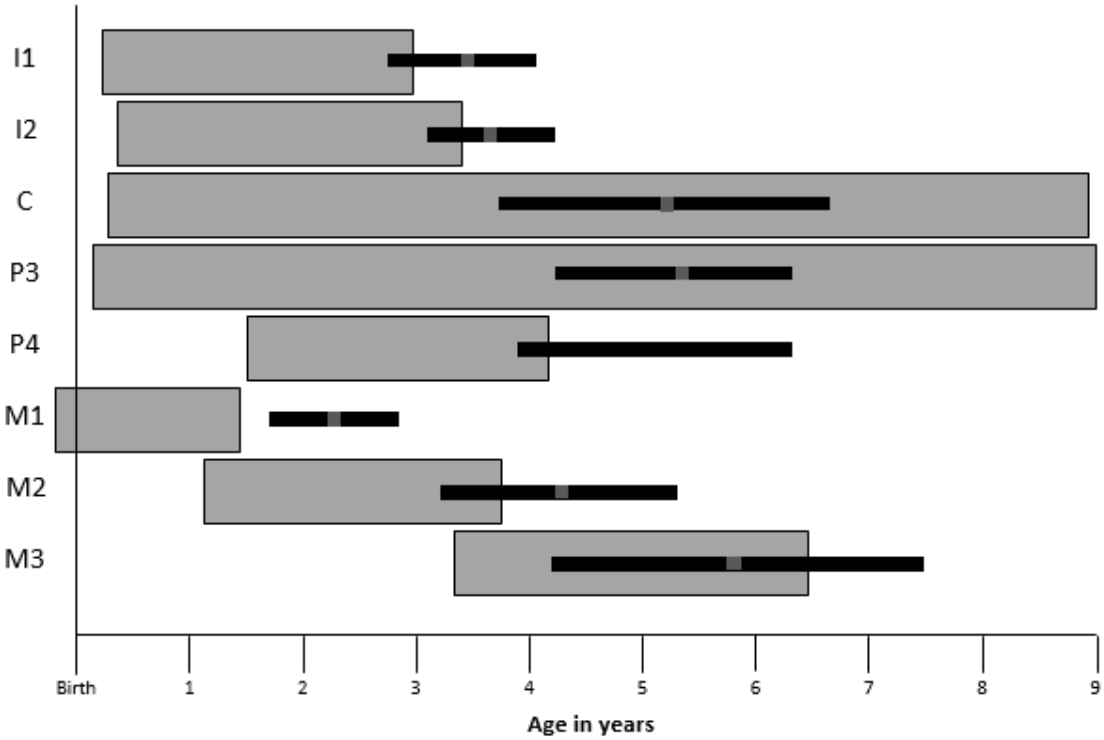

Figure 3.71: Sequence of dental development in male mandrills. The chart is a composite of data from 3 male mandrills (17E2, 5I2 and HT12_15, mandrill 2D8 excluded), with initiation based on the least worn tooth, age at crown completion based on teeth from three individuals. Grey bars indicate crown formation time, black bars indicate age at gingival emergence (range) with mid-points in grey boxes, based on published data (Setchell, 2004).

3.3.4 Retzius line periodicity and daily secretion rate

Mean female periodicity was 7 days. Periodicities were clear and consistent for 5D3A (7 days) and 16L (8 days) but PB's periodicity was difficult to establish. Neither I nor W. Dirks could obtain consistent results, but the mean of all our counts from PB's teeth was 7 days. PB was the only individual who had longer period lines visible throughout the enamel of multiple teeth, allowing me to calculate crown formation time by multiplying the number of longer period lines by the periodicity, in addition to the modified Risnes method which I used otherwise. Multiplying the number of longer period lines in PB's teeth with the periodicity of 7 resulted in a disproportionately longer crown formation time than using the modified Risnes method. Multiplying the number of longer period lines with a periodicity of 6 days matched the results of the modified Risnes method exactly. However, neither I nor W. Dirks found a periodicity of 6 days in this animal. PB's periodicity

is therefore ambiguous. Mean male periodicity was also 7 days. Periodicities were clear and consistent for all four males, with 2D8 having the lowest periodicity (6 days), 5I2 the highest (8 days) and 17E2 and HT12_15 both in between (7 days). Mean daily secretion rate was similar across the females, ranging 3.8 to 4.1μm among all teeth with a mean of 3.9 μm. Mean daily secretion for the males were similar to the females, ranging 3.8 to 4.0 μm with a mean of 3.9 μm (Appendix B).

3.3.5 Enamel extension rate

I plotted the extension rates starting from age at initiation. I do not know the actual age of initiation of the teeth due to wear. The differences along the x-axis therefore depict the differences in wear between the teeth. Mean mandibular incisor extension rate was slightly higher in males than females (Table 3.2) but there was overlap for individual teeth. PB's incisors were larger than those of the other two females, grew for longer, and had a slightly lower extension rate than the other females (Figure 3.8 & 3.9). Incisors showed an increase in extension rate toward the cervix of the crown, particularly in I_2 of 17E2 and HT12_15. Mean male C_1 extension rate was higher extension than in females and increased towards the end of towards the cervix (Figure 3.10). PB's C_1 was much larger than 16L's C_1 but both canines extended at the same rate, with PB's C_1 continuing at the same rate until completion. 5D3A's C_1 was too damaged to include. As with the incisors, there was a slight increase in extension rate towards the cervix, except for HT12_15 whose C_1 was still developing when he died. 17E2's C^1, the only maxillary canine in the sample, had the highest mean extension rate of all teeth (Table 3.2). The mean male P_3 extension rate was higher than for the female P_3 (Figure 3.11). PB, 5I2 and 2D8's P_3 extension rate increased slightly towards the cervix. The mean extension rate of P_4 was very similar among individuals and between sexes (Table 3.2) but extension rates were variable throughout the teeth (Figure 3.12), related to the P4's crown morphology. HT12_15 and PB had very little wear on their P_4 and had specific high extension rates at initiation. Extension rate increased slightly at the cervix in all individuals, but specifically for 2D8 and HT12_15. Mean M_1 extension rate was variable across the individuals (Figure 3.13, Table 3.2), unlike the extension rate of the M_2 which was very similar across all individuals (Figure 3.14, Table 3.2). HT12_15 had a higher extension rate at the cusp tip and therefore overall a higher mean extension rate than the other individuals, since his M_2 was hardly worn. Extension rates increased slightly towards the cervix in all individuals, mainly for 5I2 and 16L. M_3 had similar mean extension rates across all individuals (Table 3.2). Mainly the individuals with the least worn teeth showed the highest extension rates near the cusp (Figure 3.15). Although every tooth type had a higher mean extension rate for the males than for the males, there was is individual variation.

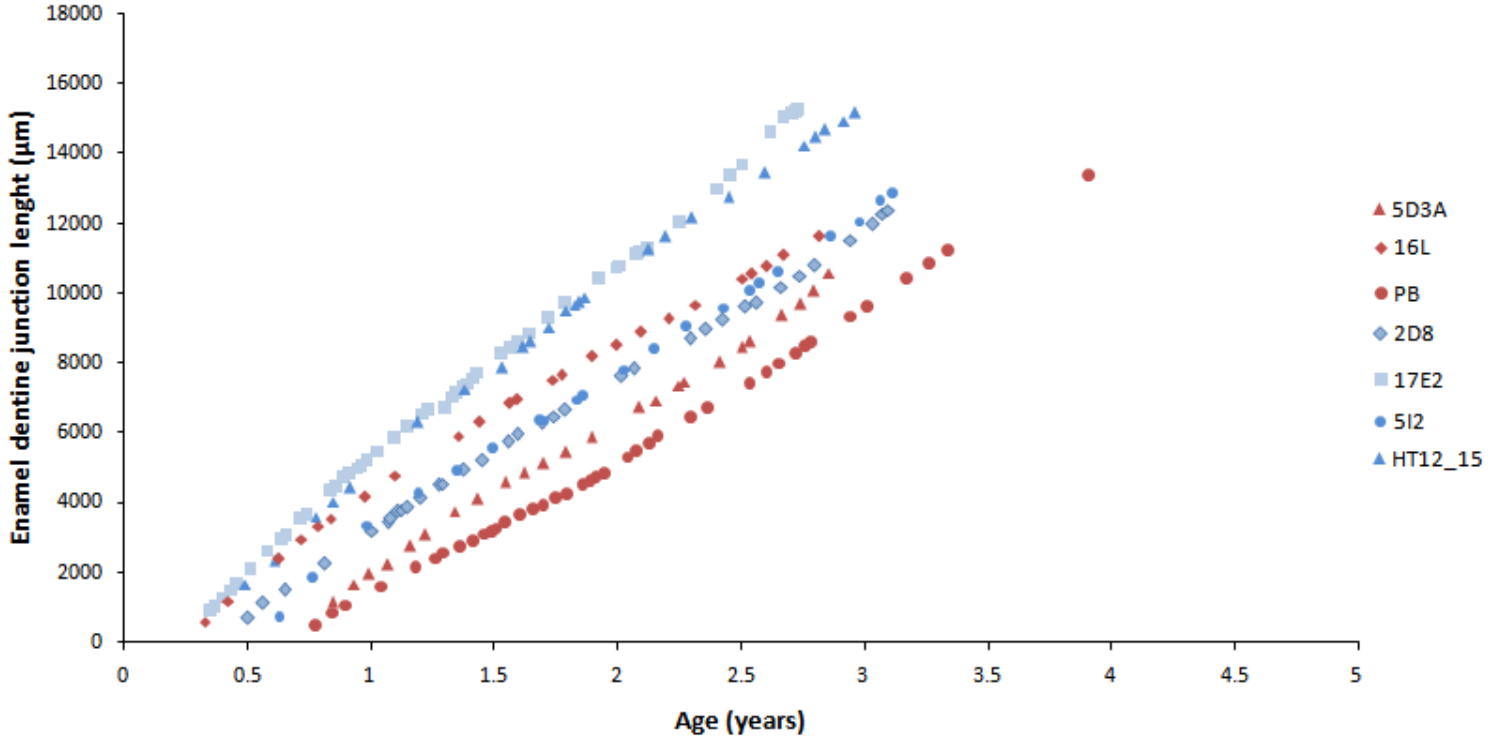

Figure 3.8: Enamel dentine junction length by age for female and male I_1 starting at age of initiation (cusp), ending at crown completion (cervix). Slope indicates enamel extension rate. Males in blue, females in red, individuals represented by different symbols.

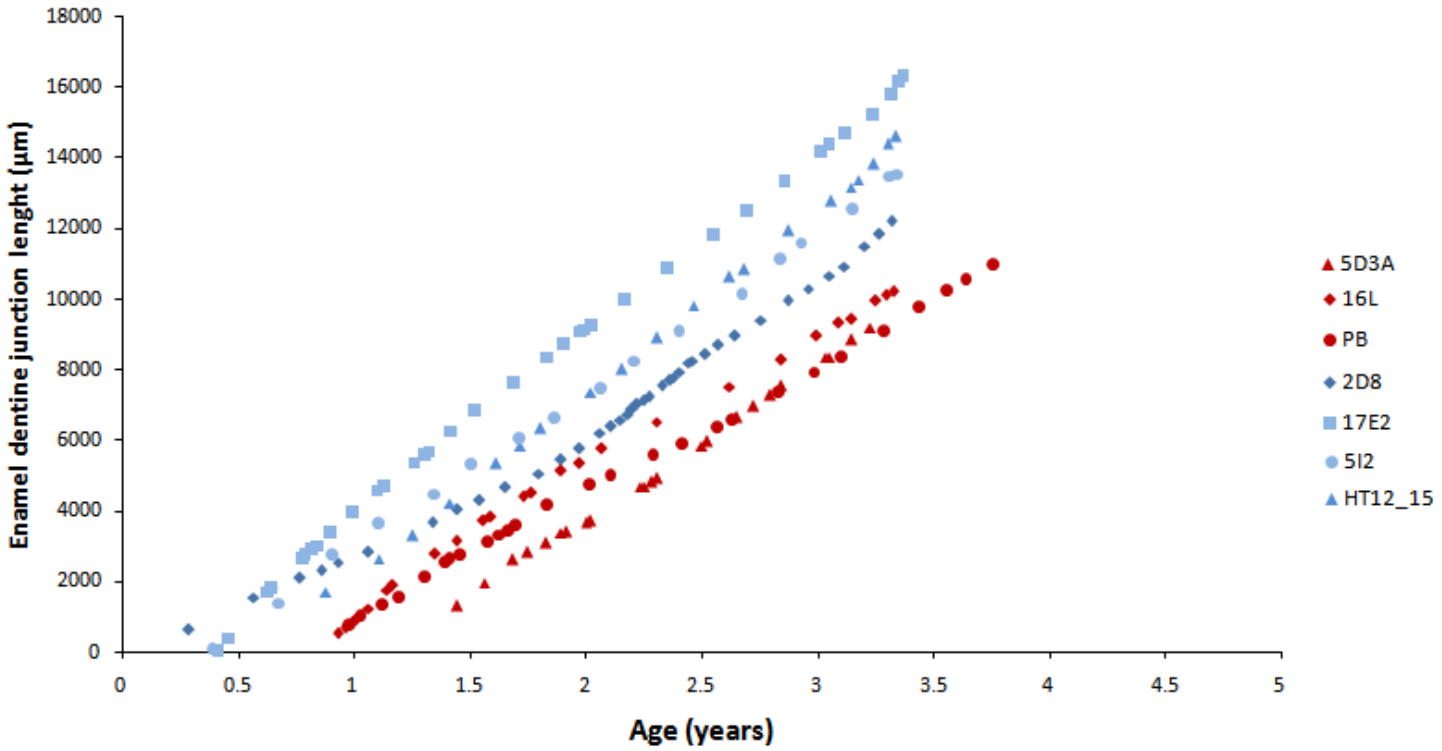

Figure 3.9: Enamel dentine junction length by age for male and female I_2 starting at age of initiation (cusp), ending at crown completion (cervix). Slope indicates enamel extension rate. Males in blue, females in red, individuals represented by different symbols.

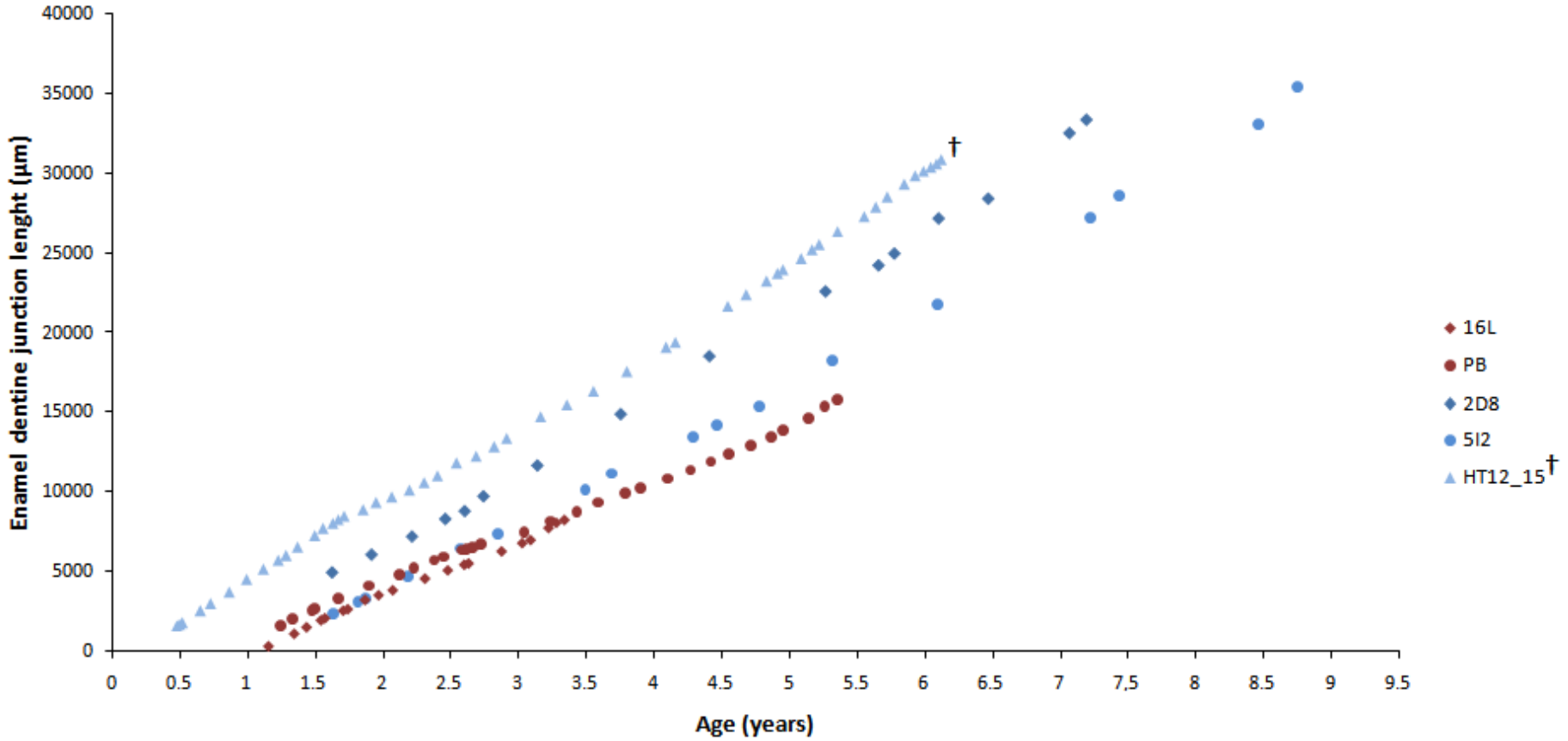

Figure 3.10: Enamel dentine junction length by age for male and female C_1 starting at age of initiation (cusp), ending at crown completion (cervix). Slope indicates enamel extension rate. Males in blue, females in red, individuals represented by different symbols. Ht12_15's crown was developing when he died (†).

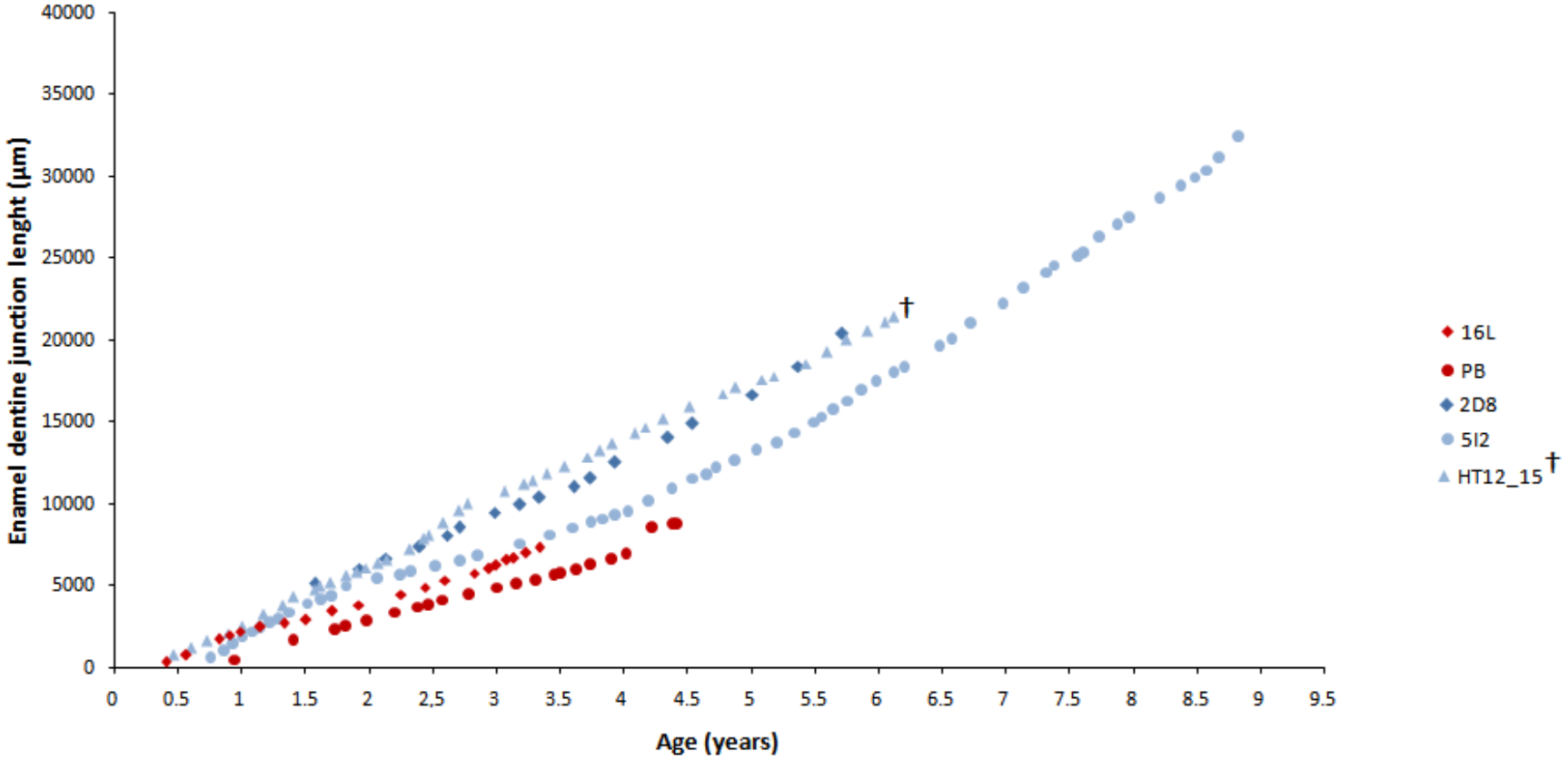

Figure 3.11: Enamel dentine junction length by age for male and female P_3 starting at age of initiation (cusp), ending at crown completion (cervix). Slope indicates enamel extension rate. Males in blue, females in red, individuals represented by different symbols. HT12_15's crown was developing when he died (†).

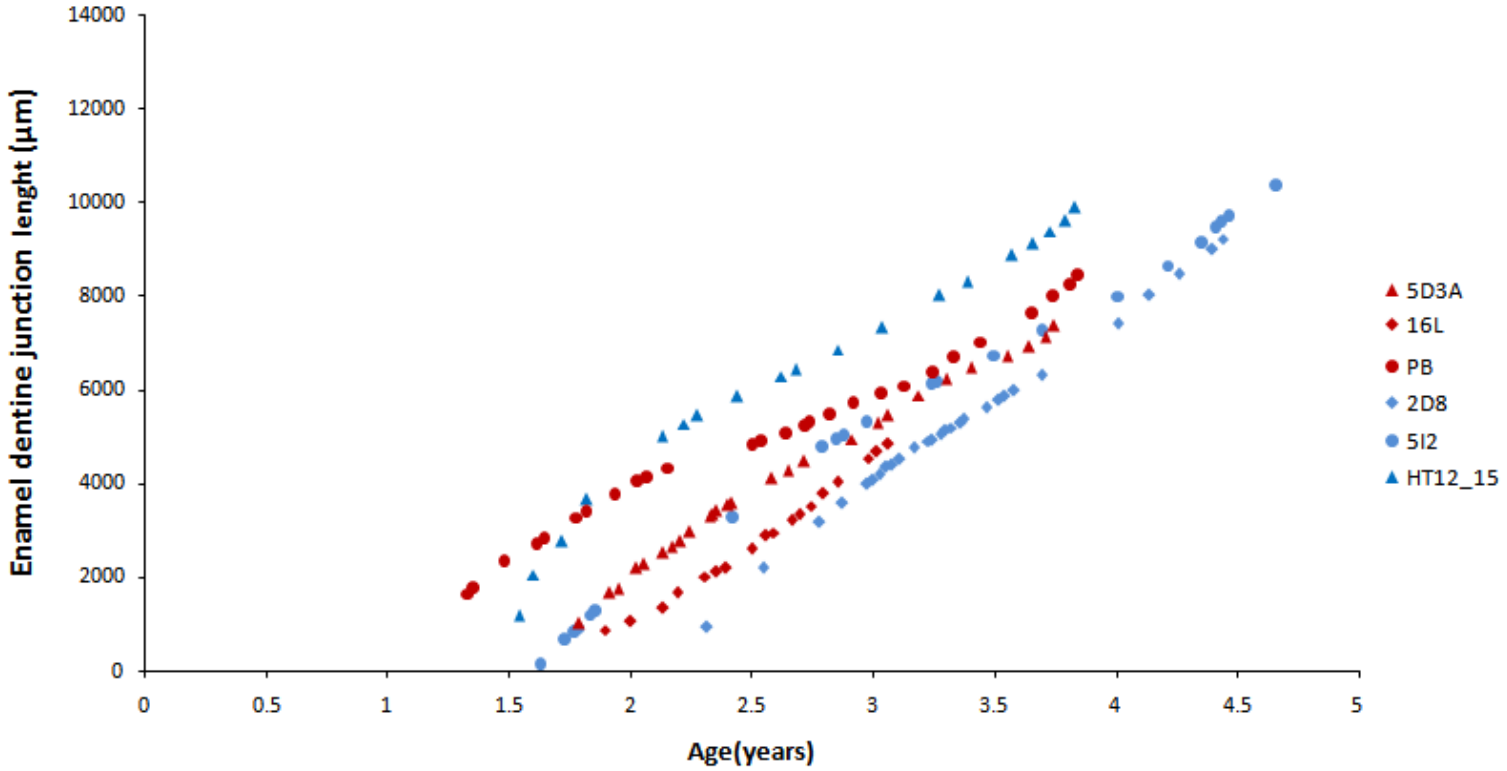

Figure 3.12: Enamel dentine junction length by age for male and female mandrill P_4 starting at age of initiation (cusp), ending at crown completion (cervix). Slope indicates enamel extension rate. Males in blue, females in red, individuals represented by different symbols.

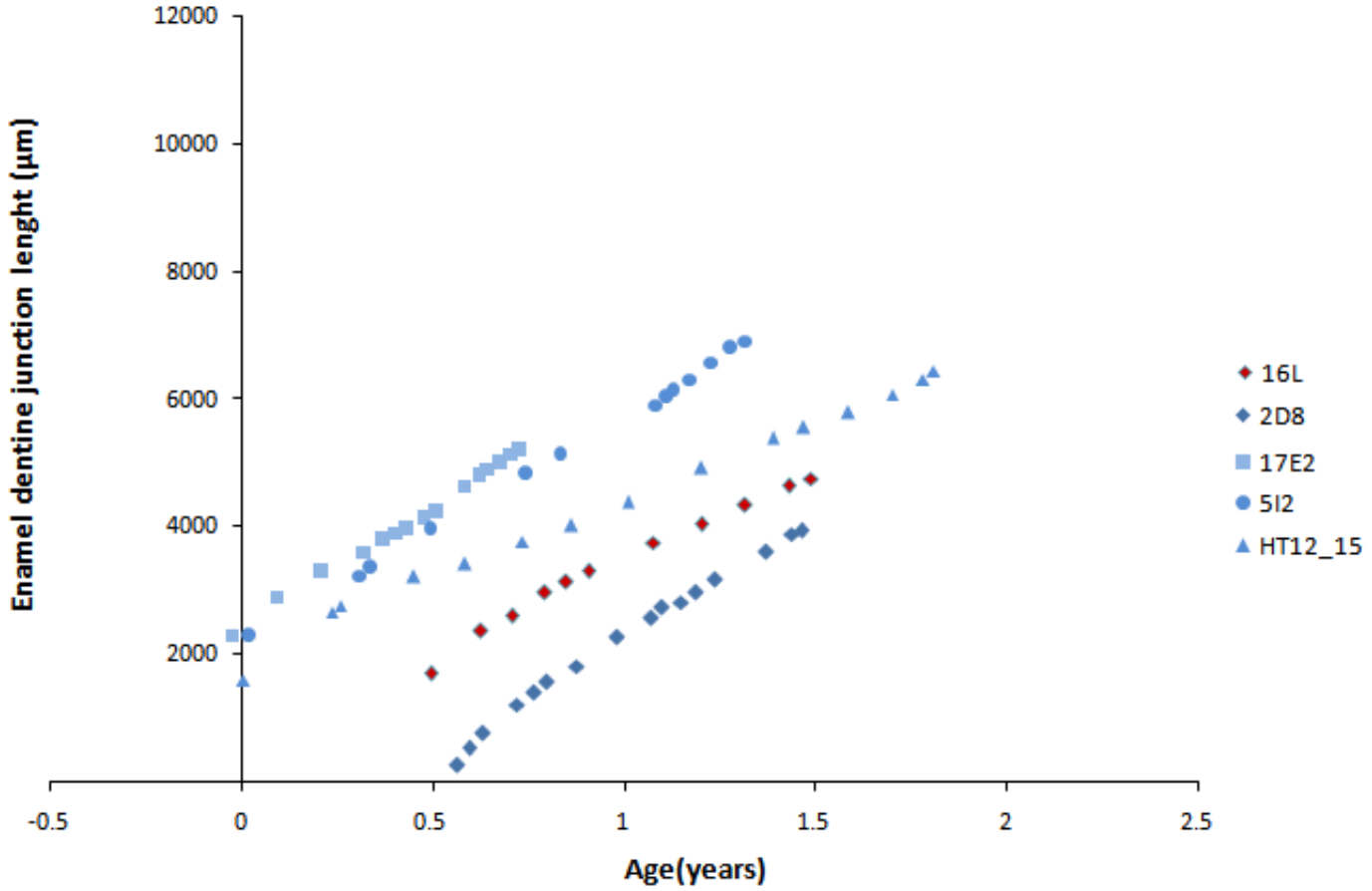

Figure 3.13: Enamel dentine junction length by age for male and female M_1 starting at age of initiation (cusp), ending at crown completion (cervix). Slope indicates enamel extension rate. Males in blue, females in red, individuals represented by different symbols. 5D3A's M_1 could not be included due sectioning damage.

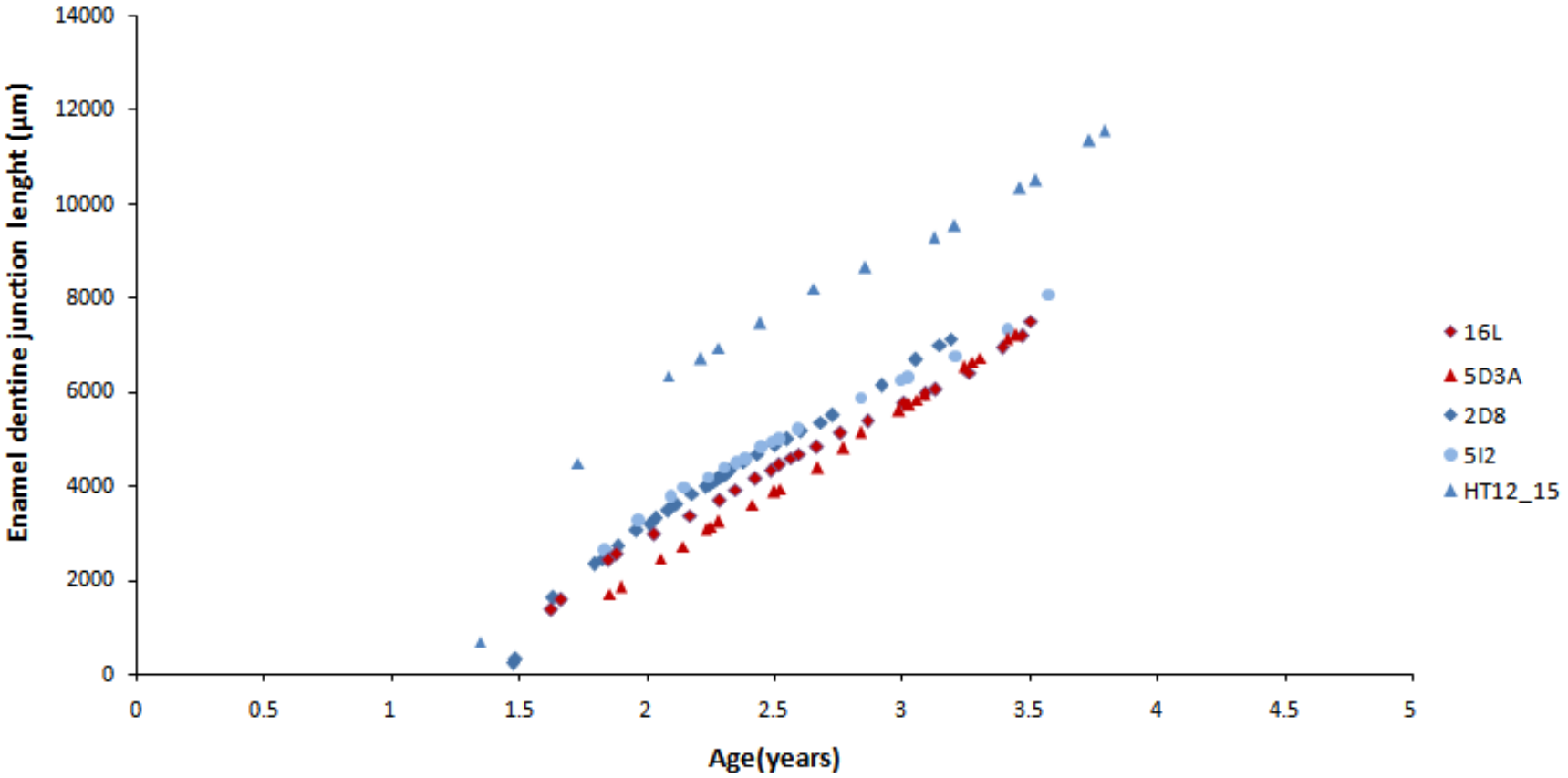

Figure 3.14: Enamel dentine junction length by age for male and female mandrill M_2 starting at age of initiation (cusp), ending at crown completion (cervix). Slope indicates enamel extension rate. Males in blue, females in red, individuals represented by different symbols.

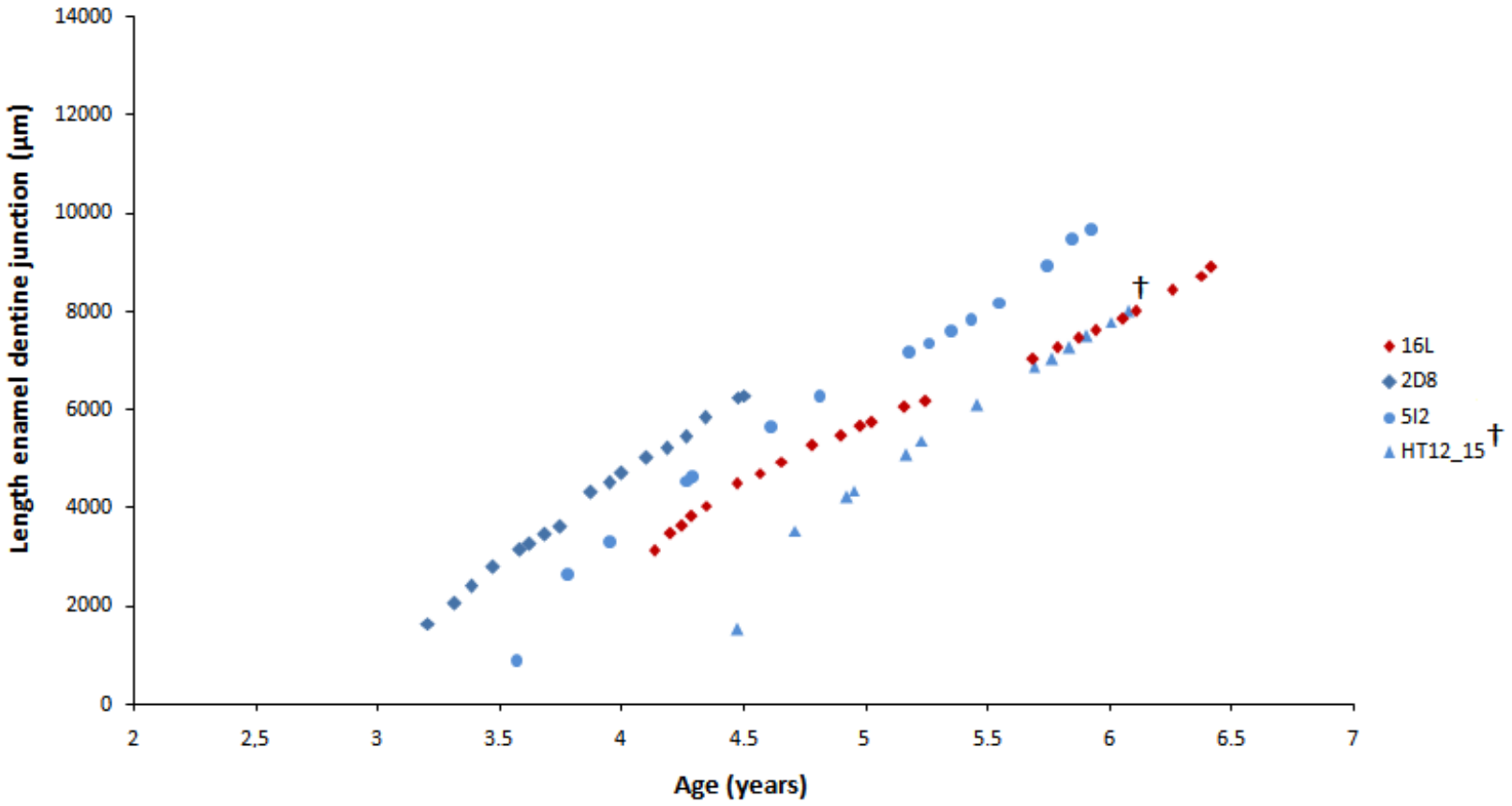

Figure 3.15: Enamel dentine junction length by age for male and female mandrill M_3 starting at age of initiation (cusp), ending at crown completion (cervix). Slope indicates enamel extension rate. Males in blue, females in red, individuals represented by different symbols. HT12_15's crown was developing when he died (†).

Table 3.2: Means and ranges of extension rates for the female and male teeth in µm/day. Some of HT12_15's crowns were still developing when he died, indicated with †. Only mandibular teeth included, except for 17E2's C_1 indicated with *.

Tooth measured		Extension rate (µm)									
		5D3A ♀	16L ♀	PB ♀	2D8 ♂	17_E2 ♂	5I2 ♂	HT12_15 ♂	Female mean	Male mean	Mean
I_1	Mean	12.2	12.0	11.7	12.4	16.6	13.8	15.3	12.0	14.3	13.4
	Min	7.9	7.7	7.7	8.6	9.2	7.6	8.9	7.8	8.5	8.2
	Max	15.9	28.7	22.4	19.9	26.9	32.2	24.9	22.3	26.4	24.4
I_2	Mean	12.5	12.1	10.3	11.9	15.6	12.3	15.2	11.6	13.7	12.8
	Min	7.3	6.9	6.6	5.5	10.2	4.1	10.3	7.0	7.5	7.3
	Max	18.9	20.0	14.0	29.2	16.7	27.8	20.7	17.6	23.6	21.0
C_1	Mean	Damaged	10.3	10.0	14.1	19.2	13.2*	14.6†	10.2	14.0	12.4
	Min	Damaged	7.1	5.7	9.3	10.3	9.3*	7.9†	6.4	8.8	7.9
	Max	Damaged	16.8	16.5	18.8	36.6	22.3*	21.6†	16.7	20.9	19.2
P_3	Mean	Damaged	7.8	6.5	10.2	Upper	11.3	10.4†	7.2	10.6	9.5
	Min	Damaged	3.6	2.9	6.6	Upper	4.0	6.4†	3.3	5.7	4.7
	Max	Damaged	23.2	22.4	16.0	Upper	23.8	19.0†	22.8	19,6	20.9
P_4	Mean	10.0	9.9	8.7	10.6	Absent	10.8	14.2	9.5	11.9	10.7
	Min	4.5	4.7	4.0	5.8	Absent	6.2	6.2	4.4	6.1	5.2
	Max	15.9	20.2	19.4	22.8	Absent	18.7	56.5	18.5	32.7	25.6
M_1	Mean	Damaged	9.2	Upper	14.1	12.0	12.7	8.5	9.2	11.8	11.3
	Min	Damaged	5.5	Upper	4.7	7.0	4.8	4.3	5.5	5.2	5.3
	max	Damaged	17.6	Upper	36.8	34.1	34.1	20.5	17.6	31.4	28.6
M_2	Mean	9.6	9.5	Upper	10.7	Damaged	9.0	11.8	9.6	10.5	10.1
	Min	7.4	5.9	Upper	7.0	Damaged	5.7	6.1	6.7	6.3	6.4
	Max	16.5	26.5	Upper	24.6	Damaged	19.8	29.7	21.5	24.7	23.4
M_3	Mean	Damaged	7.4	Upper	10.1	Upper	9.2	9.9	7.4	9.7	9.2
	Min	Damaged	3.8	Upper	4.3	Upper	6.4	6.3	3.8	5.7	5.2
	Max	Damaged	35.8	Upper	21.3	Upper	25.5	52.1	35.8	33.0	33.7

3.3.6 Dental development and life history

When female mandrills are weaned, the M_1 crown is half complete and I_1 and P_3 have initiated (Figure 3.16). When females reach peak mass velocity, the M_1, is complete, I_1 is almost complete, I_2, C_1, P_3, P_4 and M_2 are developing, and M_3, has not yet initiated. M_3 initiates just before menarche. At menarche, all other crowns are complete, except for P_3, which crown is more than 3/4 complete. By the time of first reproduction, the M_3 is developing, but has not yet emerged. Females attain adult crown rump length after the M_3 is complete and attain adult body mass at the same time as the midpoint of M_3 gingival emergence (Figure 3.16).

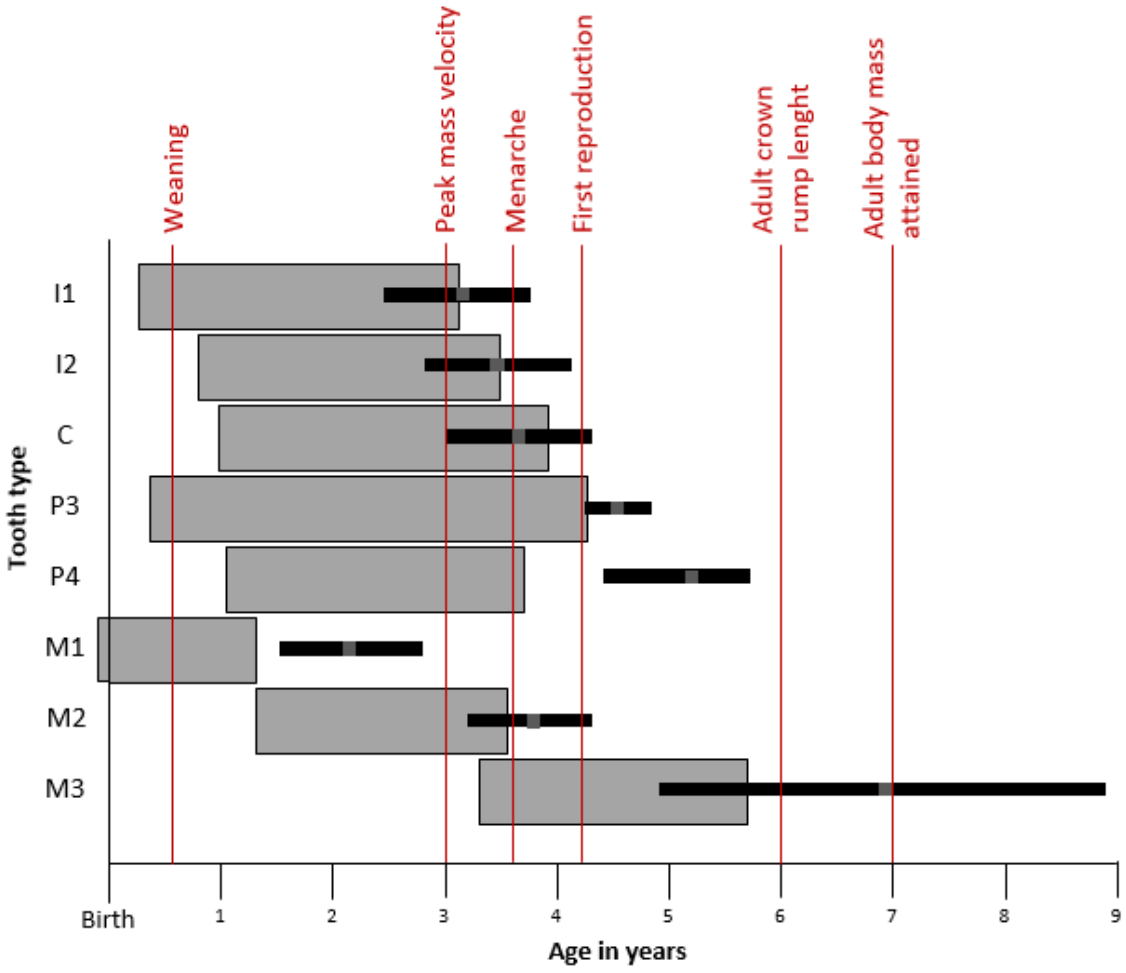

Figure 3.16: Dental development of female mandrills in relation to their life history. Grey bars: crown formation. Black bars: gingival emergence range with midpoints as grey blocks. Life history data based on published means (references in Chapter 1, Table 1.1)

Like females, male mandrills are weaned when their M_1 crown is half complete. By this time, the incisors, C_1 and P_3 have initiated (Figure 3.17). By the age the testes descend, and males are capable of siring offspring, the incisors, M_1 and M_2 are complete and emerged, the C_1 and premolars are still forming and the M_3 has initiated. Peak body mass velocity coincides is reached before the C_1 and P_3 crowns are completed. Full adult body mass, crown rump length and age at first siring, although hugely variable among individuals, occur generally after the dentition is complete.

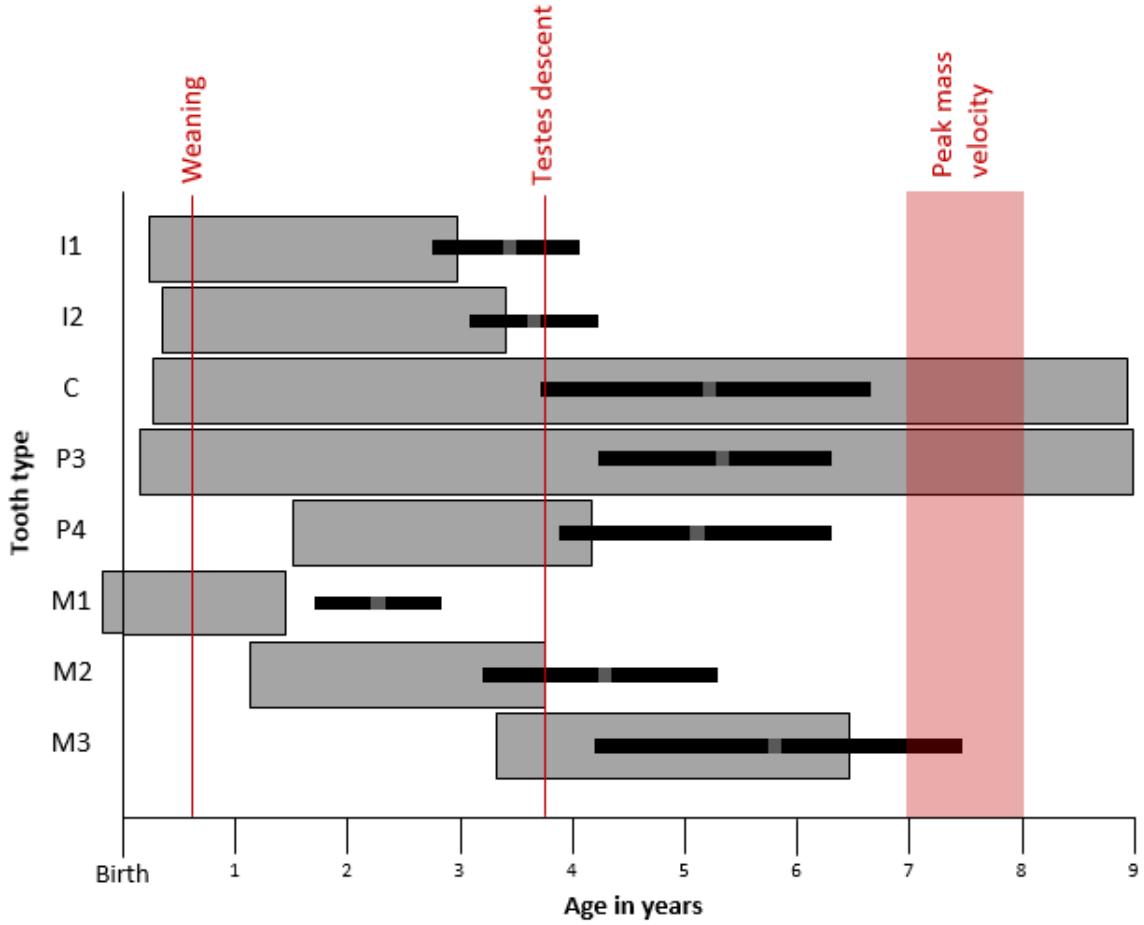

Figure 3.17: Dental development in male mandrills in relation to life history. Grey bars: Dental development. Black bars: gingival emergence range with midpoints as grey blocks. Life history data based on published means (references in Chapter 1, Table 1.1).

3.3 Summary of results

In this chapter I examined the chronology of dental development in individual male and female mandrills, combining the results with previous obtained data (Table 3.1). By doing so, I have provided the necessary framework to perform my analysis on the correlation between accentuated line formation and life history in Chapters 4 & 5. By constructing these developmental chronologies, the most interesting results were the small amount of root formation in the lower incisors in both sexes at dental emergence, the larger amount of prenatal enamel formation in male first molars and the prenatal initiation of the male C^1. Based on these individual bar charts, I constructed general sex-specific dental chronology for mandrills and investigate sex differences in dental developmental. Finally, I combined information on mandrill dental development with the previously published mandrill life history data. These results will be further discussed in Chapter 6.

Table 3.1: Summary of tooth development in male and female mandrills

Dentition Developmental stage	Age (years)		Source
	Females	Males	
Deciduous dentition completely emerged	0.4 (mid-point)	0.4 (mid-point)	Setchell & Wickings, 2004
Permanent dentition crown completion	5.6 (M_3 crown finishes development)	7.9 (canine crown finishes development last)	This study
Permanent dentition root completion	8.5 - 9.4 and later (root apex of M_3 closes last)	9.8 and later (root apex of C^1 closes last)	This study
Permanent dentition emerged through gingiva	6.8 (mid-point)	5.7 (mid-point)	Setchell & Wickings, 2004
Age maximum canine height		9 – 11	Leigh et al., 2008

Chapter 4: Accentuated lines in teeth, stress and life history in female mandrills

4.1 Chapter aims

For this chapter, my aims are (1) to determine the ages at formation of accentuated lines in the teeth of female mandrills (2) to test the hypotheses that stress associated with life history events, as well as changes in alpha male status and captures, affects tooth formation and is therefore correlated with the formation of accentuated lines in tooth sections (Table 4.1). I predict that the physiological stressors related to the mother's resumption of cycling (as a proxy for weaning), birth of subsequent siblings, first and subsequent cycles and first and subsequent parturitions will be correlated with the age at the formation of accentuated lines in the teeth of the two female mandrills (Table 4.1). In addition to life history events, social interactions can also be a source of stress and may therefore be visible on a histological level. Male dominance rank instability is a major correlate of psychological stress for some non-human primates (e.g. Barrett et al., 2002; Crockford et al., 2008; Muller & Wrangham, 2004; Sapolsky, 2005; Setchell et al., 2010; Stavisky et al., 2001). Alpha male takeovers in the colony are known to be violent and aggressive encounters (Setchell et al., 2006) and have influence on the whole structure of the group. Upheavals in the male hierarchy have a clear effect on the glucocorticoid levels of lactating and pregnant female baboons (Beehner et al., 2000) and therefore, a change in alpha-male might be a stressful event for female mandrills too, possibly correlating with accentuated lines. Furthermore, a study on macaques demonstrated that anesthetised captures could also be associated with the formation of accentuated lines (Bowman, 1991). Since the mandrills are captured and anesthetised regularly for medical examination by CIRMF staff, these capture events might correlate with the formation of accentuated lines too. Although the focus of this study lies in the correlation between accentuated line formation and life history stress, I will also take the captures and alpha male takeovers into account (Table 4.1).

Table 4.1: Summary of hypotheses and predictions Chapter 4

Life history	
Hypothesis	**Prediction**
1) Decreased attention, maternal rejection and presence of large males during resumption of cycling of the mother causes physiological stress that disrupts the formation of dental tissues.	1) Accentuated lines will form when the mother resumes her cycling. 2) Accentuated lines will form specifically when the mother is mate-guarded during her cycle.
2) Decreased attention and maternal rejection at birth of subsequent offspring to the mother causes physiological/psychological stress that disrupts the formation of dental tissues in the offspring.	1) Accentuated lines will form at the time of a sibling's birth.
3) Increasing male attention and physiological changes during first and subsequent reproductive cycles cause physiological stress that disrupts the formation of dental tissues.	1) Accentuated lines will form 'at the time a female reaches menarche and has her subsequent cycles. 2) Accentuated line will form specifically when a female is mate-guarded during her cycle.
4) Psychological and physical changes during first and subsequent parturitions cause physiological stress that disrupts the formation of dental tissues.	Accentuated lines will form at the time of parturition.
Social environment	
Hypothesis	**Prediction**
Instability in the group at times of changes in alpha male cause physiological stress that disrupts the formation of dental tissues.	Accentuated lines will form in a female's teeth during the period in which an alpha male takeover takes place.
Captivity	
Hypothesis	**Prediction**
Veterinary captures cause physiological stress that disrupts the formation of dental tissues	Accentuated lines will form at the time an individual is captured.

4.2 Results

4.2.1 Accentuated line sequence

The cusps of PB's M_1 were worn and taphonomically damaged beyond the point at which the neonatal line would be visible. Her dentition therefore covered the period from three weeks of age until her death at age 9.38 years; 99% of her total life span. The top of her I_1 was badly taphonomically damaged and thus, until she was aged 3 months, only the M_1 and M^1 were available for assessment of accentuated lines. From age 4 months to age 5.2 years, two or more crowns were forming at the same time allowing for accentuated line matching. From age 5.2 years until death only the third molars were available for accentuated line assessment (Figure 4.1). I identified accentuated lines forming from age 0.2 years until age 9.4 years, a week before her death. In total I identified 152 accentuated lines in PB's dentition, of which I classified 30 as highly accentuated (Figure 4.1). 5D3A's M_1 did show a neonatal line. Her dentition therefore covered the period from three weeks before birth to age 8.6 years, when her dental development was complete; 81 % of her total life span. For 5D3A, from age 10 weeks to age 4.9 years, two or more crowns were forming at the same time allowing for accentuated line matching. From age 4.9 until 8.6 only the third molar was in development (Figure 4.2). I identified accentuated lines from age 0.2 until age 8.2 years, 19 weeks before her dental development ended. In total I found 98 accentuated lines in 5D3A's dentition, of which I classified 43 as highly accentuated (Figure 4.2).

The number of accentuated lines formed fluctuated during the females' lives. PB had two main peaks, one at age 1-3 years and one at age 5-6 years (Figure 4.3). A third smaller peak occurred at age 7-8 years and a dense cluster of accentuated lines formed from age 8.8 years until PB's death aged 9.4 years. There were also two peaks of highly accentuated line formation, at age 1-2 and 3-4 years. There was a sharp contrast in highly accentuated line formation between the first half of PB's life, when most formed, and the second half of her life, during which I found very few. Unlike PB, I found no intense peaks in frequency of lines in 5D3A, but fewer accentuated lines formed during 5D3A's second and sixth year in comparison to other years. The formation of highly accentuated lines followed the same pattern (Figure 4.3).

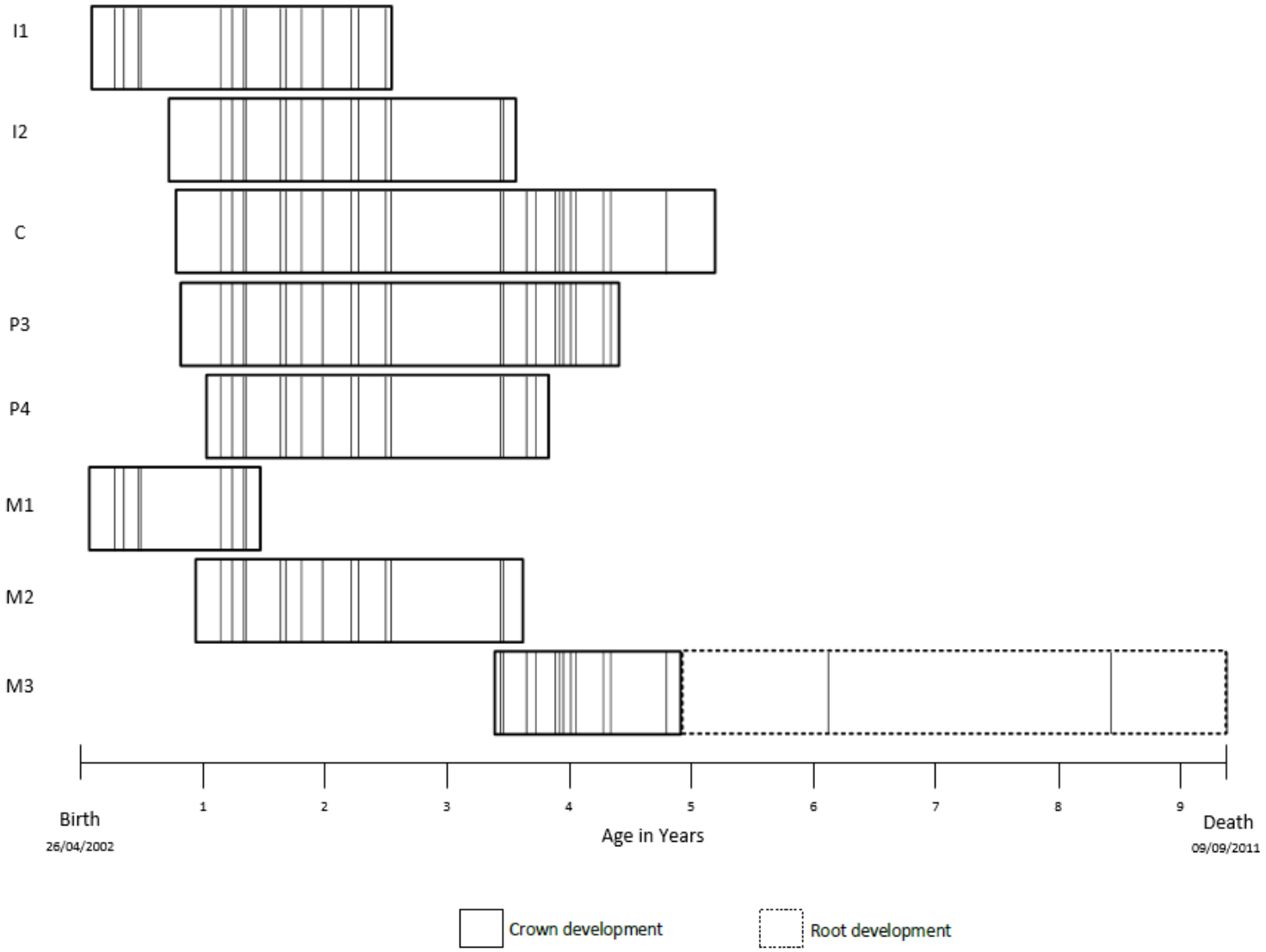

Figure 4.1: PB's highly accentuated line sequence (vertical lines) plotted on her mandibular dental development chronology (horizontal boxes).

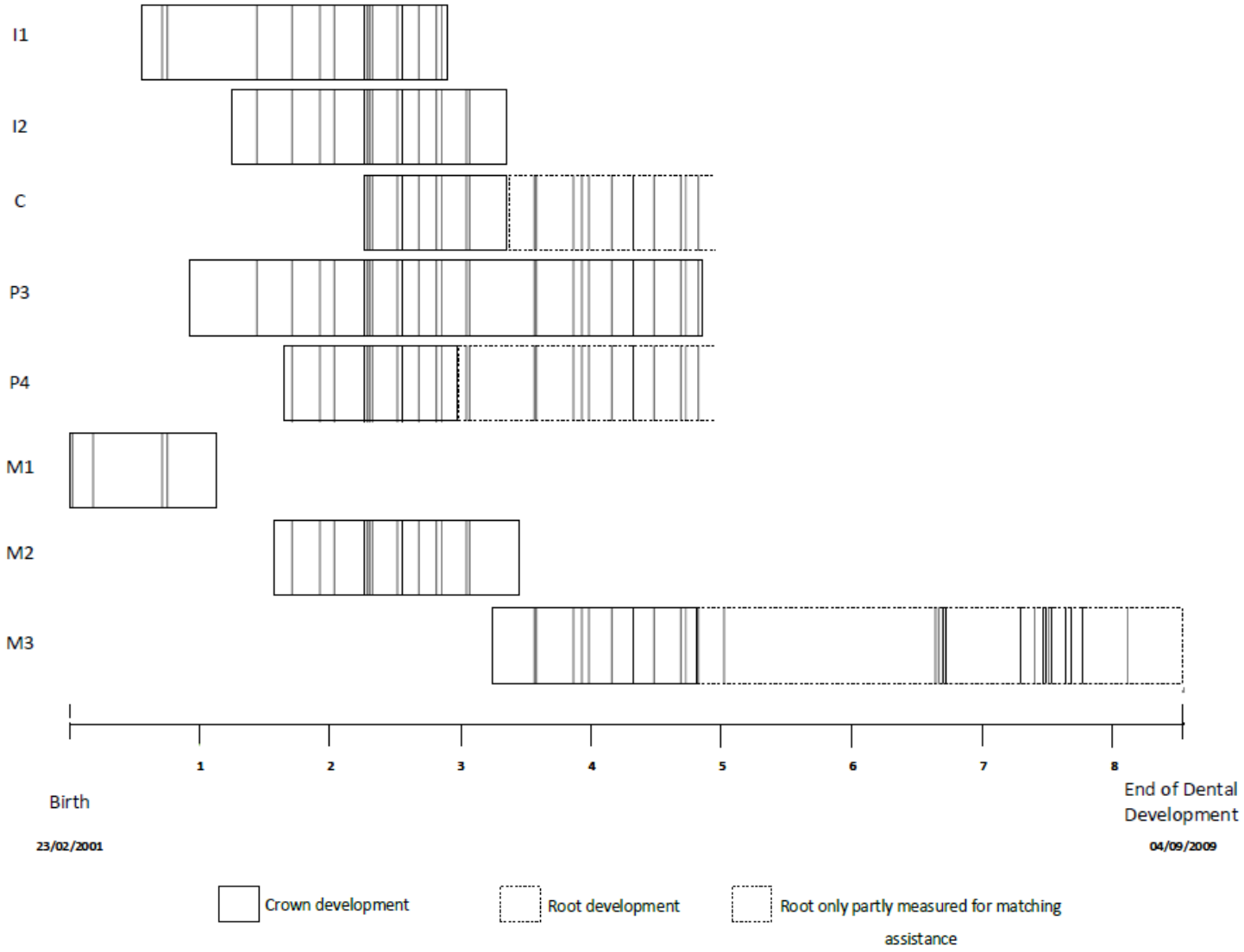

Figure 4.2: 5D3A's highly accentuated line sequence (vertical lines) plotted on her mandibular dental development chronology (horizontal boxes). Maxillary teeth indicated with *.

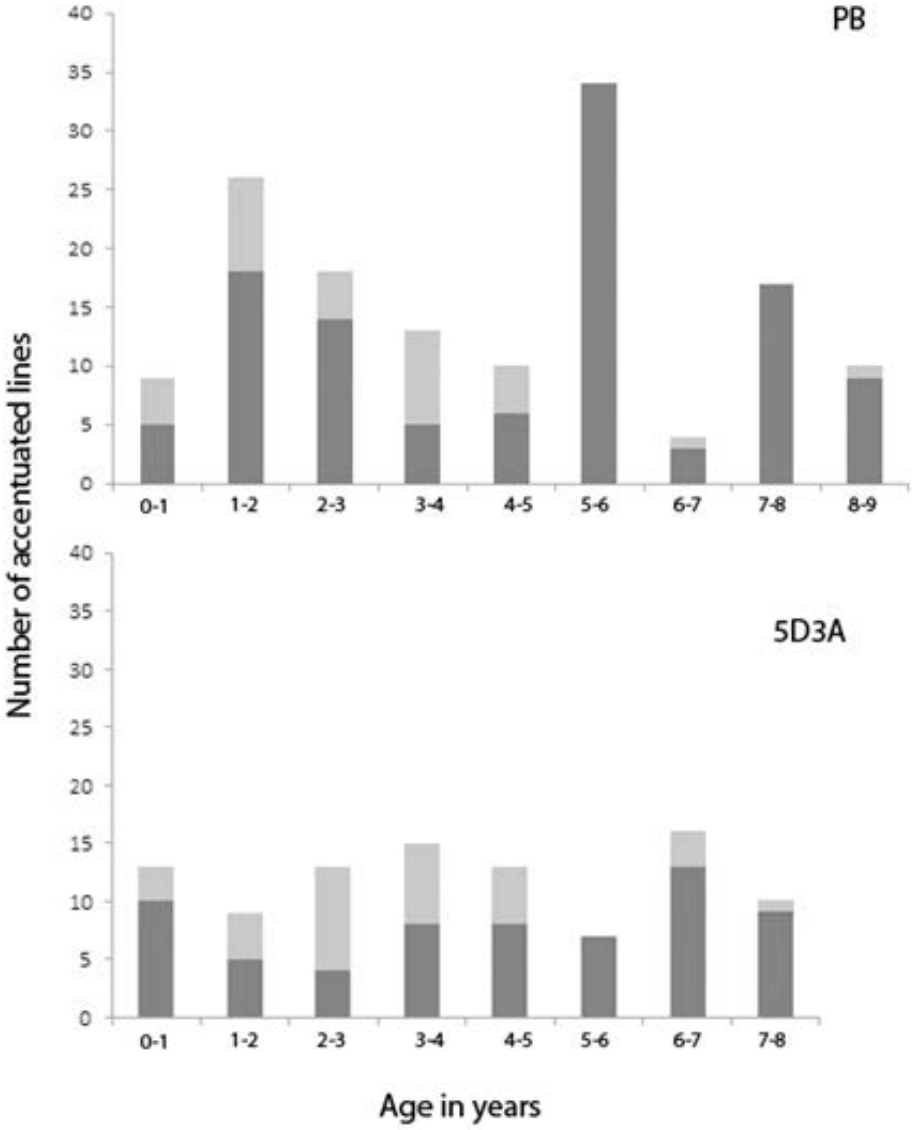

Figure 4.3: Accentuated line frequency per year (5D3A age was 8.53 at death, last 0.53 years not included in graph). Dark grey indicates the number of regular accentuated lines, light grey the number of highly accentuated lines

4.2.2 Life history

Both females showed highly accentuated lines at the time of resumption of the mothers' cycle, in contrast to the weeks leading up the resumption of the mother's cycle. Furthermore, highly accentuated lines formed in the teeth of both females at the first time their mothers were mate-guarded after resumption of cycling (Figure 4.4, 4.5 & 4.6).

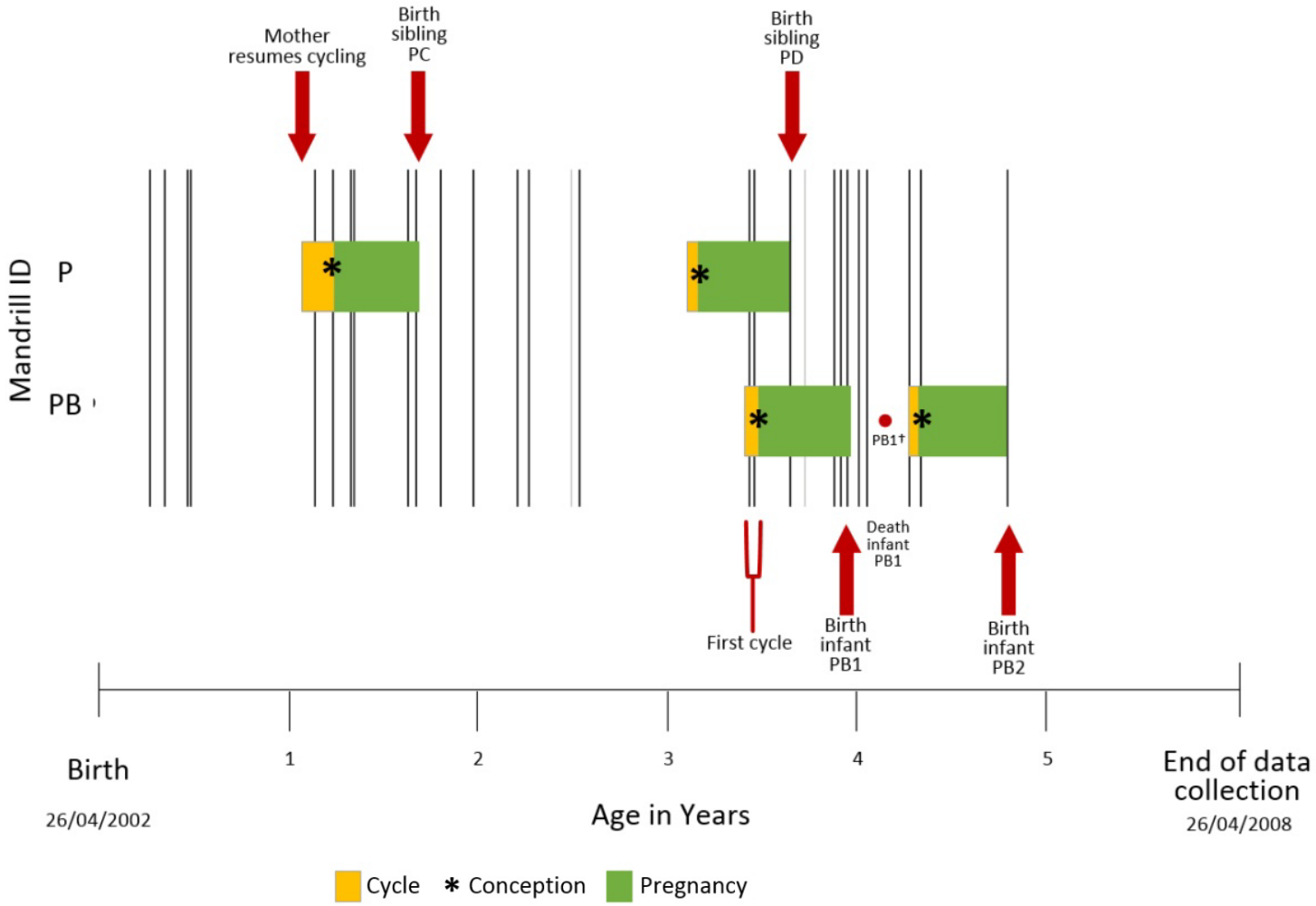

Figure 4.4: The relationship among highly accentuated lines in PB's dentition, her mother's reproductive cycle and sibling births, PB's own cycles and parturitions Highly accentuated lines associated with capture in light grey.

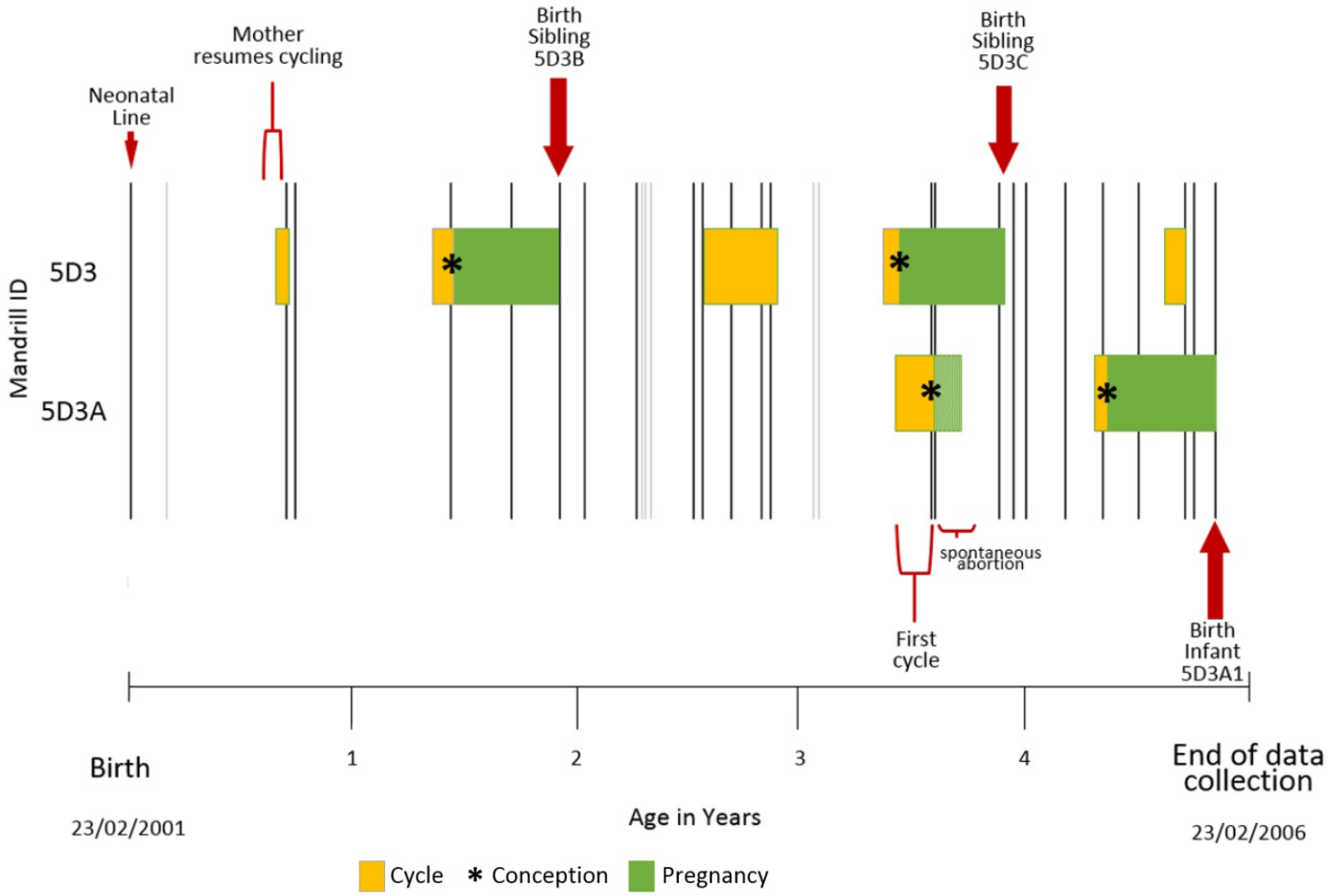

Figure 4.5: The relationship among highly accentuated lines in 5D3A's dentition, her mother's reproductive cycle and her sibling's births, 5D3A's own cycles and parturition. Highly accentuated lines associated with capture are in light grey.

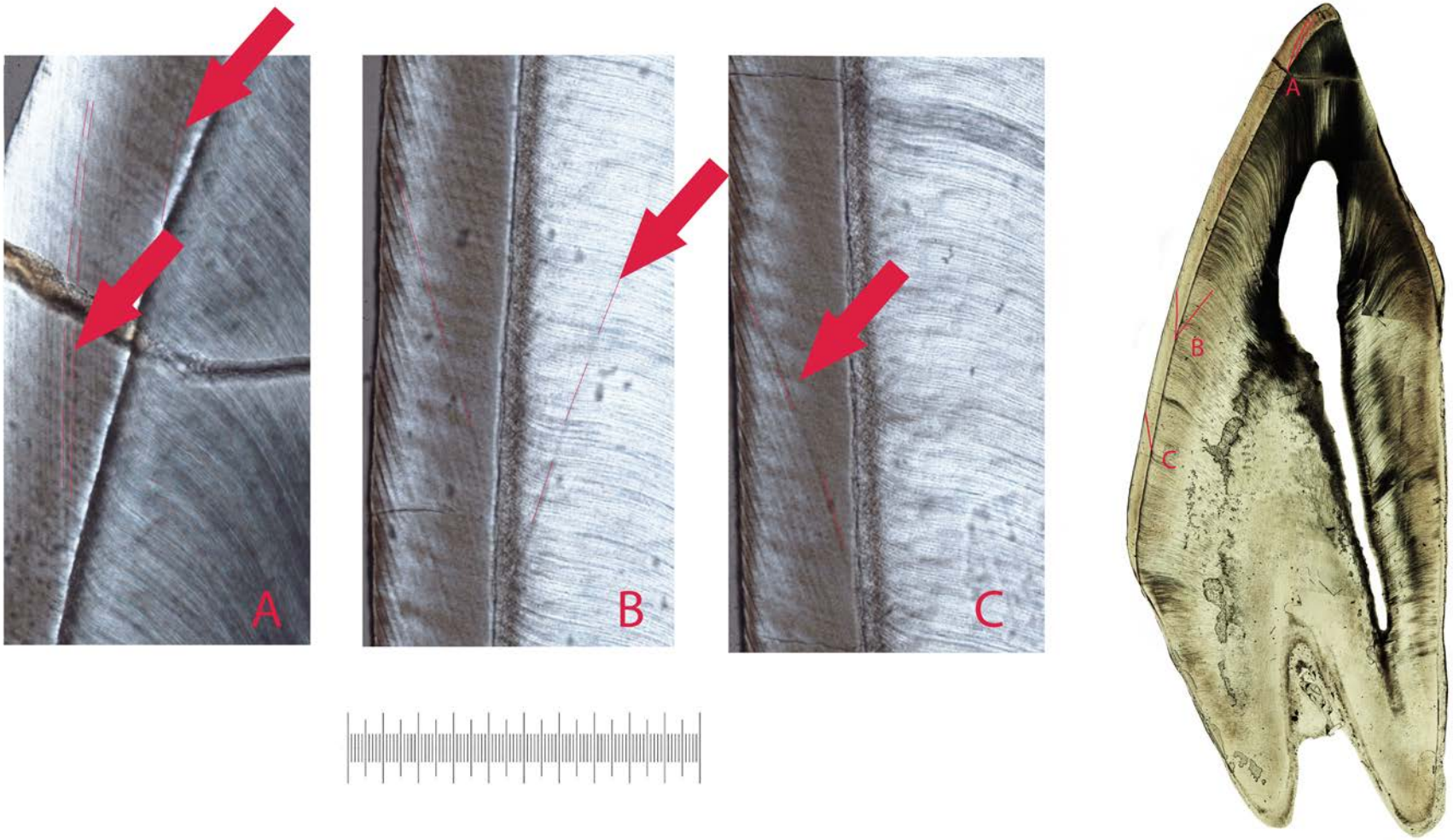

Figure 4.6: Highly accentuated lines in PB's canine (left) with their position in the canine enamel (right). A: Accentuated correlating with PB's mother's resumed cycling B: Accentuated line correlating with PB's first cycle, C: Accentuated line correlating with PB's second parturition (PB2). Scale = 1000 µm.

PB's mother, mandrill P, resumed her cycle when PB was aged 1.1 years. P showed a small sexual swelling that increased in size for two weeks, a short interval with no sexual swelling, and then had a full sexual swelling cycle (Figure 4.7). P was mate-guarded during the last week of her maximal swelling and conceived. No highly accentuated lines formed in the six months before resumption of cycling, while two formed during her resumed cycle, the second coinciding with the time she was mate-guarded.

5D3A's mother, mandrill 5D3, resumed her cycle when 5D3A was aged 0.7 years. There is a gap in the observational data from age 0.5 – 0.7 which resumes when 5D3's sexual swelling is decreasing and she is mate-guarded (Figure 4.8) but did not conceive. Judging from this sexual swelling pattern, 5D3 must have had her maximal sexual swelling the weeks preceding the observational data. The accentuated line pattern formed in 5D3A correlates with the mother's resumption of cycling: No highly accentuated lines formed during the first months of 5D3A's life apart from the neonatal line. However, the first two highly accentuated lines visible in 5D3A's teeth since the birth coincided with her mother's observed (deflating) swelling and during mate-guarding.

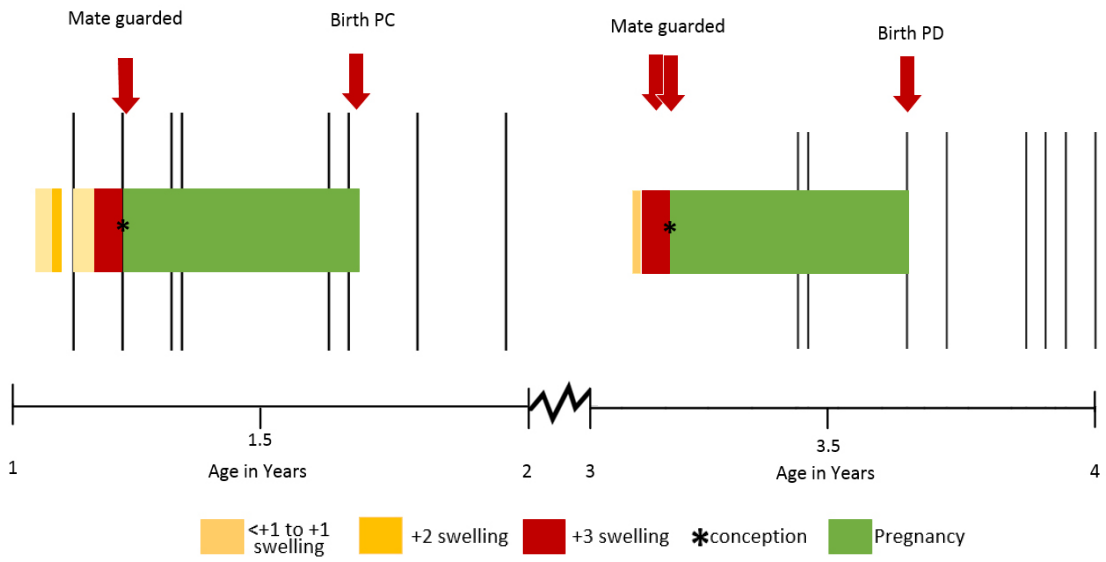

Figure 4.7: Reproductive data for PB's mother (P) plotted on the sequence of accentuated lines that formed in PB's dentition. Interruption line represents one year.

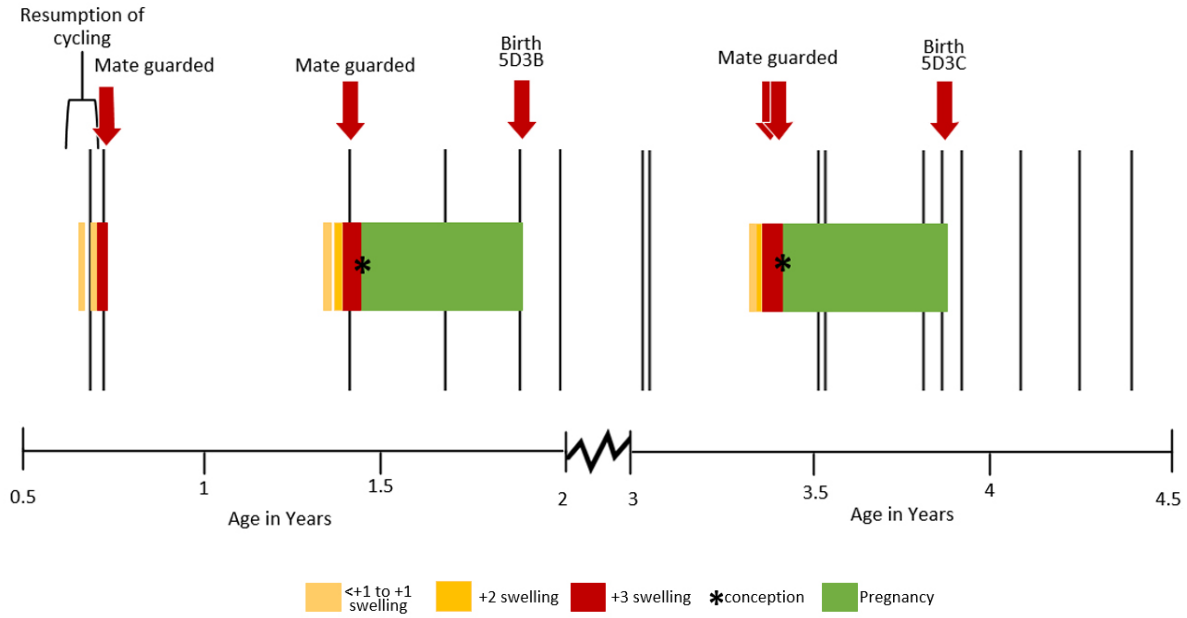

Figure 4.8: Reproductive data for 5D3A's mother (5D3) plotted on the sequence of accentuated lines that formed in 5D3A's dentition. Interruption line represents one year.

Both females formed highly accentuated lines that coinciding with the birth of one of their siblings, but not for the other (Figure 4.7 & 4.8). PB's first subsequent sibling, mandrill PC, was born when PB was aged 1.7 years with no correlated accentuated line. However, when her next sibling PD was born when PB was 3.6 years, a highly accentuated line formed. For 5D3A, the pattern was reversed, whereby the first sibling's birth corresponded with a highly accentuated line, but the second didn't. 5D3A's first subsequent sibling, mandrill 5D3B, was born when 5D3A was aged 1.9 years. 5D3A's next sibling, mandrill 5D3C, was born when 5D3A was aged 3.9 years with no correlated highly accentuated line.

The two females formed highly accentuated lines correlated with their first and subsequent reproductive cycles (Figure 4.9 & 4.10). Highly accentuated lines mainly formed when swellings were +2 or +3 and when mate guarded. PB had a hiatus of line formation during the 10 weeks preceding her first cycle. Her first swelling started when she was 3.4 years old, which was small at first but increased to a +2 within two weeks, which corresponded with the formation of two extremely clear highly accentuated lines. These lines were observable in all six teeth forming at that time (all teeth except the M_1 and M_3). Before she started her second cycle at age 4.3 there was a hiatus in accentuated line formation of six weeks. In contrast, during the following four weeks in which she cycled, two highly accentuated lines appeared. One appeared at the start of this cycle and the

second coincided with the time of conception. 5D3A had a hiatus in line formation for eight weeks preceding her first cycle Her first swelling started when she was 3.4 years as well. During the 10 weeks of her cycle, she formed two highly accentuated lines corresponding to her maximal swelling and being mate-guarded. 5D3A experienced a spontaneous termination of her pregnancy, which had lasted at least three weeks and she started a new cycle aged 4.3 years. In this timeframe, four highly accentuated lines formed with no distinct pattern. Once she started her cycle, a highly accentuated line coincided with the time she was mate-guarded for four days and conceived infant 5D3A1 (Figure 4.9).

Two out of three parturitions of the two females coincided with the formation of highly accentuated lines. One parturition did not closely correspond with a highly accentuated line. PB's first infant (PB1) was first observed when PB was aged 3.9 years (Figure 4.9) which did not correspond with the formation of a highly accentuated line. Three highly accentuated lines formed during the first 10 weeks after PB1's birth. Infant PB1 broke its leg when it was nine months old and was euthanized by the CIRMF staff. After PB1's death, no highly accentuated lines formation in PB's dentition for six subsequent weeks until she resumed cycle. PB's second infant, PB2, was born when she was aged 4.79 years. One highly accentuated line formed in PB's teeth in the week of PB2's birth. No highly accentuated lines formed for 15 weeks after PB2 was born. 5D3A's first conception ended with a spontaneous abortion (Figure 4.9). Since the exact timing of the abortion is not known, I cannot correlate it with the highly accentuated line pattern. Her second conception led to the birth of infant 5D3A1 at age 4.81 years, corresponding with a highly accentuated line.

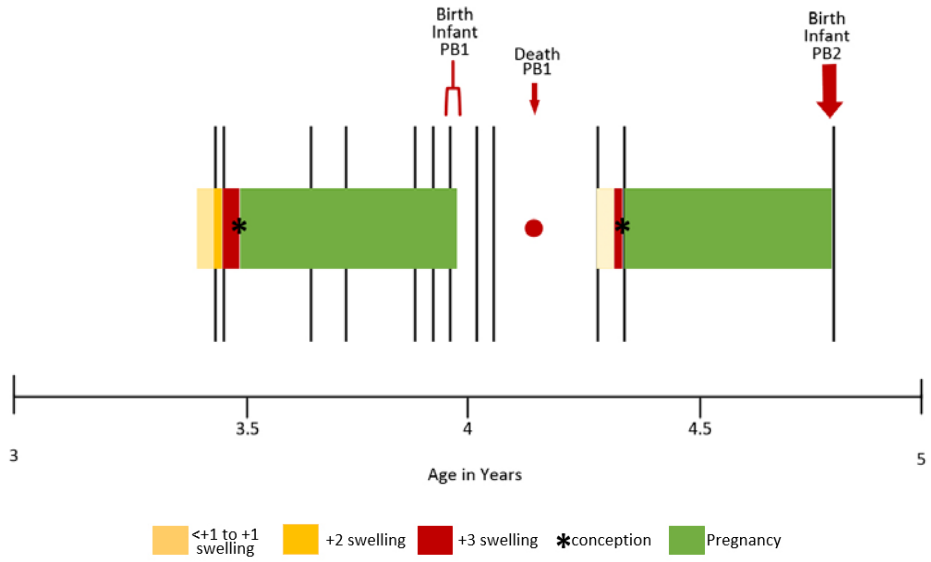

Figure 4.9: Reproductive data for PB plotted on her accentuated line sequence.

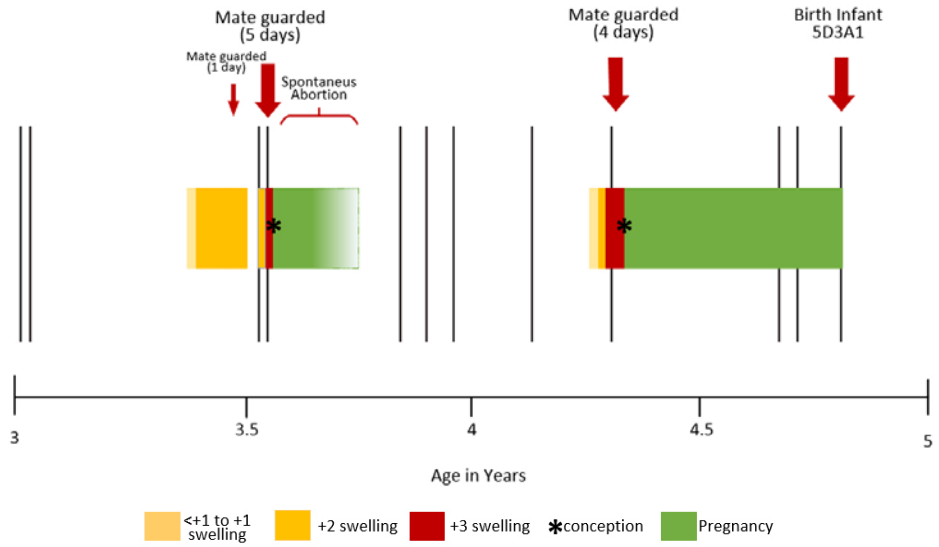

Figure 4.10: Reproductive data for 5D3A plotted on her accentuated line sequence.

4.2.3 Social environment

Highly accentuated lines did not form consistently during alpha male takeovers. PB experienced four alpha male takeovers during her lifetime. The first two takeovers took place when she was aged 0.7 and 1.4 years old. Neither takeover corresponded with the formation of an accentuated line. The third and fourth takeovers took place during a nine week-period, when PB was aged 2.26 and 2.42 years. Only the first of these takeovers was associated with a highly accentuated line.
5D3A experienced six alpha male takeovers during her lifetime of which none corresponded with the formation of highly accentuated lines.

4.2.4 Captivity

Only a few of the captures per female corresponded with highly accentuated lines; 3 out of 14 for PB and 9 out of 17 for 5D3A (Figure 4.11 & 4.12). PB had no clear pattern of highly accentuated lines in correspondence to captures but 5D3A formed mainly highly accentuated lines in correspondence to the captures that took place earlier in her life, and to the captures that took place in short succession of each other later in her life (Figure 4.12).

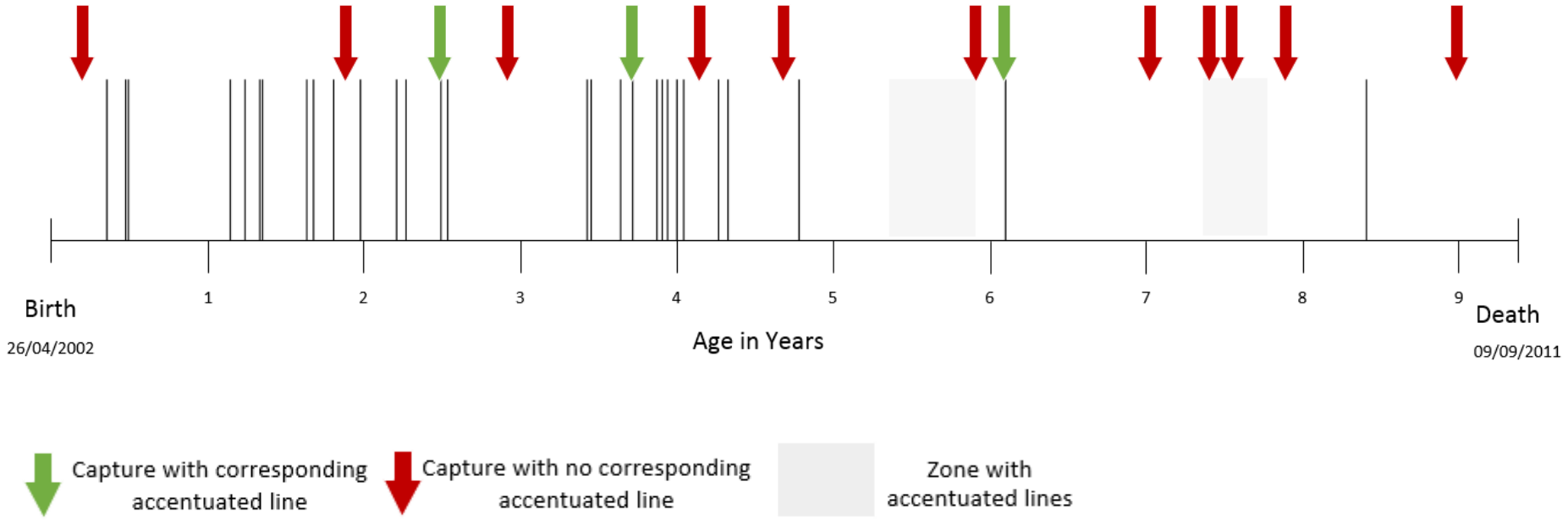

Figure 4.11: Highly accentuated line sequence for PB with the timing of veterinary captures during her life. Green arrows indicate captures that matched with highly accentuated lines, red arrows ones that do not.

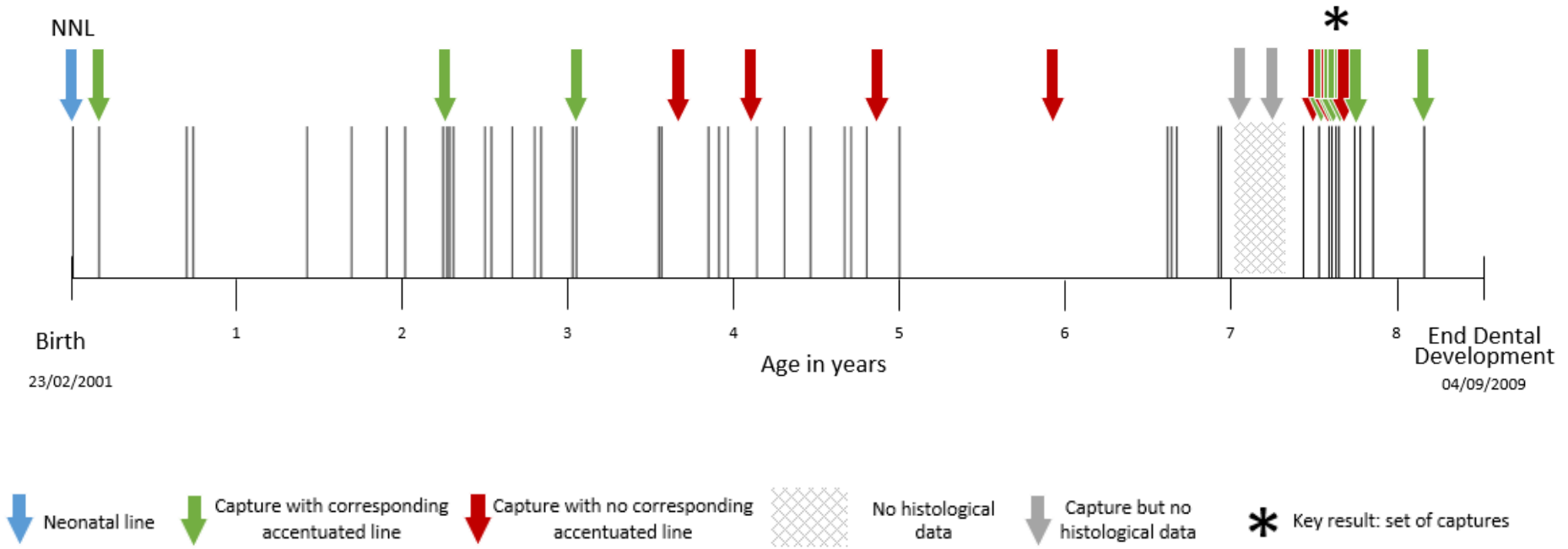

Figure 4.12: Highly accentuated line sequence for 5D3A with the timing of veterinary captures during her life. Green arrows indicate captures that matched with highly accentuated lines, red arrows ones that do not.

4.3 Summary of results

In this chapter, I aimed to test the hypotheses that stress associated with life history events, including resumption of the mothers cycling, the birth of subsequent siblings, first and subsequent sexual cycles and parturitions affect accentuated line formation in the teeth of female mandrills. Additionally, I explored if alpha male takeovers and times of veterinary captures coincided with accentuated line formation. Both females formed highly accentuated lines at the time of resumption of the mothers' cycle, in contrast to the weeks leading up the resumption of the mother's cycle. Furthermore, highly accentuated lines formed in the teeth of both females at the first time their mothers were mate-guarded after resumption of cycling. Both females formed highly accentuated lines that coinciding with the birth of one of their siblings, but not for the other. Two out of three parturitions of the two females coincided with the formation of highly accentuated lines. Highly accentuated lines did not form consistently during alpha male takeovers and only a few of the captures per female corresponded with highly accentuated lines. However, 5D3A was captured multiple times in a short timespan at the end of her dental development, which corresponded with a cluster of accentuated line formation.

Chapter 5: Accentuated lines in teeth, stress and life history in male mandrills

5.1 Chapter aims

In this chapter, I aim to (1) determine the ages at formation of accentuated lines in the teeth of male mandrills (2) test the hypotheses that stress associated with life history events, including resumption of the mothers cycling, as a proxy for weaning, and the birth of subsequent siblings cause physiological stress, could affect accentuated line formation in male mandrill teeth. Furthermore, since the mating behaviour and the presence of receptive females has proven to affect male glucocorticoids levels in seasonally breeding populations (Barrett et al., 2002; Schiml et al., 1996; Strier et al., 1999)as well as the male mandrills in the CIRMF colony (Setchell et al., 2010), I hypothesise that once males reach reproductive maturity, presence of receptive females might affects the formation of accentuated lines (Table 5.1).

In addition to life history events, I hypothesise that group instability at time of an alpha male takeover might be correlated with the formation of accentuated lines in the male teeth. Takeovers in the colony are known to be violent and aggressive (Setchell et al., 2006) and male dominance rank instability is a major correlate of psychological stress for some non-human primates (e.g. Barrett et al., 2002; Crockford et al., 2008; Muller & Wrangham, 2004; Sapolsky, 2005; Setchell et al., 2010; Stavisky et al., 2001). Social instability can increase concentrations of glucocorticoids in male primates (Bergman et al., 2005) as well as for male mandrills at CIRMF (Table 5.1). Finally, since a study on macaques demonstrated that anesthetised captures could also be associated with the formation of accentuated lines (Bowman, 1991), so might the veterinary controls of the mandrills performed by CIRMF (Table 5.1), similar as predicted for the females in Chapter 4.

Table 5.1: Summary of hypotheses and predictions Chapter 5.

Life history	
Hypothesis	**Prediction**
1) Decreased attention, maternal rejection and presence of large males during resumption of mothers' cycling causes stress that disrupts the formation of dental tissues	1) Accentuated lines form when the mother resumes cycling 2) Accentuated lines form specifically when the mother is mate-guarded during her cycle
2) Decreased attention and maternal rejection at birth of subsequent offspring to the mother causes stress that disrupts the formation of dental tissues in the offspring	Accentuated lines form at the time of a sibling's birth
3) Once males' testes descend, males experience stress during the mating season that disrupts the formation of dental tissues in their own teeth	1) More accentuated lines form during the mating season than outside the mating season from age 3.8 years onwards
Social environment	
Instability in the group at times of changes in alpha male cause stress that disrupts the formation of dental tissues	Accentuated lines form in a male's teeth during an alpha male takeover
Captivity	
Veterinary captures cause stress that disrupts the formation of dental tissues in the captured animal	Accentuated lines form when an individual is captured

5.2 Results

5.2.1 Accentuated line sequence

Although 17E2's canine root was still developing when he died, I could not properly assess the lines in this tooth. The yielded accentuated line sequence therefore covers his life from birth until the last increments measurable from his M^3 root at age 6.6 years, a total of 79% of his total life span. I found a total of 69 accentuated lines out of which I classified 31 as highly accentuated (Figure 5.1). In contrast with 17E2, 2D8's first molars were worn beyond the point at which a neonatal line would be visible and C_1 erupted after birth. His incisors were better preserved with an estimated initiation of age 0.2 years. During the last 14 weeks of dental development, material was not clear enough to identify accentuated lines, therefore restricting the retrieved accentuated line sequence to age 0.2 to 9.5 years (Figure 5.2), covering 72% of his total lifespan. In total I identified 78 accentuated lines in 2D8's dentition out of which I classified 36 as highly accentuated (Figure 5.3). The last set of highly accentuated lines in 2D8's teeth were extremely dark, more so than any other lines in his teeth.

The number of accentuated lines varied throughout the males' lives. 17E2 had most accentuated lines forming from birth until age 5 years, while 2D8 had a varying amount of accentuated lines throughout his whole life (Figure 5.34). Both had most accentuated lines forming from one to two years. 17E2 had most highly accentuated lines between birth till age 4 years. 2D8 had a complete hiatus of highly accentuated lines between 3 and 5 years and a peak in highly accentuated lines from 5 till 9 years (Figure 5.3).

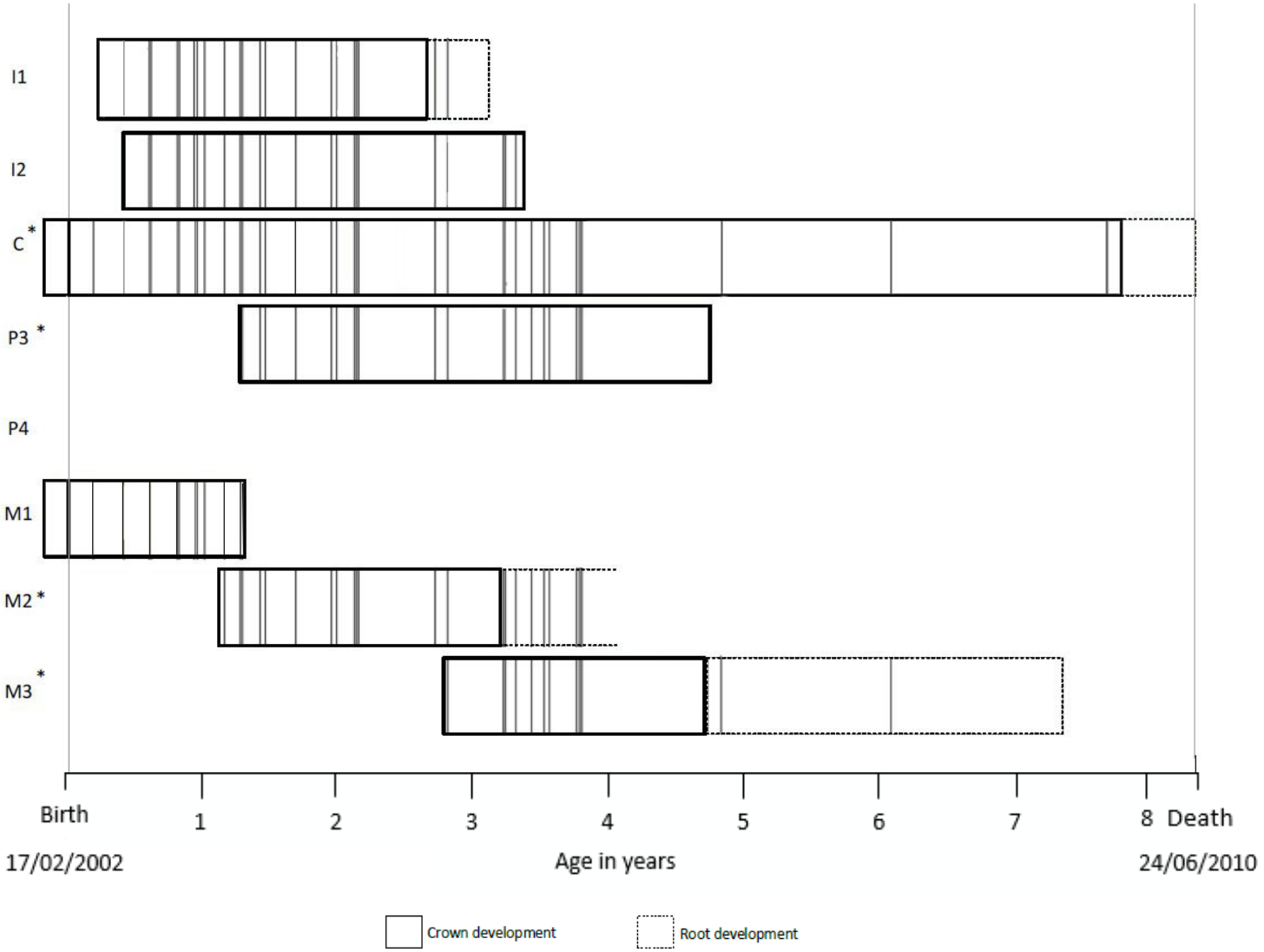

Figure 5.1: 17E2's highly accentuated line sequence (vertical lines) plotted on his mandibular dental development chronology (horizontal boxes). Maxillary teeth indicated with *.

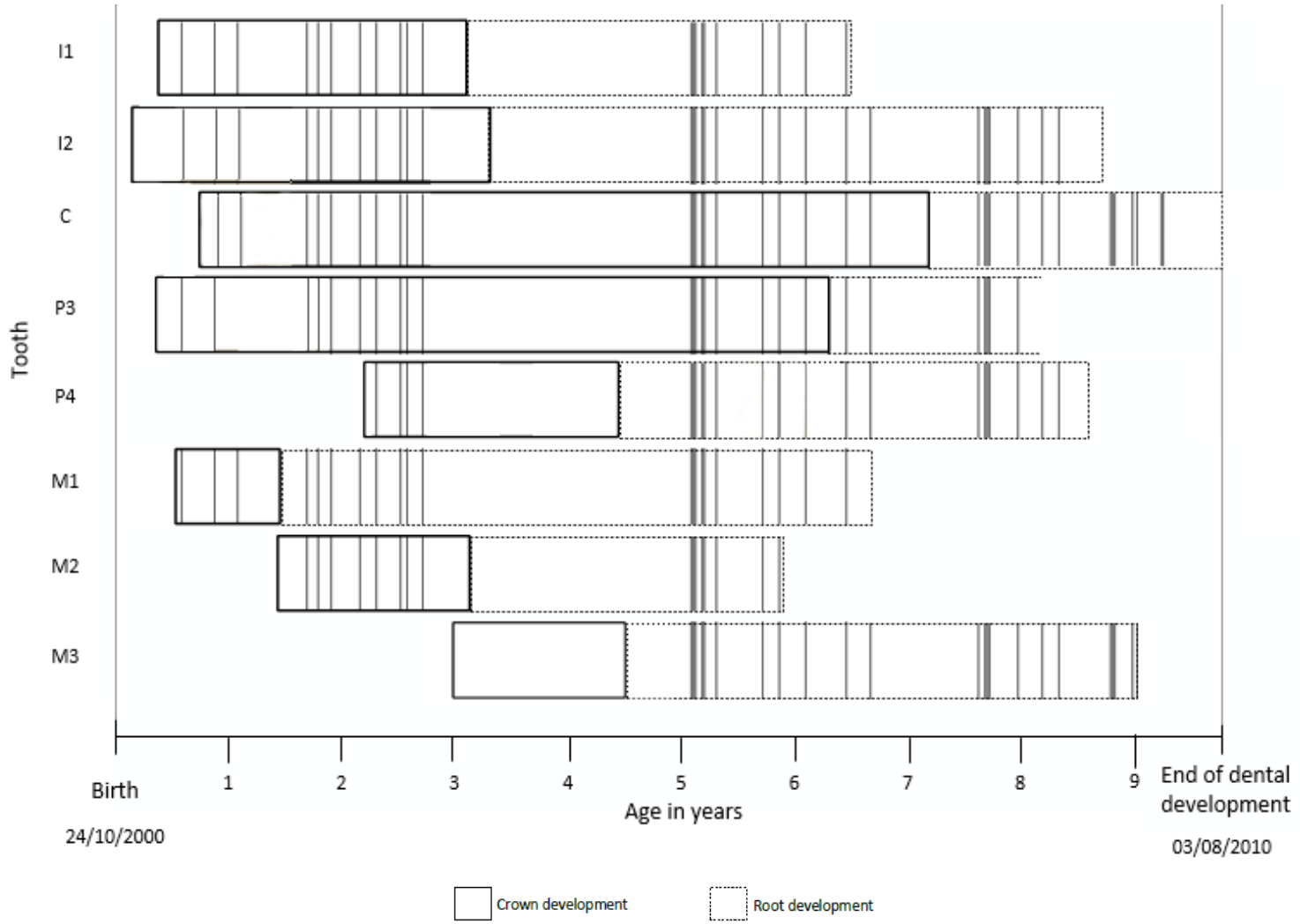

Figure 5.2: 2D8's highly accentuated line sequence (vertical lines) plotted on his mandibular dental development chronology (horizontal boxes). Maxillary teeth indicated with *.

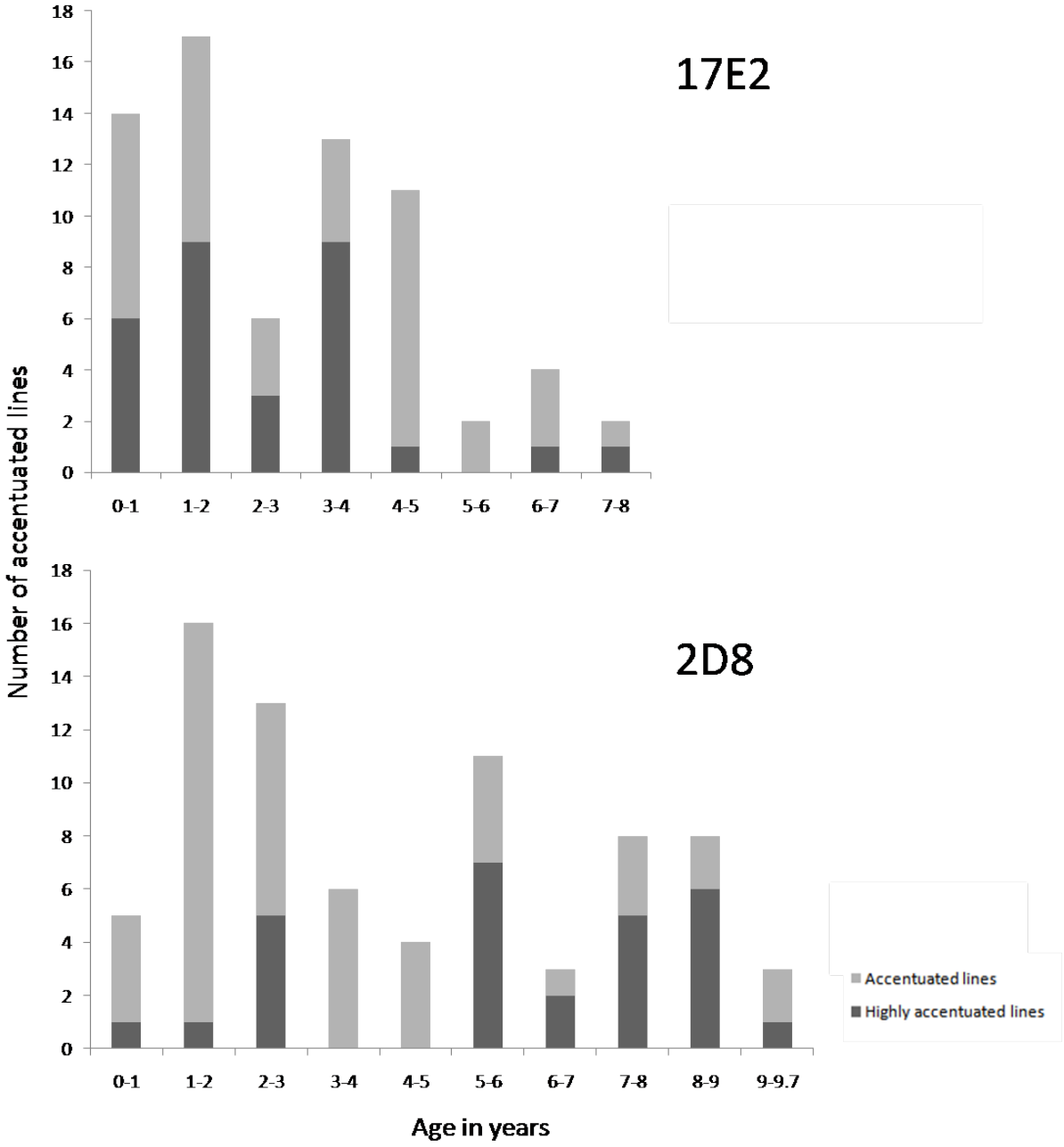

Figure 5.3: Accentuated and highly accentuated line frequency per year for the two male mandrills.

5.2.2 Life history

17E2's mother, 17E, resumed cycling when 17E2 was aged 0.5 years. Her cycle was irregular whereby her swelling fluctuated in size throughout the cycle instead of increasing to a maximal swelling, and she did not conceive. She was wounded during her cycle and mate-guarded for one day. 17E2 did not form any highly accentuated lines in his teeth up till the week of his mother's inflicted wound, which coincided with the formation of a highly accentuated line (Figure 5.4),

followed by another highly accentuated line the week after. No highly accentuated line formed when she was mate guarded. 17E2 formed two highly accentuated lines in the two weeks following the last observations of 17E's inflation, but since no swelling data were available for these following weeks, her cycle possibly continued when these lines formed. When 17E2 was age 0.8 years, 17E's swelling was observed to be flat again, followed by the formation of one highly accentuated line.

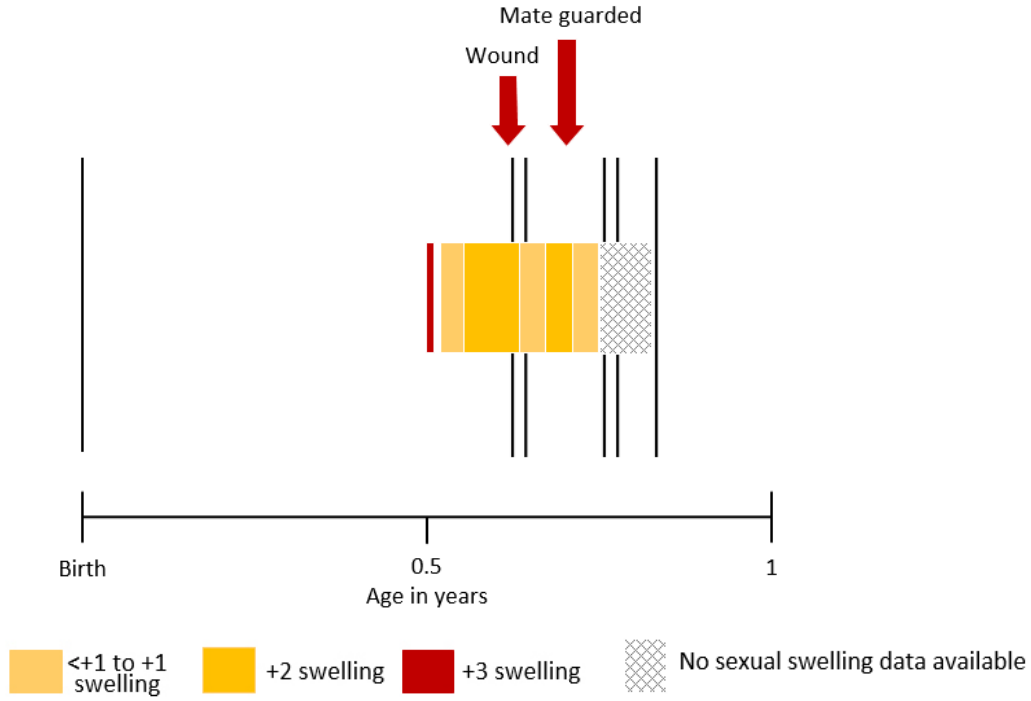

Figure 5.4: Reproductive data for 17E2's mother 17E plotted on 17E2's highly accentuated line sequence from birth to the age of 1 year.

2D8's mother, 2D, resumed her sexual cycle when 2D8 was aged 0.6 years (Figure 5.5). 2D's swelling increased in size over eight weeks. During the last week, when she had a +3 swelling, she was mate-guarded for three days and conceived. 2D8 did not form any highly accentuated lines before his mothers' cycle resumed. One highly accentuated line formed during the first weeks of 2D8's mothers' cycle. Since the accentuated line sequence is not exactly calibrated to calendar time but estimated, I do not know to which point in the cycle the line corresponds exactly. It did however certainly not correspond with the time she was mate-guarded. Two additional highly accentuated lines formed in the weeks after her cycle ended.

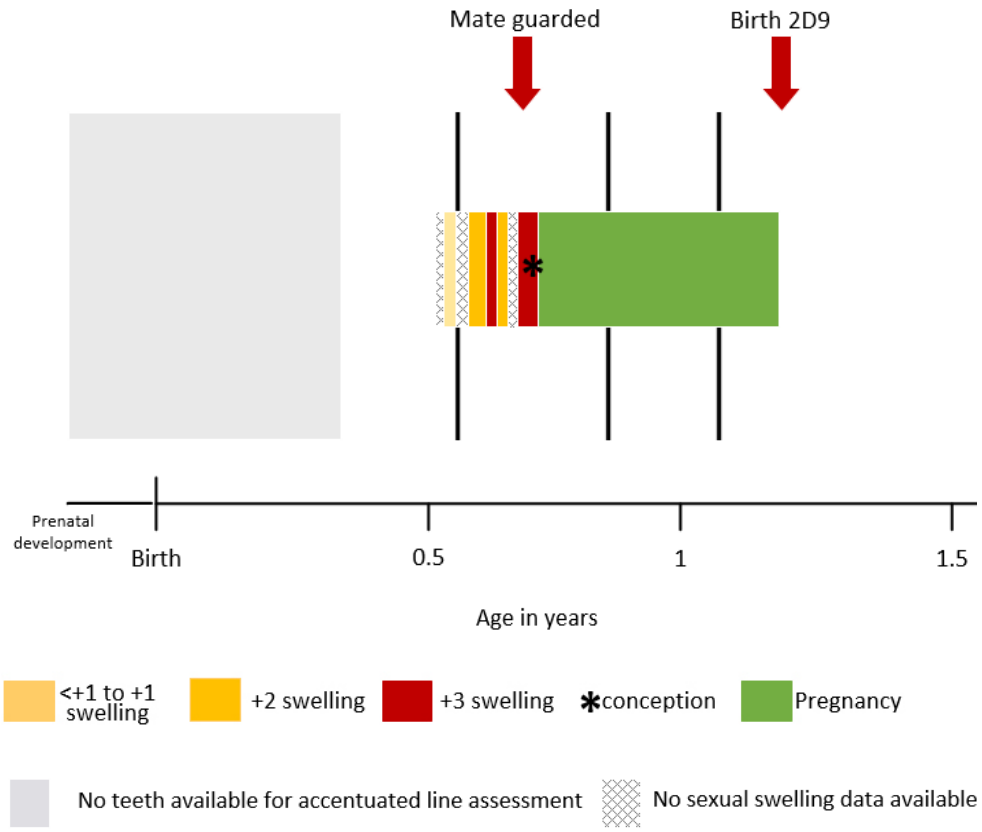

Figure 5.5: Reproductive data for 2D8's mother 2D plotted on 2D8's highly accentuated line sequence from birth to the age 1.5 years.

17E2 did not have any subsequent siblings. 2D8's mother, 2D, had another five infants after 2D8 was born (2D9 to 2D13). All were born before 2D8's dental development ended, and the date of birth is known for all but the last sibling (2D13). No highly accentuated lines formed corresponding with 2D9's birth. One highly accentuated line formed three weeks before 2D10 was born, which, given the estimated position of 2D8's accentuated line sequence, could be coinciding with the birth. No highly accentuated lines formed correlating with the births of 2D11 and 2D12.

When 17E2 was aged 3-4 years, he formed more highly accentuated lines during the mating season than the non-mating season, but for the years 4 until his death, only one or no lines formed at all. 2D8 formed more highly accentuated lines in the mating seasons between his 8-9 years compared to previous years (Figure 5.6), but there was no consistent pattern and the differences between the number of highly accentuated lines during and outside the mating season were small (Figure 5.7).

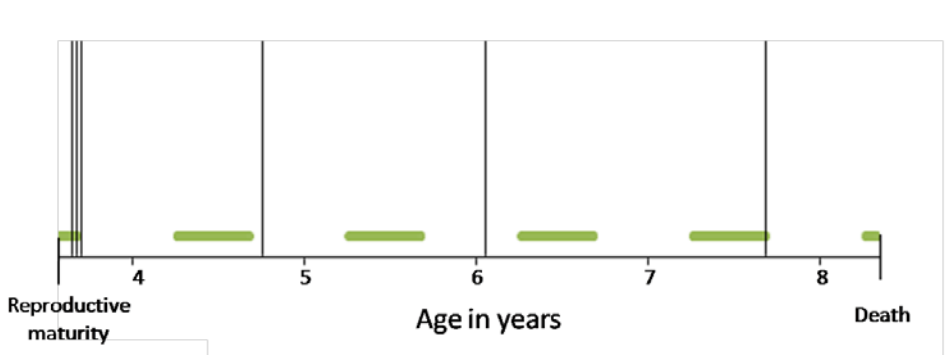

Figure 5.6: 17E2's highly accentuated line sequence (vertical lines) compared to mating seasons (horizontal lines) from age 3.8 till death.

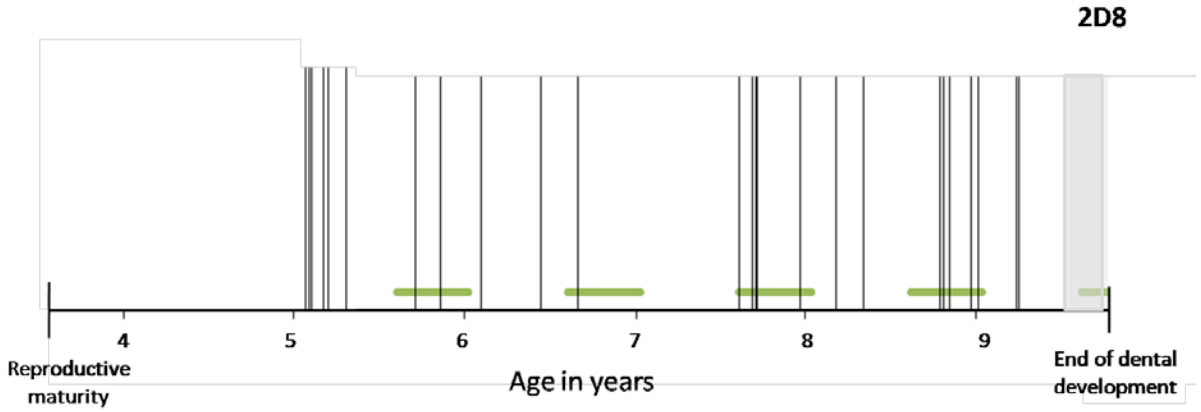

Figure 5.7: 2D8's highly accentuated line sequence (vertical lines) compared to mating seasons (horizontal lines) from age 3.8 till end of dental development. Grey zone = no accentuated lines visible due to taphonomy.

5.2.3 Social environment

During 17E2's life, there was one alpha male takeover in his enclosure (December 2004) when he was aged 2.8 years. Although the exact date of the takeover was not known, no highly accentuated lines formed in 17E2's dentition throughout the whole of December 2004. From birth until the end of 2D8's dental development, six alpha male takeovers took place in his enclosure. The last one took place when he was aged 3.9 years. None of these takeovers correlated with the formation of highly accentuated lines.

5.2.4 Captures

17E2 was captured 12 times during his life. The last two captures took place when only the C_1 was developing and since the exact calibration of this tooth is not sure and the material not clear, I did not compare these two captures to the accentuated lines. Three of the remaining 10 captures corresponded with the formation of a highly accentuated line. 2D8 was captured 19 times during the period of his dental development. Four highly accentuated lines formed within a seven-day range of a capture, two formed in a three weeks' range of captures, and one formed in a five weeks range of a capture.

5.3 Summary of results

In this chapter, I aimed to test the hypotheses that stress associated with life history events, including resumption of the mothers cycling and the birth of subsequent siblings affect accentuated line formation in the teeth of male mandrills. Additionally, I explored if the presence of receptive females affects the number of accentuated lines forming in male teeth once they reach reproductive maturity, as well as alpha male takeovers and times of veterinary captures. I found that I could not interpret male life history stress easily with this dataset. This was mainly because a large part of male mandrill life history events and phases take place past the age of dental completion. Furthermore, the life history data for the two males were difficult to work with, since the data collated ended in 2006, while a longer time period was recorded in their teeth. Additionally, the worn state of 2D8's dentition obstructed exact calibration of his dental development to calendar time. Nevertheless, the assessment of the accentuated line sequences of both males in combination with the life history data showed that resumption of mothers' cycle coincides with the formation of highly accentuated lines,

and for both males this was the first highly accentuated lines in their whole accentuated line sequence. Furthermore, results demonstrated that birth of subsequent siblings do not seem to correspond with accentuated line formation and that males did clearly form more accentuated lines during than outside the mating season past age 3.8 years up until the age at dental completion (9.7 years, male 2D8) or age of death (8.3 years male 17E2).

Chapter 6: General Discussion

My primary aim in this study was to determine the ages at formation of accentuated lines in the teeth of female and male mandrills to test the hypotheses that stress associated with life history events affects tooth formation and is therefore correlated with the formation of accentuated lines in tooth sections. To meet this aim, I first examined the chronology of dental development in individual female and male mandrills, providing the first histological information on dental development and tooth formation in mandrills including crown initiation, completion, and the associated growth processes of crown extension rate, Retzius line periodicity and daily secretion rate. I also determined sex-specific dental development chronologies for mandrills and compared mandrill dental development and chronology with other known, aspects of mandrill life history, including the sequence and timing of dental eruption (Setchell & Wickings 2004a) and the age at first cycle and reproduction in females (Setchell & Wickings 2004b). I then proceeded to obtain an accentuated line sequence from the teeth of individual mandrills and combined this newly acquired histological data with collated life history data. In this discussion chapter, I first discuss my findings on mandrill dental development and place it in the context of what we know about other African papionins. Next, I discuss my findings on the correlation between accentuated line formation and life history events, including resumption of the mothers' cycling, as a proxy for weaning, first sexual cycle, as a proxy for menarche, subsequent sexual cycles and parturitions, as well as alpha male takeovers and captures of the mandrills by the CIRMF staff. After having discussed all major findings of my thesis, I provide a discussion of my methods and possible future directions and applications for research related to this study and ending this chapter with a conclusion.

6.1 Mandrill dental development

In Chapter 3, I examined the chronology of dental development in 7 mandrills (3 females, 4 males), which was necessary to perform the research on accentuated line formation in mandrill teeth in the following chapters (4 & 5). In doing so, I examined the patterns of crown initiation, crown development duration and crown completion of individuals, examining the similarities and differences across individuals and between the sexes. By obtaining these data, I was additionally able to construct general sex-specific dental chronology for mandrills and investigate general sex-

specific differences in dental developmental (Chapter 3, Figure 3.6 & 3.7). In this discussion, I will briefly summarise these results, and place my findings on mandrill dental development in the context of what we know about other African papionins. Additionally, I discuss my findings on the relationship between life history and mandrill dental development in addition to what was previously known on their dental emergence.

The first permanent molar of mandrills (M1) has more prenatal enamel formation than other cercopithecoids studied to date (mean 50 days in mandrills: this study, mean 42 days in pig-tailed macaques (*Macaca nemestrina*, Smith et al., 2006; mean 37 days in baboons (*Papio anubis x P. hamadryas* hybrids, Dirks et al., 2002). The exact differences can only be compared properly among species once wear is accounted for, since prenatally formed enamel, positioned in the cusp tips, is rapidly lost during wear. Male mandrills have more than three times as much prenatal enamel formation in their M1 than females do. This difference cannot be attributed to wear, since some of the males had higher amounts of molar wear than females did, and still showed more prenatal enamel than females. The difference in amount of prenatal enamel formation could theoretically be due to the cusp we sectioned, because female 53DA's neonatal line was present in the mesial cusps and the males' neonatal lines were visible in the distal cusps. However, we found a neonatal line in male 5I2's metaconid with 62 days of prenatal crown formation, meaning that the male M1 undoubtedly initiates earlier than those of females. Although the sample size is small, this indicates that sexual differences in the adult dentition are present from the onset of development *in utero*, leading to sexual dimorphism. The frequency of worn first molars in skeletal remains means that differences between males and females in prenatal enamel formation are difficult to collect and rarely reported. In a study of dental development in orangutans (*Pongo pygmaeus* and *P. abelii*, Smith, 2016), another highly sexually dimorphic primate, males also seem to have either more or similar amounts of prenatal enamel in the M1 as females, but never less.

Additional to the M1, the incisors, P_3 and M_2 also initiated earlier in males than in females and the all crowns except the I_1 and P_4 had longer formation times in males than in females. Because the incisors and molar crowns are complete at similar ages in both sexes, earlier initiation is necessary to compensate for the longer duration of crown formation in males and male crowns may be larger at completion as a result. Differences may also relate to spatial relationships within the jaws and the requirements of accommodating the highly dimorphic canines and third premolar, all of which are developing simultaneously.

These sex differences in dental development reflect the extreme sexual size dimorphism in mandrills (Setchell et al., 2001) and the fact that males have the largest canines of any primate (Leigh et al., 2008). Sexual dimorphism in the adult canine increases through ontogeny in cercopithecines and although female canines generally erupt earlier than in males, the male canine erupts more rapidly and for longer than female canine (Leigh et al., 2005). The same is true for mandrills (Setchell & Wickings, 2004a). Additionally, I found that the upper male canine initiates prenatally. Prenatal development of permanent teeth is generally restricted to M1, although exceptions are occasionally reported (I_1 in a gibbon, *Hylobates lar*, specimen NYU008 (Dirks, 1998, 2003), I_1 and I_2 in humans (*Homo sapiens,* Dean & Beynon, 1991; Takiguchi, 1966) and C_1 in the fossil remains of *Anapithecus hernyaki* (Le Cabec et al., 2017). Early initiation of the male canine allows a longer period of crown formation and cranial growth before the tooth erupts, reaches occlusion, and attains its full height, which is directly correlated with reproductive success (Leigh et al., 2008). Early initiation is also related to facial morphology. The mandrill upper canines grow horizontally in the jaw before erupting in a vertical plane, clearly visible in the scan of HT12_15's cranium, the 6.1 year old male mandrill from my sample (Chapter 3, Figure 3.5). Prenatal initiation of the upper male canine may not be unique to mandrills, and likely to be present in male drills too. However, maxillary teeth are often not included in histological studies, since they are difficult to extract due to their curved root morphology (Van Beek & Downer, 1975), as well as being a precious tooth in the context of museum collections. Therefore, there are few comparative histological data for male primate upper canines (Reid, Schwartz, et al., 1998) and none for other highly sexual dimorphic primates. More work on the upper dentition is necessary to examine the underlying mechanism of prenatal initiation of the male mandrill's upper canine.

When looking at the general mandrill dental development chronologies (Chapter 3, Figure 3.6 & 3.7), mandrill molars develop stepwise with overlapping crown formation in the M_2 and M_3. The stepwise development pattern is similar to that in baboons (Figure 6.1) and geladas (Figures 6.2 & 6.3). However, whereas both mandrills and geladas have overlap in the development of their M_2 and M_3 development, baboons do not (Figure 6.1). The timing of molar M3 development compared to M2 is hypothesised to be related to feeding ecology, and in some species hypothesised to relate to life history pace (e.g. Dirks, 1998). Mandrills and baboons both have tough diets, but with a strong focus on incisal preparation (Fleagle & McGraw, 1999; Galbany et al., 2014; Hoshino, 1985; Jolly, 1970; Jouventin, 1975). In contrast, geladas mainly consume grass (Jablonski, 1993). Gelada molars are highly adapted to this graminivorous diet; their molars are large and high crowned, and have a distinctive structure with high, rather columnar cusps, large ridges and deep and complex folding of

their occlusal enamel (Jolly, 1970). Gelada M_1 and M_2 are usually severely worn by the time the M_3 comes into occlusion. The rapid succession of the M_3, which already initiates when the M_2 is still forming, is probably an adaptation to this graminivorous diet (Jolly, 1970).

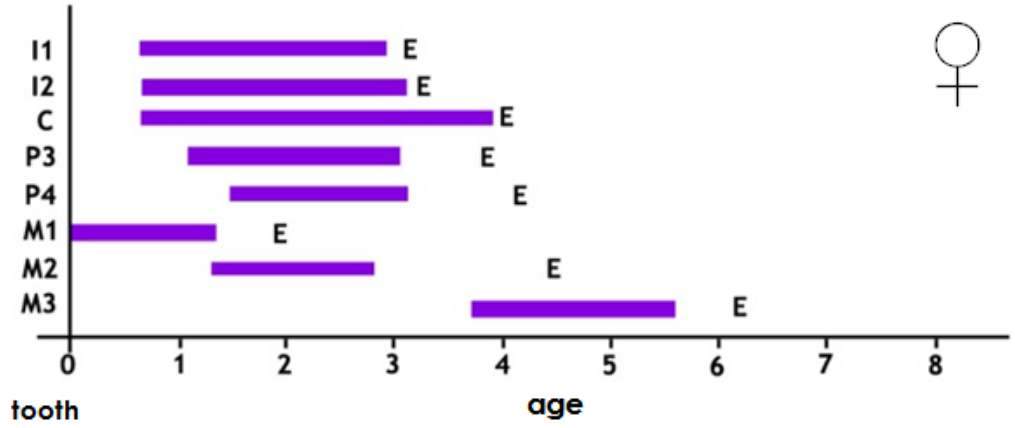

Figure 6.1: Published mandibular dental development for female baboons (purple bars) (redrawn from Dirks et al., 2002), combined with eruption means (Phillips-Conroy & Jolly, 1988).

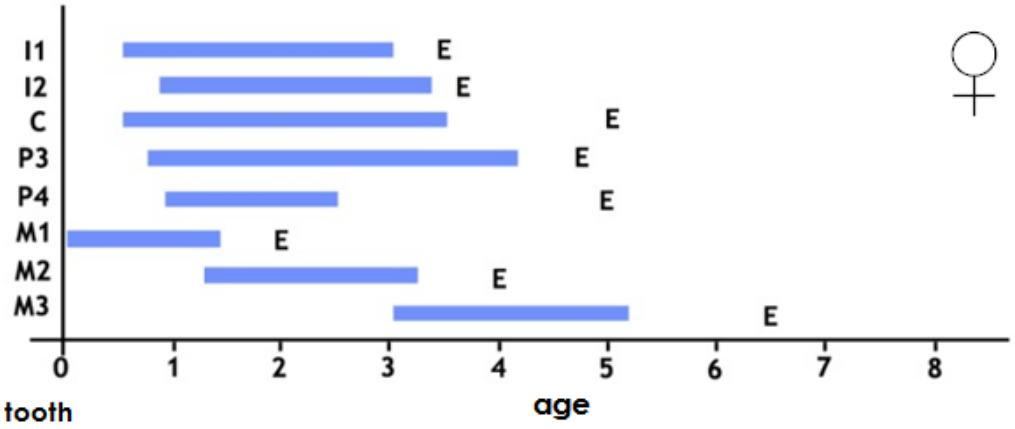

Figure 6.2: Published mandibular dental development for female gelada (blue bars), combined with eruption means (E) (redrawn after Swindler & Beynon, 1993) .

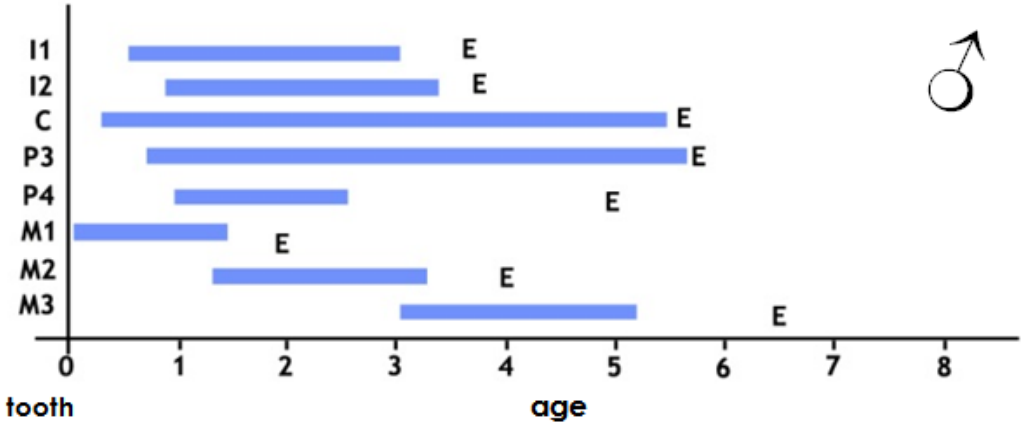

Figure 6.3: Published mandibular dental development for male gelada (blue bars) combined with eruption means (E) (redrawn after Swindler & Beynon, 1993).

When combining my new data on mandrill dental development with published mandrill emergence data, it became clear that in male mandrills, the canines (both C_1 and C^1) and P_3 emerge when the crowns are only partially developed. Male geladas also have large canines and P_3, and the eruption age for the canines and P_3 is similar among these two species, but geladas have shorter crown formation times (Swindler & Beynon, 1993) and the crowns are already completed by the time the male gelada canine and P_3 erupt (Figure 6.2 & 6.3). The P_3 canine-honing complex's main function is related to social signalling and male competition and has different selective pressure on its development and timing of eruption than the incisors. The P_3 has a very elongated honing facet, angled to hone the C^1. It lies almost parallel to the jawbone. HT12_15's dental development at death shows that the P_3 first moves in a vertical plane towards occlusion, as all teeth generally do during crown formation end eruption. However, after alveolar eruption, the tooth turns and continues to grow in a horizontal plane. Alveolar remodelling must occur to allow the tooth to turn during eruption (Newman et al., 2011). Analysis of 17E2's C^1 and the other male mandrill's C_1 showed that the canines and P_3 all develop and erupt at similar times. This suggest that the pressure of the C^1 on the P_3 may push the tooth in the right direction during eruption. Clinical dentistry shows that teeth turn and alveolar remodelling may occur in reaction to pressure due to occlusal trauma or parafunctional habits (Newman et al., 2011). The canines and P_3 may erupt while developing instead of after crown completion because of their size. Male mandrill canines are extremely large (mean 4.5 cm, Leigh et al., 2008), much larger than those of geladas. As visible in the X-ray of HT12_15, there would not be enough room in the jaw of a juvenile mandrill to accommodate a fully developed canine or P_3 including its root.

When combining my new histological data on mandrill dental development with published mandrill emergence data for the incisors, I found that the incisors also have little or no root when the crowns emerge. No other anthropoid primate incisors studied to date emerge in the same way as mandrills. Incisal root formation was once thought to be part of the eruption process (Chiego, 2014; Nanci, 2003), but we now know that root formation is not essential for eruption to proceed (Gowgiel, 1961; Kjær, 2014; Marks & Schroeder, 1996). Rootless incisal emergence has only been reported for species with ever-growing incisors (e.g. in rodents, Koenigswald, 1985, bovids such as *Myotragus balearicus*, Jordana & Kohhler, 2011, and one primate, the aye aye (*Daubentonia madagascariensis,* Hill, 1953). Although these ever-growing incisors have a different developmental trajectory whereby their continuous growth compensates for extensive wear, it does indicate flexibility in the necessity of root presence during emergence. Not the root, but the un-erupted portion of the developing crown can serve as an anchoring point within the alveolar bone, which could serve the purpose of

stabilizing that tooth during eruption before reaching occlusion. Furthermore, eruption is a process, and therefore the age of gingival eruption is earlier than the age a tooth comes into occlusion and functional use: By the time the mandrill incisors erupt, they will not be fully functioning yet. When comparing my findings on mandrill incisal development and eruption to that of baboons (*Papio anubis-hamadryas* hybrids, Phillips-Conroy & Jolly 1988; Dirks et al., 2002) and geladas (*Theropithecus gelada,* Swindler & Beynon, 1993), I found baboons have little root development of the anterior teeth at eruption too, although not as extreme as in mandrills. Geladas however have more root development for all anterior teeth at eruption (Chapter 3). Since mandrills and baboons have very different diets and food processing strategies, feeding ecology possibly plays a role here. Mandrills and baboons both have tough diets requiring a lot of incisal preparation (Fleagle & McGraw, 1999; Hoshino, 1985; Jolly, 1970; Jouventin, 1975) and both show extreme tooth wear of the anterior dentition (Galbany et al., 2014). Geladas on the other hand mainly consume grass and do not intensely use their anterior teeth for food processing (Jablonski, 1993), but rely more heavily on their molars (Jolly, 1970). However, a diet relying mainly in incisal preparation would suggest early incisal development (including the root), and therefore seems contradictory to my results. Alternative explanations might be necessary to explain this phenomenon than just feeding ecology. Possibly, cranial growth and morphology plays a role too. Significant sexual differences in the papionin facial skeleton do not emerge until the eruption of M2 has taken place (O'Higgins & Jones, 1998; O'Higgins & Collard, 2002). Therefore, if small amount of root formation at eruption of the incisors is connected to facial morphology, it should be present in both males and females, since the incisors erupt earlier than the M2. Both male and female mandrills indeed show little incisor root formation at eruption. Early facial morphology could therefore technically be an additional driving force. This in turn might also relate to root extension rates. If the roots of the different taxa extend at different rates, this will mean that even if incisors emerge with different amounts of root formation, they still might come into occlusion in a similar state. Despite emerging with less root, incisors of mandrills may take a shorter time to reach functional occlusion, at which point they have all the root they need to be sufficiently anchored into the jaw. An examination of root extension rates among these three species is necessary to establish this further. To shed further light on the correlation between eruption age and root formation in papionins, we recently performed a comparative study of papionin dental development, which demonstrated that mangabeys (*Cercocebus atys)* have a very similar state of incisal development at eruption as mandrills (Lemmers et al., 2016; Appendix D). The similarities between mandrills and mangabeys may be related to their close genetic relationship and similar foraging strategies (Fleagle & McGraw, 1999).

While constructing dental development chronologies, I also calculated mandrill Retzius line periodicities and daily secretion rates. Mandrills have a mean Retzius line periodicity of 7 days, with a range of 6 - 8 days and no sexual differences. Mandrill periodicities are therefore similar to baboons (7 days, Dirks et al 2002) and geladas (7 days, Swindler & Beynon, 1993), higher than in macaques (4 days, *Macaca nemestrina*, Smith, 2006), slightly lower than great apes (mean 8/9, range 5-12: Kawasaki et al., 1980; Dean, 1989; Beynon et al., 1991a; Dean & Beynon, 1991; Dean et al., 1993; Huda & Bowman, 1994, 1995; FitzGerald, 1996; FitzGerald et al., 1996; Reid & Dean 2006, Reid et al., 1998), but higher than for gibbons (4 days, Dirks 1998). Periodicity is hypothesized to be linked to the Havers-Halberg Oscillation (HHO), a biorhythm that regulates bone growth and metabolism (Bromage et al., 2009, 2012; Mahoney et al., 2017). In addition to body mass, periodicity in primates might also correlate with life history variables, metabolic rate and the rate at which osteoblasts proliferate (Bromage et al., 2009, 2012). The findings for mandrills therefore fit the pattern that heavier primates have higher periodicities (Bromage & Janal, 2014; Bromage et al., 2012; Dean, 1995; Dean & Scandrett, 1995; Smith et al., 2003). The meaning and aetiology of Retzius line periodicity however is not yet fully understood (Bromage & Janal, 2014; Bromage et al., 2011, 2012), making and the interpretation of variation, ranges and means of periodicities within and among primate species complicated. For example, recent work on the fossil remains of *Anapithecus hernyaki*, a primitive catarrhine (Le Cabec et al., 2017) showed a periodicity (3 days, Le Cabec et al., 2017), which based on the HHO theory, would be unexpected for its body mass (8 and 15 kg, Begun, 2002; Nargolwalla et al., 2005). Recent work on human Retzius periodicity showed a positive correlation of periodicity with deciduous enamel thickness as well as a moderate association with the rate of enamel secretion and osteocyte proliferation in bones (Mahoney et al., 2016; 2017). These new data may suggest periodicities might be used to infer enamel thickness and stature of individuals. Additionally, periodicities are useful to establish for individuals and species since they can assist in crown formation time calculation. Multiplying the number of perikymata from a tooth with a mean periodicity allows for non-destructive crown formation time assessment, specifically valuable when material cannot be sectioned due to limitations preservation or access. However, as the results from this study demonstrated, accurate periodicity calculation can be difficult, even when histologically assessed, and an error of 1 day can result in markedly different crown formation times. I therefore do not recommend to use periodicities for crown formation time establishment unless periodicity can be calculated consistently and repeatedly, without having to use a mean for an individual.

Mean enamel daily secretion rate in mandrills was 3.9 µm for both sexes. Mandrill values therefore fall within the range of hominoid daily enamel secretion rates, with a lower limit of 2 - 3 µm per day and an upper limit of 6 - 7 µm per day (Smith, 2004). However, secretion rates vary across a tooth. A mean per species is therefore very overarching and measurements of enamel daily secretion rate are particularly useful when they are measured in standardised distances along the enamel dentine junction, since this allows for better inter and intra species comparison. In this thesis, I measured enamel daily secretion rates specifically to establish crown formation times and to determine the position of accentuated lines (Chapters 4 and 5). My results are, however, useful in contributing to the larger body of data dealing with variation in rate of enamel formation among primates (Beynon et al., 1998; Dean et al., 1998; Reid et al., 1998; Smith, 2004;2007;2008), which in turn will hopefully assist in the wider debate on dental development and biorhythms (Bromage & Janal, 2014; Chapple, 2016; Mahoney et al., 2017).

I calculated extension rates for all individuals and all tooth types, which indicated that male mandrills had higher mean extension rates than females for all teeth. Canines and incisors had the highest mean extension rates in both sexes, and the M_3 had the lowest mean. 17E2's C^1 had the highest mean extension rate of all teeth. The higher extension rates in males is likely to be related to their overall tooth size and age at dental emergence: males need a higher extension rate to complete crown formation and erupt teeth at the time required to maximise reproductive success. Females mandrills emerge their permanent teeth earlier than males (Setchell & Wickings, 2004a). Males have longer crown formation times than females. Male teeth initiate earlier, emerge later and their crowns extend at a higher rate (mean) than female teeth. However, just discussing mean extension rates does not give a complete picture, since extension rates vary within teeth. The highest extension rates in mandrills occur at initiation. The rate then drops and increases again towards completion in most of the teeth. Increased extension rates towards the end of the cervix are unexpected since the perikymata spacing, and thus the Retzius line spacing, generally decreases down the crown side in humans and other great apes (Hillson, 2014), meaning that extension rate decreases. The increased cervical extension rate in mandrills may be related to differences in crown morphology and the accompanying perikymata spacing.

As a final part of my mandrill dental development analysis, I compared the newly acquired data on mandrill dental development with mandrill life history data. I found that mandrill mean weaning age falls 6 months before their M1s complete. This is earlier than the general pattern for primates, in

which weaning occurs after M1 completion and around the time of M1 eruption (Smith, 1991). Baboons also wean their infants before M1 eruption (Dirks & Bowman, 2007). Geladas, however, have completed and erupted M1 when weaned (gelada weaning cited in Lee et al., 1991; Swindler & Beynon, 1993), as do most great apes. If we think of the deciduous teeth as 'learning teeth' and the permanent teeth as indicative of independent feeding, tooth eruption can characterize weaning as early or late, which is probably co-evolved with environmental pressures and diets (Smith, 1991). The dichotomy between cercopithecoid and great ape weaning ages matches the overall pattern of faster and slower life histories in these two families of catarrhines. Earlier weaning means shorter inter-birth intervals, which maximises reproductive success in an environment of higher adult mortality (Harvey & Zammuto, 1985; Promislow & Harvey, 1990). The seasonal or more terrestrial environments in which ancestral cercopithecoids evolved may have increased the risk of predation and starvation, favouring faster life histories, with shorter inter-birth intervals to optimise reproductive success. In contrast, selection would have acted to slow hominoid life histories, maximizing their reproductive success in an environment of low adult mortality (Jablonski et al., 2000; Kelley & Smith, 2003). As semi-terrestrial primates, mandrills fit the predicted cercopithecoid life history pace. However, among the cercopithecoids, mandrills also seem to wean relatively early compared to their dental development. Diet is likely a driving force since the eruption of the M1 greatly increases the chewing surface of the deciduous dentition, enabling the transition to an adult diet, which explains the correlation between M1 eruption and weaning (Smith, 1991). However, primates have diverse diets, and diverse ways of shifting from mother's milk to solid foods. This can for example clearly be illustrated by looking at humans (*Homo sapiens*), who are extreme outliers to the weaning and M1 eruption correlation in primates; they wean their infants multiple years before their M1 erupts. This is only possible because of specific weaning foods offered to infants that can easily be processed with merely the deciduous dentition (Dettwyler & Fishman, 1992; Humphrey, 2010). Across mammals, herbivores have extremely accelerated development and eruption of the adult dentition compared to weaning, which prepares them for their heavy masticatory plant-based diet. The graminivorous gelada may therefore need the M1 at weaning more than mandrills and baboons, who are probably able to get by with their deciduous dentition at weaning. The extremely worn deciduous teeth left in the mandible of mandrill HT12_15 show that mandrills use their deciduous teeth heavily post-weaning.

Female mandrills reach menarche and start reproduction at the same time as their M3 develops, but before it emerges. The common primate pattern is for first reproduction to occur after the emergence of M3, except for the cercopithecoids (Dirks & Bowman, 2007). In cercopithecoids, M3

eruption tends to occur prior to first reproduction (Dirks & Bowman, 2007; Kralick et al., 2017; Machanda et al., 2015). This suggests that early reproduction might be a derived trait in cercopithecoids. Based on the dental development data presented in Chapter 3 of this thesis and published emergence data (Setchell & Wickings, 2004), mandrills fit this cercopithecoid pattern well. Male mandrills have a different pattern of dental development related to sexual maturity and first reproduction than females. Although males reach reproductive maturity at similar ages to females, they rarely sire before the age of 10. The size of the male canine is strongly correlated with reproductive success with a peak in reproduction corresponding with maximum tooth height (Leigh et al., 2008), which means the canines are complete and in occlusion, but have not yet started to wear down (Leigh et al., 2008). The mandrill lower P_3 follows a very similar developmental course, as part of the canine-honing complex.

6.2 Stress, life history and accentuated line formation

Once I acquired the data on mandrill dental development, I proceeded to analyse the accentuated lines in the teeth of two male and two female mandrills for which accurate life history data was available. Here I will summarise the results of both the females (Chapter 4) and the males (Chapter 5) and discuss the implications. First, I will discuss results related to the overall accentuated line sequence found in females and males, followed by a discussion on the correlation between accentuated lines and weaning and sibling birth, which I examined for both sexes, followed by menarche, subsequent cycles and parturition, which I examined in females. Next, I discuss my findings on male post-weaning life history stress in correlation with accentuated line formation and I conclude this section with a discussion on the correlation between accentuated line formation and changes in alpha male and captures for both sexes.

I found that the number of accentuated lines, before applying the classification between accentuated and highly accentuated, was very high for all mandrills. The high frequency of accentuated lines might have multiple causes. Firstly, histological assessment of accentuated lines is bound to contain variation due to the way samples are prepared (e.g. Guatelli-Steinberg, 2001; McFarlane et al., 2014) and accentuated lines might be more visible in one sample or set of samples than in others. Secondly, the living circumstances of the mandrills might influence the overall stress levels of the individuals, affecting the formation of accentuated lines. The animals live in semi-free ranging conditions in their natural environment and except for the founder males did not show self-

directed behaviour like hair plucking observed in zoo mandrills (Pansini, 2006; Setchell, *pers comm*). Overall, the mandrill living conditions are considered to be fairly good (Setchell, *pers comm*). However, the CIRMF mandrill group probably has more males aged 10+ than what we know of in the wild outside the mating season (Hongo, 2014; Rogers et al., 1996). More males in a group could increase competition and aggression which might influence stress levels as well. Furthermore, in the wild most males only join the group during the mating season (Abernethy et al., 2002; Hongo, 2014) and afterwards leave the group, which is not possible at CIRMF. Additionally, the CIRMF enclosures might be large but home ranges in the wild are as large as 40-50 km^2 (Hoshino, 1985; Jouventin, 1975), leaving more space for males to become peripheral. Although in the wild animals will experience additional stress related to risks as predation, poaching, habitat disruption and untreated wounds and illnesses (Bowen-Jones & Pendry, 1999; Brockmeyer et al., 2015; Harrison, 1988), the overall day-to-day sources of stress may be different for the CIRMF animals, such as due to daily additional food provision, introducing additional competition for food. It would be interesting to compare the accentuated line sequences from wild mandrills with the CIRMF individuals to find out if the dense accentuated line sequence is an artefact of the CIRMF set-up. Finally, to make true statements on the high frequency of total accentuated line frequency in the CIRMF mandrills, comparative studies need to be performed whereby total counts of accentuated lines from complete dentitions are made. To this date no such studies exists yet, and therefore it is difficult to make a final statement on the overall accentuated line frequency.

There was variation in the frequency of accentuated lines among the individuals. When comparing the two females, PB had more accentuated lines in her teeth than 5D3A. PB was born to the lowest ranking mother in the group, while 5D3A was high ranking, suggesting that the difference in accentuated line frequency may be rank-related. The correlation between rank and the amount of stress an individual experiences is however not straightforward. In many mammals, including primates such as olive baboons (*Papio anubis*), low-rank leads to chronically elevated glucocorticoid levels (Creel, 1996; Sapolsky, 2004) and subordinates may suffer chronic stress due do acts of aggression (Goymann & Wingfield, 2004; McEwen, 1998; McEwen & Wingfield, 2003; Silk, 2002), few stress-reducing relationships (Abbott et al., 2003) and fewer grooming partners (Sonnweber et al., 2015). Low ranking female CIRMF mandrills however do not show chronically elevated cortisol levels, explained by stable female social hierarchy, overall low levels of aggression, a system of social support, and large enough enclosures to avoid aggressive encounters with dominants (Setchell et al., 2008). These findings correspond with those of for wild chacma baboons (*Papio ursinus*) (Engh et al., 2006; Weingrill et al., 2004) and long tailed macaques *(Macaca fascicularis)* (Carel P. van Schaik et

al., 1991). The high number in accentuated lines in PB compared to 5D3A is therefore not easily explained by their rank differences. It may be that PB is an outlier since she was the absolute lowest ranking individual in her whole group. Furthermore, Setchell et al (2008) suggest that subordinates may react only transiently to specific aggressive events, rather than continuously expecting them which is reflected in their cortisol levels not being continuously chronically elevated. The higher frequency in accentuated lines in PB might only record brief moments of mild disturbance which are not intense enough to chronically elevate her cortisol levels. In contrast with the total number of accentuated lines, the frequency of highly accentuated lines was similar between the two females, which is much more consistent with the previous research on high and low-ranking cortisol levels in the CIRMF colony.

The males also showed differences in accentuated line sequence when compared to each other. Although their frequency of accentuated lines was comparable to each other, the lines were differently distributed. 17E2's highly accentuated lines mainly formed during the first part of their life, while 2D8 had a formation hiatus between the ages of 3 and 5 and a peak of highly accentuated lines from age 5 till 9 years. The different patterns of accentuated line formation in the males could be related to the different group size and enclosure size of the two separate enclosures in which the individuals were placed. Furthermore, rank may play a role, since 17E2 was born to a low-ranking mother and 2D8 to a high-ranking mother. However, a study on the relationships among glucocorticoid levels, testosterone and secondary sexual ornamentation in male mandrills from the CIRMF colony found that glucocorticoid levels did not vary systematically with dominance rank (Setchell et al., 2010). 17E2 had a lower frequency of highly accentuated lines in the latest part of his sequence than 2D8. This may in part be an artefact from the material available and the methods used. For the last 3.5 years of 17E2's life, only the root of his M^3 and the C^1 were developing. The canine was very difficult to accurately assess due to the condition of the enamel, and the dentine was difficult to measure as well. Therefore, only the root of the M^3 was available for accurate accentuated line assessment. Since the teeth of 2D8 had been very difficult to match to each other, I included the roots of his teeth to a further extend than I did for 17E2. This results in more material to examine for the presence of accentuated lines. The higher number of lines in 2D8's later years in life in comparison to 17E2 might therefore be, in part, influenced by the material examined.

After having identified the pattern of accentuated lines in the teeth of the females and males, I examined the correlation between accentuated line formation and life history events for mandrills, starting with resumption of the mothers' cycling as a proxy for weaning.
for all four mandrills I found a link between accentuated line formation and the resumption of the

mother's sexual cycle. There was however individual variation as well as differences between the sexes in the way the accentuated lines manifested.

For the females, the first highly-accentuated lines forming in their dentition post-birth corresponded with the resumption of the mother's cycling, specifically at times when the mothers were mate-guarding during their cycle. This result is consistent with previous research stating that weaning conflict would be particularly intense when mothers resume cycling (e.g., Berman et al., 1994), when the mother shifts her attention away from her infant and directs her behaviour to mating (e.g. Lee, 1996). The mother's increased mobility and activity during resumption of cycling gives the infant less access to her physically, including decreased time on the nipple and fewer rides, which may increase infant stress levels (Setchell *pers comm*, Barrett *pers comm*) and could cause the appearance of highly accentuated lines, in contrast to minor acts of rejection during other times of the weaning phase that might have taken place at earlier stages. The infants' formation of highly accentuated lines when the mother was mate- guarded during resumption of cycling might indicate stress related to the proximity of dominant male mandrills, who are up to three times larger than their mothers in mandrills (Setchell et al., 2005a). The presence of large males and inter-male aggression may seems to have increased the weanling's stress levels, comparable to 'spectator stress' (Jackson, 2013; Sapolsky, 2004).

For the males, as for the females, the highly accentuated lines that formed at the time their mothers resumed their sexual cycle were the first highly accentuated lines that formed in their teeth post-birth. Male 17E2 formed a highly accentuated line when his mother was wounded during her cycle resumption and 2D8 formed a highly accentuated line at the start of his mother's cycle resumption. The proximity of a possibly large male as well as the aggressive encounter towards his mother seems to have been threatening situation for 17E2, enough to increase his stress levels resulting in the formation of a highly accentuated line in his teeth at this point in his mother's cycle. Although for 2D8 the first highly accentuated line observed in his teeth corresponded with the mothers' resumed cycle, a large part of his first molar was worn away which theoretically could have contained highly accentuated lines as well. Surprisingly, no highly accentuated lines formed in the males' teeth when their mothers were mate guarded. For 17E2, this might be explained due to the brevity of the mate guarding, which was only one day. Furthermore, it might relate to the irregularity of his mother's resumed cycle; Her swelling fluctuated in size throughout the cycle and the cycle did not lead to conception. The mate guarding possibly was not as consistent as when she would have had a regular

cycle with an increasing swelling, ovulation and conception. It could be that the mate-guarding therefore was less invasive and psychologically threatening for the infant. For 2D8, the mate guarding did take place when his mother had a maximal swelling and did result in a conception. This may be because the first approach of larger males earlier in his mother's cycle evoked a stress-response intense enough to form a highly accentuated line, and the infant adjusted to the presence of males after this initial increased attention towards his mother. However, 2D8's dental sequence was extremely difficult to calibrate, and the absence of a highly accentuated line might also be an artefact of the calibration method used.

In summary, my results suggest that weaning stress correlates with the formation of highly accentuated lines and may be detectable in teeth of individuals with unknown life histories. Females showed a correlation between accentuated lines and the timing their mothers were mate-guarded during their resumption of cycling. Males, also showing highly accentuated lines at the time of their mothers' cycle resumption, did not show accentuated lines specifically at the time their mothers were mate-guarded. This may be partly due to poorer condition of one of the males' teeth which resulted in non-exact calibration of the accentuated lines with calendar time. However, it may also indicate that females experience the resumption of their mother's cycle differently to males and the key study of baboons that led to the hypothesis that weaning leads to the formation of accentuated lines was indeed specifically based on two females (Dirks et al 2002). Additional to variation between the sexes, there will likely always be a degree of variation in how the weaning process is experienced by individual animals (Dirks et al., 2002). Individual variation markers of stress in teeth is also reported for chimpanzees (Skinner et al., 2012), whereby notable variation was observed in the ages of onset and cessation of enamel defects, which the authors hypothesised to reflect variation in the weaning process as experienced by individual animals.

My results do not show a convincing link between accentuated line formation and sibling birth. Both females formed highly accentuated lines coinciding with the birth of one out of two subsequent sibling births, but not for the other; 5D3A in response to the first sibling birth, PB only to the second. 17E2 did not have subsequent siblings and 2D8 did not form highly accentuated lines correlating to the birth of his subsequent siblings, except possibly when his second subsequent sibling was born. This makes explaining the accentuated line pattern in correlation to sibling birth complex. A stress response to a siblings' birth can be explained by attachment theory and parent-offspring conflict theory, when the reduction in maternal care causes an increase in offspring distress (Bowlby, 1969; Devinney et al., 2001, 2003; Trivers, 1974). This would be particularly the case at the birth of a first subsequent sibling when an individual is still juvenile, reliant on maternal support, and has not

experienced the presence of a sibling before. This may be the case for 5D3A. She formed a highly accentuated line at the time of her first sibling being born, but not for the second. By the time her second sibling was born she was already a cycling female herself and less maternally dependant. PB's reversed pattern is more difficult to explain. No highly accentuated line forming at first subsequent sibling birth would suggest less conflict over maternal resources with the new sibling. As a juvenile, she might have increased in play, grooming, and contact with other members of her social group after the birth of a sibling (Bateson, 1994; Devinney et al., 2001, 2003) which might mediate a stress response. 2D8 showed the same result and did not form a highly accentuated line at the time of his first siblings' birth. The CIRMF mandrill group is a stable social environment (Setchell et al., 2008b), so PB and 2D8 might have easily replaced their mother's attention. Furthermore, dynamic assessment models propose that cooperation and compromise between mothers and infants over levels of care may prevail instead of causing conflict and distress (Bateson, 1994). This however does not explain why PB formed a highly accentuated line at the time of her second sibling's birth, but not the first. Possibly, an explanation can be found within the stress physiology and its translation to accentuated line formation itself. For both females, the sibling births that did not correspond with accentuated line formation took place at a time when multiple highly accentuated lines had already formed in the weeks before the sibling birth itself. The other two sibling births that did correlate to highly accentuated line formation had no additional lines forming shortly before. Hence, the absence of accentuated lines to the sibling births might be a side effect of already increased stress-levels, which might have happened for other, undocumented reasons. Finally, studies have shown that maternal care decreases more intensely when mothers resume cycling than when subsequent offspring is born (Berman et al., 1994; Devinney et al., 2001; Schino & Troisi, 2001). A similar pattern seems to be the case for the female mandrills, since I found a more distinct pattern of accentuated line formation during the resumption of the mother's cycle than around the time of subsequent sibling birth. In summary, from the results of the male and females together, the prediction that sibling birth affects the formation of accentuated lines is not confirmed by my data.

I found that highly accentuated lines correlated with maximal swellings and mate-guarding during a female's first and subsequent cycle, and my findings suggest that menarche and the accompanying increase in male attention may have a stronger effect on the formation of accentuated lines than subsequent cycles. Since the highly accentuated lines stopped forming as soon as breakdown occurred, these results support the prediction that first and subsequent reproductive cycles are associated with the formation of accentuated lines. Two mechanisms might be responsible for the formation of the accentuated lines during female cycles. Menarche, and to a lesser extent subsequent cycles, are linked to physiological (Dixson, 2012; Plant & Zeleznik, 2015) and

morphological (Setchell & Wickings, 2004; Zinner et al., 1994) changes in the body of female primates which may affect the formation of accentuated lines. Furthermore, social circumstances change considerably during these times, when females are in much closer contact with males than before and are mate-guarded. The costs of mate-guarding are often discussed from a male perspective (e.g. Alberts et al., 1996; Girard-Buttoz et al., 2014; Matsubara, 2003; Setchell et al., 2005b). However, mate guarding may also be costly for females (e.g., Palombit, 2014; Smuts & Smuts, 1993). Thus, both physiological and psychological aspects of the first cycle are likely to be a stimulus in the formation of the accentuated lines, throughout the cycle and at the time of mate-guarding. The accentuated lines associated with PB's first sexual swellings were extremely marked, uniform in all teeth forming at the time and were the main connecting point when matching her teeth for dental development. In contrast, the accentuated lines forming during her second cycle were less intense, and although very clear in the M_3 enamel and M_2 root, they had a less distinct appearance in the canine. These results from PB's teeth suggest that menarche and the accompanying increase in male attention may have a stronger effect on the formation of accentuated lines than subsequent cycles. Since the accentuated lines correlated specifically with times when females were mate-guarded, accentuated line formation may relate most to the psychological stress induced by the presence of and interaction with males. Altogether, my findings therefore support the hypothesis that the cyclical pattern of accentuated lines beginning at about the age of 4 years observed in the teeth of hybrid baboons corresponds to the age at which females undergo their first menstrual cycles (Dirks et al., 2002).

Two out of three parturitions experienced by the two females in my study correlated with the formation of highly accentuated lines. These results fit with previous research on parturition lines in teeth of mammals, whereby markings in teeth represented minimum number of parturitions or 'calving episodes' rather than accurately recording every parturition that took place (Klevezal & Myrick, 1984; Trunova et al., 1999; Okada, 1943; cited in Dean & Elamin, 2014). PB's first parturition did not exactly coincide with the formation of a highly accentuated line and no highly accentuated line formed either when the new-born infant was euthanised due to a leg injury. Loss of an infant is thought to affect some primates judging from mourning behaviour (e.g., Anderson, 2011; Biro et al., 2010; Fiore, 2013) and mothers, including mandrills, may carry the body of a dead infant for multiple days (*pers observ* at CIRMF, Setchell *pers comm*). Since PB's infant was euthanized, carrying her infant was not possible. Judging from the absence of highly accentuated lines after her infant's death, PB may have returned to more juvenile, playful behaviour instead of a stress response to infant loss. PB's second and 5D3A's first parturition did correlate with a highly accentuated line. This

suggests that PB's second parturition and care for her subsequent new-born was less stressful for her than the period after her first parturition. 5D3A's successful full-term pregnancy and parturition took place when she was around the same age as PB's second parturition. Maturity therefore may play a role in accentuated line formation in response to parturition and post-parturition period, which fits well with the hypothesis that early reproduction may be a derived trait in cercopithecoids whereby females can reproduce before reaching full adult body size, but at the risk of first reproduction not always being successful. If infants do survive, the reward for taking that risk of early reproduction may result in higher reproductive success (Dirks & Bowman, 2007) although not always, as for rhesus macaques (*Macaca mulatta)* whereby rapid reproductive maturation neither led to an increase nor a decrease in their overall lifetime reproductive success (Bercovitch & Berard, 1993). It is difficult to explain why some parturitions correlate to accentuated lines and others do not. When physiological stress is minimal and delivery occurs very quickly, parturition lines may not be detectable (Dean & Elamin, 2014). Furthermore, the formation of accentuated lines at parturition may be related to an individual's physical condition before parturition. However, physiological events surrounding parturition and the many transient shifts in blood chemistry that might affect accentuated line formation at this time are likely to be very complex, and there is currently no information yet on how an individual's physical condition prior to parturition might increase or decrease susceptibility to parturition line formation (Dean & Elamin, 2014).

Neither of the males had a distinctly higher amount of highly accentuated lines during the mating season than during the other months of the year after the age of 3.8 years. The most likely explanation for this is that the males at the ages recorded in their teeth were not yet enough engaged in reproductive activity and therefore did not respond to the presence of receptive females as much as males aged 10+ would have (Setchell et al., 2010). Probably, if more accentuated lines would be present in than outside the mating season, this would only become clear at a later age, by which age the teeth are already formed. For 2D8, the accentuated lines do increase in frequency later in his life and are slightly more regular during the mating season than outside, but the differences are small and could, based on these results, be by chance. It could however be indicative for a trend that would have manifested at a more advanced age. Furthermore, most females in 17E2's enclosure had contraceptive implants, and females with implants show no sexual swellings (Setchell et al., 2008a). The low numbers of receptive females in 17E2's enclosure could have contributed to the low number of overall highly accentuated line forming in his teeth from age 3.8 onwards, in comparison to 2D8's number of highly accentuated lines. However, since the lines in 2D8 are not confined to just the mating season, I cannot state this with certainty. The prediction

that more accentuated lines form in the males' teeth during the mating season than outside is therefore not supported by my data.

Neither male nor female mandrills consistently formed accentuated lines in correlation with alpha male takeovers in their social group. This is probably best explained by the take-overs not posing a threat to individuals at the specific life stage they were in during a take-over. Alpha male takeovers are expected to be stressful for individuals when they endanger an individual's life, their infant's life, or their position in a group. For example, according to infanticide theory (Engh et al., 2006; Hrdy, 1979; van Schaik & Janson, 2000), infants are in danger of being killed if they are not sired by the newly established alpha male, while juveniles are not at risk. A lactating female might be affected by a takeover since she is at risk of losing an infant, and an adult male risks being involved in aggressive encounters with other males. However, when a female has no infant to protect and a male is too young to challenge other males for rank, take-overs are not likely to increase stress levels. Thus, the life history stage or phase of an individual during the take-over is likely to be the determining factor in accentuated line formation in correlation with alpha male take-overs. Studies of female baboons found elevated levels of glucocorticoid during takeovers in females who are at risk of infanticide, but none in females who are either cycling, pregnant or in a non-reproductive state (Beehner et al., 2000; Bergman et al., 2005; Engh et al., 2006). This suggests that lactating females would be more likely to form accentuated lines during a take-over. Neither of the female mandrills was lactating during any of the takeovers, which might contribute to the absence of accentuated lines at these times. The one take-over that did corresponded with the formation of a highly accentuated line, in PB's teeth, was one that took place in a small time-frame of nine weeks with another take-over. Alpha males at CIRMF generally have long tenure (mean 1.6, SD +/- 0.5 years in enclosure 1, range 0.2–3.5 years, Setchell et al., 2005a). The short time frame in which these two takeovers took place suggests a high degree of male conflict and social instability during these weeks. If this is true, then the way a take-over takes place and the amount of social instability related to a transition period may be correlated with the formation of highly accentuated lines since more highly accentuated lines formed during a prolonged period of social instability than during brief takeovers. Finally, the lack of highly accentuated lines in response to most takeovers in both females suggests that alpha male takeovers were generally not intensely stressful situations for the two females at CIRMF. This is in correspondence with research performed by Setchell *et al* (2008) on the glucocorticoid levels of females and males in the colony, explained by the fact that females will only be influenced by upheavals in the male hierarchy when these pose a direct risk to themselves or their offspring (Engh et al., 2006), which was not the case for at the time of any of these takeovers for the two females.

For the males, no highly accentuated lines formed in the teeth in correlation with alpha male takeovers at all. Since male mandrills have proven to have increased levels of glucocorticoid levels when at times of unstable dominance hierarchy (Setchell et al., 2010), the absence of highly accentuated lines at times of alpha male takeovers is unexpected. However, this can, as for the females probably best be explained by the life stage and social situation the males were in during the time of the take-over; neither of the males was yet reproductively mature or competing for rank and access to receptive females when the takeovers took place. A change in alpha male might therefore not have many implications for the two males in this study, and therefore did not stimulate a stress-response leading to accentuated line formation. Witnessing a threatening situation could cause a stress-response in bystanders (Sapolsky, 1994), but since the alpha male takeovers at CIRMF generally happen fast (Setchell et al., 2005), the experience of merely being part of the group in which an alpha male takeover takes place seems not stressful enough to result in the formation of a highly accentuated line for the two males of my sample. The prediction that more accentuated lines form in the mandrills' teeth at times of alpha male take-overs is therefore not supported by my data.

Captures of the CIRMF mandrills did not correlate consistently with the formation of highly accentuated lines among the individuals. This result is unexpected, as previous studies showed that captures, transfers, hospitalisation and possibly anaesthesia administration may correlate with accentuated line formation (Bowman, 1991; Schwartz et al., 2006). Possibly, individuals may habituate to captures, which may become less stressful over time to individuals than unexpected stressful events (Creel, 2001; Sapolsky, 2004; Silk, 2002). However, if this is true, then captures that occurred earlier in life should correspond with highly accentuated lines more often than those later in life, which was the not the case for the mandrills. Possibly, intensity of a capture could explain variability in accentuated line formation. CIRMF captures are known to be variable in their intensity; sometimes animals are effectively darted, other times it takes longer to target the right individual (*pers comm* Setchell), or individuals might be accidentally darted twice. Furthermore, CIRMF captures can go on for multiple days whereby animals see others being caught (some of whom are relatives). Individuals may be trapped in the feeding pen with other targeted animals multiple times (Setchell *pers comm*), while other captures might involve less commotion and animals are caught and anesthetised instantly. The execution of the capture might affect the stress response of the individual involved, which could be explaining the variation in accentuated line formation in response to captures. The exact execution of the capture, and how rapid it was performed is not documented in the CIRMF files. I therefore could not make a differentiation between different types of captures. What did stand out is that when one female (5D3A) was caught multiple times in a short

time span, these captures let to a distinctive cluster in accentuated line formation, suggesting the opposite of a capture habituation effect.

Since the mandrills were anesthetised at every capture, my findings show that merely the administration of an anaesthetic is not enough to affect an individual's homeostasis sufficiently to consistently result in the formation of a highly accentuated line, otherwise a highly accentuated line would have correlated to every capture. Although Bowman (1991) reported the presence of accentuated lines in correlation with a capture whereby anaesthesia administration was involved, she also indicated that the effect of anaesthetics on accentuated line formation was not yet clear. The dose of anaesthetic varies during CIRMF captures (Setchell *pers comm*). Possibly, if the applied dose of anaesthesia during a capture succeeded the standard set by CIRMF, highly accentuated lines would form more regularly at times of captures. A combination of the amount of anaesthetic applied, how efficiently the capture is conducted and how much psychological stress an individual experiences before being sedated may all affect highly accentuated line formation.

6.3 Discussion of methods

Histological analysis of teeth, specifically when employed to reconstruct dental development sequences, are often based on a small number of individuals due to the time-consuming nature of the work. The same situation applies to this thesis, and the results of mandrill dental development as well as life history stress related to accentuated lines are based on a limited number of individuals. However, depending on what kind of analysis are performed and what kind of questions are asked to the material, small sample sizes do not necessarily pose a problem for study reliability. The general sex-specific dental development chronologies presented in this thesis are based on three animals of each sex. Although this might seem a low number at first, dental development is thought to be under strong genetic control (Saunders et al., 1993), less variable among individuals than ages at tooth eruption, and much less variable than timing of skeletal growth and development, which can be heavily affected by extrinsic factors such as nutrition and disease (Lewis & Garn, 1960; Cardoso, 2007). Thus, a small sample as presented in this thesis can be considered representative of a species, and comparable to other published means of anthropoid primates such as for humans (Reid et al., 1998), baboons (Dirks, 2003; Dirks & Bowman, 2007; Dirks et al., 2002), geladas (Swindler & Beynon, 1993), langurs (Dirks & Bowman, 2007; Dirks, 2003), orangutans (Kelley & Schwartz, 2010; Smith, 2016), chimpanzees (Reid et al., 1998), gorillas (Schwartz et al, 2006; Kelley &

Schwartz, 2010), gibbons (Dirks & Bowman, 2007; Dirks, 2003) and siamangs (Dirks & Bowman, 2007; Dirks, 2003).

Nevertheless, dental development is affected by extrinsic factors and varies among individuals of the same species (e.g., Mays, 1998; Gustavson & Koch 1974). Species' means calculated from small samples are more sensitive to individual variation, which is a general problem in dental development studies and not just restricted to dental histology (e.g., Beynon et al., 1991; Kralick et al., 2017; Kuykendall et al., 1992) I found slight variation in dental development among individuals of the same sex. The main variant was a distinctly larger C_1 in one female (PB) compared to the other female canines. Furthermore, although I_1 initiates before I_2 in most mandrills, in two males (2D8 and 5I2) the I_2 initiated before than the I_1. Wear however inevitably obscures initiation timing, regardless of sample size. This can only be improved when more individuals are analysed with unerupted or unworn teeth, which is, as I found in this study, very difficult to obtain. Variation in molar crown formation times is also related to the cusps available for assessment, and the sectioning plane. Given that maternal characteristics in mandrills, such as rank, age and parity can exert significant effects on growth, development and growth-related endocrine factors of their offspring (Bernstein et al., 2012; Setchell et al., 2001, 2006), maternal factors may also affect an individual's dental development, which may be interesting to test in a future study.

For the second part of the thesis, whereby I tested the hypothesis that accentuated lines correlate with life history events, I had four individuals available, two males and two females. This sample size was determined by the material and data available (crania with well enough preserved teeth, combined with known ID's and detailed life history data). Furthermore, the sample size was determined by time constraints due to the time-consuming nature of matching accentuated lines across whole dentitions. Matching lines from one tooth to the next to create a continuous pattern of accentuated lines is very difficult, particularly when working with a new species for which we do not yet know how each tooth develops in comparison to the others. Although the published eruption sequence for mandrills (Setchell & Wickings, 2004a) and dental development sequences of other papionins (Dirks et al., 2002; Swindler & Beynon, 1993) were very useful guides for matching teeth, it was still challenging to find the right positioning of the mandrill teeth. Once I had achieved this for the first individual, subsequent individuals were much easier to match. The number of individuals included in this study was therefore the maximum number possible given the time and material available. Although I used the full extent of material available for this study, it can debated what an

ideal sample size would be for such a study as mine if no limitations would be present regarding availability and time constraints. This is however not an easy question to answer and a statistical power analysis or probability test to analyse the pattern of accentuated line formation may be challenging to apply. The main issue is that most of the events in which I was interested regarding life history, such as resumption of the mothers' cycle and menarche, only happen once in an individual's life. It is therefore difficult to statistically approach the probability of a highly accentuated line coinciding with a one-off event, even when using many individuals. The best way to statistically the probability of an event and a highly accentuated line corresponding would be to test a series of similar events that happen at specific dates. The CIRMF captures would have been ideal for this test. However, my results indicated that captures do not always coincide with the formation of a highly accentuated line. Another way to approach the data could be to group all events predicted to be associated with highly accentuated line formation and predict that the presence of an event, regardless of its specifics, increases the likelihood of highly accentuated line formation. This can easily be tested using for example a Fisher's Exact test. However, this approach has two problems. First, it states that each type of event is just as likely to correlate with an accentuated line, which is not necessarily the case. Menarche for example is more likely to correlate with an accentuated line that first sibling birth, as my results have shown. Furthermore, not all life history data incorporated in this thesis concern events, but rather short periods of certain activity. Captures, alpha male take-overs, parturitions and sibling births indeed can be regarded as events, taking place on a single day, or at least within one week. In contrast, resumption of the mothers' sexual cycle, menarche, and subsequent cycles are episodes in time: they can still span multiple weeks, and represent periods of increased swellings, including weeks marked as +1, +2, +3, mate-guarding and conception. In this thesis, it was my intention to explore if highly accentuated lines would form during these periods of increased sexual activity, and if so, at what times. To test the probability of accentuated line formation statistically, a study would be more successful when focuses on events of shorter duration or specific timing, thereby for example only test if mate-guarding or the week of ovulation coincides with accentuated line formation. For my thesis however, I was interested in the whole period of female cycling and accentuated line formation.

All the mandrill tooth sections had very dense accentuated lines. Thus, many accentuated lines in the teeth were present that did not correlate with my collated life history or observational data. This is to be expected, since our records cannot encompass all the physical and social stressors an animal experiences (Austin et al., 2016; Birch & Dean, 2014). There are no comparative studies of the number of accentuated lines in the complete dentition of other primates, so I currently cannot

assess if the total number of accentuated lines in the mandrill teeth is common for primates. The visibility of accentuated lines, and with that the results on frequency and positioning of accentuated lines, inevitably depended on tissue and section quality. Generally, daily increment structures are very visible in sections less than 70 µm thick, but highly accentuated lines are better visible when sections are around 100 µm thick. Thin sections contain multiple layers of material (Chiego, 2014; Nanci, 2003), and thinner sections are composed of fewer stacked layers of daily increments, facilitating accurate analysis. However, the presence of multiple layers of tissues makes regions of altered tissue deposition stand out more clearly from the neighbouring tissue, which improves accentuated line visibility. It is difficult to find the right balance for making a section that shows both types of structure as well as possible. Because the thickness of a section influences the visibility and the clarity of accentuated lines, an accentuated line that formed at the same time in multiple teeth of the same individual has a different appearance in different sections. This made matching lines between teeth complicated. However, lines were generally consistent in their visibility within a section. Furthermore, teeth with thicker enamel were often easier to assess for accentuated line formation than those with thinner enamel: the crowns of the second and third molar were consistently the clearest, and incisors and canines consistently the most difficult. The presence of multiple cusps on molars also increases the chance of finding an area that is well preserved, while only one section is available for canines and incisors, and therefore less chance in finding clear accentuated lines. However, first molars were generally the most difficult teeth to assess and match due to the absence of teeth that initiate earlier and the amount of tooth wear.

I found that accentuated lines are more consistently visible in enamel than in dentine, if enamel is well preserved and section thickness is optimal. This suggests that a study of this sort should use accentuated lines in enamel and use dentine only to check difficult zones. Furthermore, the enamel cross striations are unambiguously observable structures, whereas the daily increments in dentine have often other dentinal microstructures running parallel to them, which makes the border between one daily increment and the next much more difficult to establish with certainty. Hence, measurements in dentine are likely to have a larger error margin than those in enamel. Although an open root can be used to calibrate a dental sequence to age of death, the neonatal line therefore gives better calibration, if it is available.

Finally, wear poses a serious obstruction to dental histology studies. In my sample, wear mainly hindered the calculation of initiation ages of teeth, and all initiations are estimates of the maximum age of initiation. Otherwise, wear was only a problem in older animals, where the first molar was worn down and the neonatal line was lost. These lines are the main point for calibration of the

dental development sequence and accentuated line sequence to calendar time. Without this point of calibration, correlation between accentuated lines and life history events is not exact. However, teeth have evolved to accommodate a lifetime of food processing, and wear along the way. If we want to study the lives of adult animals via dental remains, we must accommodate damaged or worn material. Material from young individuals is also extremely difficult to obtain due to its fragility and small sizes. My analysis of a male with very worn teeth (2D8) shows that it is possible to retrieve information even from worn teeth showing that wear might complicate analysis but does not prohibit it.

6.4 Future directions

It is difficult to increase the sample size in histological studies, but this can be partially resolved by targeting specific teeth. Accentuated lines correlating to weaning stress in mandrills occur half-way down the crown of the first molar, and in the top of the first and second incisor crowns. The most time-consuming aspect of this study was establishing the dental development sequence and matching the teeth of an individual to each other. Now that we have this information, studies of weaning stress and accentuated lines would benefit from targeting first molars and incisors. This requires teeth with little wear, so that neonatal lines are preserved. The neonatal lines themselves must be distinct enough to be unambiguously identifiable, which I found is not always the case. Now that I have established the likely positioning of the neonatal line in male and female mandrills and that weaning stress is likely to be visible in the first molar, the sample size could theoretically be increased, if we could obtain more crania and mandibles from individuals from the CIRMF colony weaned before 2006 (i.e., for whom we have data on the mothers' resumption of cycling). However, animals that would die now (2017+) will have very worn teeth, since they will be of advanced age. This indicates how difficult it is to obtain the right material to perform a study of combining life history data with dental samples of known individuals, and that the sample I used in this thesis was a rare opportunity to study.

Future research could also specifically target upper male canines, because this tooth covers the complete period of dental development. Like the first molar, it initiates prenatally and the upper canine root and the root of the third molar are the last to close. Working on one tooth instead of eight per animal could therefore theoretically drastically reduce analysis time. However, the line classification system I used in this study requires more than one tooth (Chapter 2), which would therefore still require the sampling of additional teeth. Furthermore, canine enamel is very thin, making analysis of the dentine necessary, which is more difficult and more prone to error. Although

the upper canine is an interesting tooth to target for accentuated line assessment due to the time period it covers, it therefore does pose a challenge for assessment. Future analysis of upper canines would also be interesting from a dental development perspective. This study only contained one upper canine and increasing the sample size would indicate whether the prenatal initiation I observed is a general trend in male mandrills.

Radiographic imaging of mandrill dental development would be very useful in future, as radiographic information is useful for a complete understanding of dental development (Kuykendall, 1996; Kuykendall & Conroy, 1996). X-ray imaging can non-destructively increase sample size, making dental development calculations more robust. I was fortunate to have access to the cranium and mandible of one young mandrill (HT12_15) (Chapter 3). This animal provided a guide to initiation ages of male teeth and the dental development of the other mandrills, due to the presence of the neonatal line and multiple teeth with open roots and crowns in development. X-ray imaging could provide additional information on the development of the lower P3 and the angle it makes during eruption. Furthermore, it could indicate whether the incisor erupting with little or no root is common in a larger sample. X-ray imaging shows the initiation of calcification rather than of matrix deposition, so initiation ages will be slightly later in X-ray studies than in histological studies. This should be considered by observers who compare ages at formation stages obtained via the two different methods.

Expanding the study of dental development and accentuated lines in teeth of mandrills to wild individuals would also be useful. Possibly, the semi-free ranging mandrills I studied show accelerated dental development and dental eruption compared to wild conspecifics (Machanda et al., 2015; Phillips-Conroy and Jolly, 1988; Smith and Boesch, 2011; Zihlman et al., 2004), but the effect might be small (Smith and Boesch, 2011). Analysing the dental development sequence from wild mandrills would indicate how much difference there is between wild and semi-free ranging individuals in this species regarding to dental development and improve our knowledge on mandrill biology. It would also be interesting to study accentuated lines in wild mandrills. Wild animals may have increased stress related to predation and the absence of veterinary treatment of injuries and illness. The absence of daily food provisioning, interference with group size, and home range confinement might also influence accentuated line formation.

Future work might also aim to examine why some accentuated lines are more distinct than others. The manifestation of an accentuated line may relate to the severity and intensity of the disruption or stressor. Neonatal lines in human infants are more distinct when delivery is complicated than when

vaginal delivery is smooth or a caesarean is used (Eli et al., 1989; Kurek et al., 2016; Witzel, 2014). The duration of the stressor seems to influence line formation, since lines hypothesised to correlate with prolonged parturition events were more distinct than those associated with fast delivery (Dean & Elamin, 2014; Klevezal & Myrick, 1984). The visibility of parturition lines in mammalian dentitions may therefore depend on the magnitude and duration of the psychological and physiological stress during labour and birth (Eli et al., 1989; Klevezal & Myrick, 1984; Zanolli et al., 2011). If this is true, human parturitions should leave a more distinct accentuated line behind than in other primates or mammals, since human female pelvic morphology complicates birth (Gruss & Schmitt, 2015; Rosenberg & Trevathan, 2002). Furthermore, high resolution Scanning Electron Microscopy (SEM) studies which showed that the underlying mechanism of accentuated line formation in enamel is related to the obstruction of the Tomes' processes also indicated variation in the type of obstruction (Kierdorf, 1997; 2000). Additionally, these studies indicated that the intensity of an accentuated line might be related to the functional stage of the active ameloblast at the time of disruption (Kierdorf, 1997; 2000). A systematic SEM study of accentuated lines correlated with known events might give insight to why the intensity of accentuated lines varies and whether the intensity is related to a change to the direction of the prism or the absence of prism formation.

Accentuated line assessment may also contribute to studies of animal welfare. My results indicate that accentuated lines formed in correlation with some, but not all the captures at CIRMF. A comparison of the presence or absence of accentuated lines in extracted teeth from deceased individuals with the details of a capture might show which procedures are likely to disrupt homeostasis severely enough to result in accentuated line formation. For example, variation in line formation may be associated with the amount of anaesthetic administered, how quickly the individual was darted following capture and how many times it was darted. This in turn can then be used to tailor capture protocols.

The major finding in this thesis, that accentuated lines indeed hold a correlation to life history events, also is of relevance to interpreting life history from teeth found in the fossil record. Since patterns of dental development by themselves are not in direct lock-step correlation with skeletal development or other maturation processes (Schwartz et al., 2002, Dirks, 2003, Dean & Liversidge, 2015) life-history variables derived from dental maturation should be made cautiously (Dirks & Bowman, 2007, Smith et al., 2015b). The formation of accentuated lines in teeth in relation to weaning and age at first reproduction in females is a better biological definition of adulthood than the end of tooth and/or bone development (Dean, 2016). Therefore, the fact that these accentuated lines do seem to form in correlation with these major life history events is a large step forward in

interpreting life history information from fossil remains, since it allows for bringing aspects of reproductive biology into context with the timing of skeletal as well as dental maturation stages (Dean & Elamin, 2014; Dirks & Bowman, 2007). With these accentuated lines, we can now superimpose aspects of reproductive biology onto the chronological record of skeletal and dental development, which has the ability to throw new light on the question of how, when and where currently existing life history trajectories came to be (Dean, 2016; Dirks et al., 2002), including that of the human life history trajectory. However, the research presented in this thesis also shows that it is likely not enough to just use patterns of accentuated lines in a small number of individuals for interpreting life history events. This is likely to be true for interpreting the timing of life history events for fossilized individuals too. First of all, a way forward is, as mentioned previously, increasing sample sizes. This holds true for fossil remains as well. As Smith et al (2015) demonstrated, synchrotron radiation virtual histology has the ability to show dental microstructure on a highly detailed level. Access to beamlines to analyse dental microstructure is currently limited, but more facilities are being constructed and tailored to a wider range of applications, such as the Canadian Light Source at Saskatoon, Canada (http://www.lightsource.ca/), as well as Argonne, Illinois (http://www.anl.gov), and the SESAME facility in Jordan (http://www.sesame.org.jo), allowing more researchers to access these facilities and experiment with the application to different types of material. In addition to improving visibility and sample size, accentuated line research can also be combined with other techniques such as trace element analysis and isotope analysis in combination to gain more information about life history events (Dirks et al. 2010). Combining dental histology with trace element analysis, four dietary stages in the weaning process can be established, including prenatal intake, a period of exclusive suckling, a period of mixed feeding including both suckling and independent foraging, leading to exclusive dependence on independent foraging. Such studies can be combined with accentuated line formation to further refine the stress experienced during the transition to independent feeding and can be applied to the fossil record as well. Work on barium distribution in teeth from captive macaques and human children also focused on early-life dietary transitions (Austin et al., 2013), demonstrating that barium distributions are correlated with early dietary transitions from the introduction of mothers milk and the addition of solid foods throughout weaning. Their research also included a sample of a Middle Palaeolithic juvenile Neanderthal, giving insight into dietary transitions in the period of breastfeeding (Austin et al., 2013). The way forward for life history assessment from the fossil record may be to seek a combination dental histology and accentuated line formation, as presented in this study, external defect observation such as coronal waisting (Skinner et al., 2012), trace element studies (Austin et al., 2013, 2016; Dirks et al., 2010; Humphrey, 2014; Humphrey et al., 2008) or stable isotope assessment (Humphrey, 2014; Tacail et

al., 2017; Tsutaya & Yoneda, 2015). Knowledge of the incremental development of teeth visible in histological sections is vital for trace element and isotope studies, since it assists in correct and specific sampling (Dirks et al., 2010). Similarly, a deeper understanding of accentuated line formation in teeth may adjust and target specific regions of teeth for sampling to obtain information of changing properties within a tooth, which may relate to life history transitions. In addition to uncovering signals related to the dietary shift of weaning, the combination of techniques may also be informative to pinpoint the timing of other life history events such as menarche first reproduction. As my thesis has shown, accentuated lines do form at the timing of menarche and reproduction, suggesting an increase in stress-levels at this time of these life history events. A recent study on captive macaques showed that stressors such major disruptions in body weight trajectory and periods of illnesses influenced biochemical signatures in their teeth (Austin et al., 2016). Stress related to life history events may therefore also be examined biochemically, which could add to the results of this thesis and improve the research on life history from fossil remains.

6.5 Conclusions

In this thesis, I determined the chronology of dental development for individual mandrills and I established sex-specific dental chronologies. I used this to provide the first histological information on dental development and tooth formation in mandrills, finding that males initiate their teeth earlier than females, and that the upper canine initiates prenatally. I showed that mandrills have a unique pattern of incisal eruption where lower incisors emerge with little or no root formation, probably related to their food processing strategies. I determined the timing of physiological stressors that disrupted normal tooth formation in the form of accentuated lines visible via dental histology. By comparing mandrill dental development and pattern of accentuated lines in the teeth of individual animals with detailed life history information I tested the hypothesis that the relationships among dental development, accentuated lines and life history events including weaning, first menstrual cycles, sibling birth and parturitions hold at the level of the individual. My results show that weaning stress and menstrual cycles do correlate with accentuated line formation, but that correlation with sibling birth and parturitions were not consistent. I also found that accentuated line formation can, but does not always, correlate with veterinary captures and that accentuated line formation does not correlated with alpha male takeovers. With these results, I have improved our understanding of when, how and why accentuated lines form in relation to stressful events and life history. These results therefore contribute to future research on individuals with unknown life histories such as paleoanthropologists, who would be able to use stress lines in teeth to infer weaning and maturation in fossil taxa.

Appendix A: General Methods

Appendix A.1: Protocol for the preparation of hard tissue (English)

This protocol is to assist in the collection and treatment of deceased primates to ensure possibilities for future research using their hard tissues, consisting of the skeletal remains and dentition. It is a step by step guide for how to deal with the remains from the death of an individual to the storage and archiving of the hard tissue. This is followed by additional notes and a skeletal inventory form used during step 10.

1. **Notice the absence and possible death of an individual**

   Daily observation of the mandrill colony allows observers to note the absence of individuals at feeding times. If an individual is not seen for several days in a row, the chances are high this individual has died. Record the absence in the individual's file. After 3 days of absence, search the enclosure for the missing individual. The smell of decomposition also serves as an indication of a death. Search the enclosure as soon as the smell is detected.

2. **Confirm and record the death of an individual**

   When an individual is found dead in the enclosure, dies on the operating table or dies under other circumstances, record this in the individual's file with the exact date of death. If a decomposed body is retrieved, note the date, the state of decomposition and estimate the date of death based on the state of decomposition and the date on which the animal was last observed at feeding time.

3. **Collect the remains of a recently deceased individual**

   Collect all remains available for controlled decomposition. If the body is fresh, collect the remains as a whole. If the remains of an individual are already in advanced decomposition and skeletal elements have become detached from one another, pay attention to the collection of loose elements. If the body has fallen apart, collect the material according to skeletal regions. These regions are:

   - The cranium, consisting of the skull and lower jaw. Check the area around the cranium for loose teeth.
   - The thorax (consisting of the vertebral column, the sternum, shoulder blades, pelvis (hip bones) and sacrum) and the extremities (consisting of the arms and legs).

- The hands and feet. Collect material from each side separately to avoid difficulties with determining the side of the material later. Pay extra attention to checking the area around the hands and feet, since there are many small bones here which could get lost.

The most important thing is not to miss any material. In cases where more than one individual died at the same time, make sure the material is kept separated during collection.

4. **Place the remains of the individual in a plastic bag for controlled decompositions.**
   Puncture the bag to facilitate the decomposition process so that liquids can leave the bag and insects and other animals can enter to remove the soft tissue. In the case of large individuals, place the head, feet and hands in bags for decomposition on the cemetery, and place the rest of the body for decomposition in the forest next to the enclosures for decomposition. Check the remains regularly.

5. **Add clear ID labels made of non-degradable material (ear-tags are ideal) to the bag and place an individual in the cemetery for decomposition**
   Do not just write the ID number on the plastic bag in which the remains are kept for decomposition, because this will degrade, losing the ID information which is vital for further research. Note the date on which the remains are placed in the cemetery in the individual's file. When more individuals are placed on the cemetery at the same time, place the bags at least 1m from one another to avoid mixing of material.

6. **Check the state of decomposition monthly**
   During decomposition, the first material to degenerate is the soft tissue such as organs and muscles, followed by tougher material such as hair, cartilage and ligaments. Later, mainly hard tissues are left, consisting of dental elements and the skeleton. Although hard tissue is more resistant to degeneration than the other softer tissues, it also degenerates when the remains of an individual are left for too long. The remains of infants and juveniles are less robust than the remains of adults, so need extra attention when monitoring decomposition, shorter decomposition times and more regular checks.

7. **Collect the remains from the cemetery**

   Once all the soft tissue is gone, collect the remains.Check the bag in which the remains were placed carefully for all bone and dental elements, as well as the soil under and surrounding of the bag. Ensure **that you collect all dental elements (teeth) after decomposition**. Molars are usually securely fixed in the jaw, even when soft tissues are lost, but single rooted teeth, such as the incisors and the canines become detached from the maxilla and mandibular bones easily when soft tissues are no longer present. It is very important to collect these too.

8. **Clean the bone material with water and alcohol.** Take all the material out of the bag, gently remove excess soft tissue, place in a solution of Chloramine T and water (5%) and leave it for 7 days. After that, clean the bones carefully with a soft brush. **Do not use aggressive chemicals such as bleach for cleaning the skull and dentition.** Bleach has a negative effect on the condition of the tooth enamel and removes dental calculus, which is of interest to researchers. After one week in chloramine T, the material can be stored under refrigeration in a 2% Chloramine T solution or dried in a ventilated room and stored until shipped.

9. **Ensure that you keep the ID label with the remains at all times and that you do not mix the remains of more than one animal together.**

   If you retrieve more than one individual from the cemetery at the same time, take care to keep the remains of each individual separate. Use separate buckets for the cleaning process.

10. **Label the bone material**

    Once the material is dry, write the full ID code of the individual on the skull with a permanent marker. Label all available large bones as well. These consist of: the femur, tibia and fibula for the legs; the humerus, ulna and radius for the arms; the left and right sides of the pelvis, the sacrum and the left and right shoulder blades (scapula) for the thorax. Collect the other bones by zone: place the hand bones from the left hand in one bag, labelled Left Hand. Place the hand bones of the right hand in another bag labelled Right Hand. Do the same for the bones of the left and right feet, the left and right side of the ribcage, the vertebral column including the hyoid and the sternum. Label the bones with the whole ID code of the individual, for example 17D1A. Use permanent marker for all labelling and write the ID code on an area of the bone where it is clearly visible. Avoid joint surfaces and areas of muscle attachment when labelling.

11. Fill in the skeletal inventory recording sheet

After the bones are cleaned and labelled, fill in the skeletal inventory form (see attachment). This facilitates future research and helps to keep the material organised. Add the skeletal inventory form to the individual's file, after the autopsy report.

12. Organised storage

Keep the remains of each individual together during storage. Store material in a dry place and avoid contact with moisture. Write the location of storage on skeletal inventory recording sheet. If material is moved to a different location, note this on the skeletal inventory recording sheet.

13. Note that the bone material was collected and stored after death in the individuals file

Notes

1 Collect and store as many skeletal elements as possible.

The long bones of primates are studied in the context of locomotion and its effect on morphology, age estimation, plasticity, influence of diseases, and so on. The fact that the individuals at CIRMF are closely monitored during life and the possibility of collecting their hard tissues after they die creates a unique combination which allows us to address many research questions if material is carefully collected and curated. Knowledge of the individual's ID is crucial here (see point 1 above). Collect and store skeletons as completely as possible.

2 Collect the remains of infant and juvenile individuals.

The hard tissues of infants and juveniles allow the study of growth and development in a way that cannot be achieved by only studying the remains of adults. Although the remains of infants are often more difficult to retrieve from the enclosures due to their small size and quick decomposition in combination with the dense forestry, take advantage of any possibility of collecting infant remains. This includes infants and juveniles who die in the volieres or during veterinary procedures. Infant remains are fragile, therefore take extra care during handling.

3 Visual documentation of material

If possible, take photographs of the dead individual to record the initial state of the material. This can range from highly decomposed / completely skeletonised in the enclosure to completely intact. Also record the remains after cleaning. These images should accompany the inventory form. When taking photographs, place a clear label close to the remains stating the ID of the individual and the date the photograph was taken.

This protocol was written on the basis of the knowledge of the authors, as well as the knowledge and experience of Dr Barthelemy Ngoubengoye, Dr Anais Herbert, Ivan-Cyr Moussadji Kinga and Oloussou Dieu-Donnée, Centre de Primatology, CIRMF Gabon.

Appendix A.2: Protocole pour la conservation des tissus des os et des dents

Le protocole a pour but de contribuer à la collecte et au traitement des primates décédés, à garantir la possibilité de futures recherches utilisant leurs tissus durs, composés de la dentition et des restes du squelette. C'est un guide qui détaille étape par étape le protocole de conservation des restes des individus morts et l'archivage des tissus durs. Enfin, on retrouvera des commentaires supplémentaires et un inventaire du squelette utilisé lors de l'étape 10.

1. Notifier (ou remarquer) l'absence et la mort (probable) d'un individu

Une observation quotidienne de la colonie de mandrills permet aux observateurs de remarquer l'absence d'individus lors des repas. Si un individu n'est pas aperçu pendant plusieurs jours, il est possible que cet individu soit décédé. Notez l'absence dans le dossier de l'individu. Après 3 jours d'absence, recherchez dans l'enceinte l'individu disparu. L'odeur de décomposition est aussi une indication de la mort de l'individu. Recherchez dans l'enclos dès que l'odeur est détectée.

2. Confirmer et enregistrer le décès d'un individu

Quand un individu est retrouvé mort dans l'enceinte, mort sur la table d'opération ou mort dans d'autres circonstances, indiquez-le dans le dossier de l'individu avec la date exacte de la mort. Si un corps décomposé est retrouvé, notez la date, la phase de décomposition et estimez la date du décès sur l'état de décomposition et la date à laquelle l'animal fut observé pour la dernière fois.

3. Recueillir les restes d'un individu décédé

Recueillir tous les restes disponibles pour la décomposition contrôlée. Si les restes viennent d'un individu mort récemment, recueillir les restes tous ensemble. Si les restes viennent d'un individu qui est déjà en décomposition avancée et des éléments du squelette sont détachés, une attention toute particulière est nécessaire pour collecter les petits éléments pouvant être détachés. Recueillir les divers éléments en fonction de la région du squelette. Ces régions sont les suivantes:

- Le crâne, composé du crâne et de la mâchoire inférieure. Vérifiez dans la zone proche du crâne si des dents se sont déchaussées.
- Le thorax (composé de la colonne vertébrale, le sternum, les omoplates, le bassin et le sacrum) et les extrémités (composé des bras et des jambes).
- Les mains et les pieds. Récupérer les restes de chaque côté séparément pour éviter les difficultés lors de la détermination postérieure de la côté des restes. Une attention toute

particulière est nécessaire à la vérification de la zone autour des mains et des pieds, car l'on pourrait perdre de nombreux petits os.

La chose la plus importante est de ne pas oublier un quelconque reste. Dans les cas où plus d'un individu est décédé en même temps, assurez-vous que les restes sont maintenus séparés lors de la collecte.

4. **Placez les restes de l'individu dans un sac en plastique pour les décompositions contrôlées.**

Percez le sac pour faciliter le processus de décomposition afin que les liquides puissent sortir du sac et les insectes et autres animaux puissent entrer pour enlever les tissus mous. Dans le cas de grands individus, placez la tête, les pieds et les mains dans des sacs pour que la décomposition ait lieu au cimetière, et placez le reste du corps en décomposition dans la forêt à côté de l'enclos pour la décomposition. Vérifiez régulièrement les restes.

5. **Placez des étiquettes d'identification claires, faites de matériaux non dégradables (étiquettes d'oreille sont idéales) dans le sac et placez l'individu dans le cimetière pour la décomposition**

N'écrivez pas le numéro d'identification seulement sur le sac en plastique dans lequel les restes sont conservés pour la décomposition, parce qu'il se dégradera, entraînant la perte d'information d'identification qui est essentielle pour mener les recherches. Notez la date sur tous les restes qui sont placés dans le cimetière dans le dossier de l'individu. Lorsque plusieurs individus sont placés dans le cimetière en même temps, placez les sacs au moins 1 m les uns des autres pour éviter de mélanger les restes.

6. **Vérifiez l'état de décomposition tous les mois**

Au cours de la décomposition, les premiers matériaux qui se décomposent sont les organes à tissu mou et les muscles, suivi par des matériaux plus durs comme les cheveux, le cartilage et les ligaments. Plus tard, il ne reste plus que les tissus durs, constitué du squelette et d'éléments dentaires. Bien que les tissus durs soient plus résistants à la dégénérescence que les autres tissus doux, ces restes se décomposent s'ils sont laissés trop longtemps en décomposition. Les restes des nourrissons et des jeunes sont moins robustes que les restes d'adultes, ils nécessitent donc une attention particulière lors de la surveillance de la décomposition, des durées de décomposition plus courts et des contrôles plus réguliers.

7. **Récupérez les restes du cimetière**

Quand tous les tissus mous sont disparu, recueillez les matériaux osseux/dentaires. Vérifiez l'état du sac contenant tous les éléments osseux et dentaires, ainsi que le sol en dessous et autour du sac. Assurez-vous que vous collectez tous les éléments dentaires après décomposition. Les molaires sont normalement solidement fixées dans la mâchoire, même lorsque les tissus mous sont perdus, mais les dents mono radicules, comme les incisives et les canines se détachent du maxillaire et de la mandibule plus facilement lorsque les tissus mous ne sont plus présents. Il est très important de les recueillir.

8. Nettoyer la matière osseuse avec de l'eau et de l'alcool.

Videz le contenu du sac, retirez délicatement les restes de tissus mous, placez-les dans une solution de Chloramine T et de l'eau (5%) et les laisser pendant 7 jours. Après cela, nettoyez soigneusement les os avec une brosse douce. N'utilisez pas de produits chimiques agressifs comme la javel pour nettoyer le crâne et la dentition. La javel a un effet négatif sur l'émail des dents et enlève le tartre dentaire, -qui est important pour les recherches. Au bout d'une semaine dans la Chloramine-T, conservé les restes sous réfrigération dans une solution à 2% de Chloramine T, ou laissez les sécher dans une pièce ventilée, et conservez les jusqu'à leur envoi.

9. Assurez-vous que vous gardez tout le temps l'étiquette d'identification avec les restes et que vous ne mélangez pas les restes des animaux ensemble.

Si vous récupérez plus d'un individu du cimetière en même temps, faites attention à garder les restes des individus séparément. Utilisez des seaux séparés pour le processus de nettoyage.

10. Marquez les os

Quand les restes sont secs, écrivez le code d'identification complet de l'individu sur le crâne avec un marqueur indélébile. Étiquetez aussi tous les grands os disponibles: le fémur, le tibia et le fibula pour les jambes; l'humérus, l'ulna et le radius pour les bras; les côtés gauche et droit du bassin, le sacrum et la gauche et la droite des omoplates (scapula) pour le thorax. Recueillez les autres os par zone: placer les os de la main gauche dans un sac étiqueté 'main gauche'. Placez les os de la main droite dans un autre sac étiqueté 'main droite'. Faites de même pour les os des pieds gauche et droit, la gauche et le côté droit de la cage thoracique, la colonne, y compris l'os hyoïde et le sternum vertébrale. Étiquetez les os de l'ensemble du code d'identification de l'individu, par exemple 17D1A. Utilisez un marqueur indélébile pour toutes les étiquettes et écrivez le code d'identification sur une zone de l'os où il est clairement visible. Évitez les surfaces et les zones d'attache des muscles lors de l'étiquetage.

11. Remplissez le formulaire d'enregistrement de l'inventaire du squelette

Après que les os soient nettoyés et étiquetés, remplissez le formulaire d'inventaire squelettique (voir pièce jointe). Cela facilite les futures recherches et permet d'être ordonné dans le rangement du matériel. Ajoutez le formulaire d'inventaire squelettique au dossier de l'individu, après le rapport d'autopsie.

12. Gardez le matériel de manière ordonnée

Gardez les restes de chaque individu ensembles pendant le stockage. Entreposez le produit dans un lieu sec et évitez tout contact avec l'humidité. Donnez l'emplacement de stockage sur le formulaire de l'inventaire du squelette. Si les restes sont déplacés vers un autre emplacement, indiquez-le sur le formulaire de l'inventaire du squelette.

13. Notez que la matière osseuse a été recueillie et stocker après la mort dans le fichier de l'individu

Remarques

1. Recueillez et gardez tous les éléments squelettiques possible.

Les os longs des primates sont utilisés pour la recherche dans le cadre de la locomotion et son effet sur la morphologie, l'estimation de l'âge, de la plasticité, l'influence des maladies etc. Vu que les primates à CIRMF sont étroitement surveillés pendant leur vie et la possibilité de recueillir leurs tissus durs après leur mort crée une combinaison unique qui nous permet d'aborder de nombreuses questions de recherche si les restes sont soigneusement recueillis et conservés. La connaissance de l'identité de l'individu est cruciale ici (voir point 1 ci-dessus). Recueillez et conservez les squelettes de manière aussi complète que possible.

2. Recueillez les restes de jeunes squelettes et d'individus juvéniles.

Les tissus durs des enfants et d'adolescents permettent d'étudier le développement d'une manière qui n'est pas possible par l'étude exclusive des restes des adultes. Bien que les restes des enfants soient souvent plus difficiles à récupérer des enceintes à cause de leur petite taille, de leur décomposition rapide en plus de la dense végétation, profitez de toutes les chances permettant de recueillir des restes d'enfants. Cela inclut les enfants et les jeunes qui meurent dans les volières ou pendant les procédures vétérinaires. Les restes des enfants sont fragiles, donc veuillez prendre des précautions supplémentaires lors des manipulations.

3. La documentation visuelle des restes

Si possible, prenez des photos de l'individu mort afin d'enregistrer l'état initial des restes. Cela peut aller de très décomposé, état squelettique dans l'enceinte à complètement intact. Prenez aussi des photos des restes après le nettoyage. Ces images doivent accompagner le formulaire d'inventaire. Lorsque vous prenez des photos, placer une étiquette claire à proximité des matériaux indiquant l'identification de la personne et la date à laquelle la photo a été prise.

Ce protocole a été rédigé sur la base de la connaissance des auteurs, ainsi que les connaissances et l'expérience du Dr Barthélemy Ngoubengoye, Dr Anaïs Herbert, Ivan-Cyr Moussadji Kinga et Oloussou Dieu-Donnée, Centre de Primatologie, CIRMF Gabon.

Appendix A.3: Tooth replication protocol

When using President Fast Soft Putty, we took 50/50 material base and catalyst. We mixed these two components together by hand and surrounded the tooth crown and part of the root. We marked the putty with the mandrill's identity, and left the material to set. Once it was dry and hard, we marked the tooth and putty with a small line using a permanent pen to facilitate correct positioning of the tooth back in the mould at a later stage. The replicas cover the crowns and top parts of the root, so that the replicas fit back into the original jaw easily. Once the putty was set, we took a sharp razor blade and cut length ways through the mould to release the tooth. We then cut a small hole in the mould at the tip of the root so we could use a pipette to pour in the resin. We sealed the cut back up with putty. As replica resin, we used Bosworth Trim © which is made up of a liquid solution plus powder. We pipetted out a small amount of liquid into a plastic cup and then slowly added the powder until it turned into a creamy solution. Once the right thickness was reached, we pipetted the liquid resin into the mould and let it run in on an angle, to avoid trapping air bubbles. We took the mould off after 24 h. We placed the replica into the correct alveolar of the jaw. For more detailed casts we used President light body to cover the inside of the former cast. We pushed the tooth back into the mould, to get a detailed imprint of the tooth. Next we used Spurr resin © to make the replica, which gives a highly detailed replication of the tooth. We let the material set for 24 h, cut away the mould and placed the tooth in the jaw.

Appendix B: Accompanying material for Chapter 3

Appendix B.1 Crown initiation, formation and completion

Table 1: Crown initiation, completion and formation times 5D3A. '<' indicates teeth initiation ages and '+' crown formation time for worn teeth. Negative values for time from crown completion to gingival emergence indicate that gingival emergence started before crown formation was complete.

5D3A									
Tooth	Age at crown Initiation (years)	Age at crown completion (years)	Crown formation time	Age at gingival emergence		Mid-point age at gingival emergence (years)	Time between crown completion and gingival emergence (years)		Mean time between crown completion and gingival emergence (years)
				Last age when tooth was recorded absent	First age when tooth was recorded present		min	max	
I_1	< 0.56	2.88	+ 2.32	2.27	3.05	2.66	-0.61	0.17	-0.22
I_2	< 1.25	3.36	+ 2.11	2.27	3.05	2.66	-1.09	-0.31	-0.70
C_1	< 2.26	3.35	+ 1.09	3.66	4.10	3.88	0.31	0.75	0.53
P_3	< 0.90	4.83	+ 3.93	4.10	4.87	4.49	-0.73	0.04	-0.35
P_4	< 1.65	2.99	+ 1.34	4.10	4.87	4.49	1.11	1.88	1.50
M_1	-0.06	1.09	+ 1.15	0.16	2.27	1.22	-0.93	1.18	0.13
M_2	1.57	3.47	1.9	3.05	3.66	3.36	-0.42	0.19	-0.12
M_3	3.24	4.77	1.53	5.90	7.05	6.48	1.13	2.28	1.71

Table 2: Crown initiation, completion and formation times 16L '<' indicates teeth initiation ages and '+' crown formation time for worn teeth. Negative values for time from crown completion to gingival emergence indicate that gingival emergence started before crown formation was complete.

16L									
Tooth	Age at crown Initiation (years)	Age at crown completion (years)	Crown formation time	Age at gingival emergence		Mid-point age at gingival emergence (years)	Time between crown completion and gingival emergence (years)		Mean time between crown completion and gingival emergence (years)
				Last age when tooth was recorded absent	First age when tooth was recorded present		min	max	
I_1	< 0.27	3.17	+ 2.90	2.86	3.79	3.36	-0.31	0.62	0.16
I_2	< 0.86	3.33	+ 2.47	2.86	3.79	3.36	-0.47	0.46	-0.01
C_1	< 1.09	3.34	+ 2.25	3.79	4.95	4.37	0.45	1.61	1.03
P_3	< 0.36	3.33	+ 2.96	3.79	4.95	4.37	0.46	1.62	1.04
P_4	< 1.74	3.83	+ 2.09	3.79	4.95	4.37	-0.04	1.12	0.54
M_1	< 0.23	1.49	+ 1.26	1.56	1.96	1.76	0.07	0.47	0.27
M_2	< 1.30	3.51	+ 2.20	2.86	3.79	3.33	-0.65	0.28	-0.19
M_3	3.89	6.42	2.53	6.96	8.04	7.50	0.54	1.62	1.08

Table 3: Crown initiation, completion and formation times PB. '<' indicates teeth initiation ages and '+' crown formation time for worn teeth. Negative values for time from crown completion to gingival emergence indicate that gingival emergence started before crown formation was complete.

PB									
Tooth	Age at crown Initiation (years)	Age at crown completion (years)	Crown formation time	Age at gingival emergence		Mid-point age at gingival emergence (years)	Time between crown completion and gingival emergence (years)		Mean time between crown completion and gingival emergence (years)
				Last age when tooth was recorded absent	First age when tooth was recorded present		min	max	
I_1	< 0.71	3.16	+ 2.45	2.92	3.31	3.31	-0.24	0.54	0.15
I_2	< 0.79	3.59	+ 2.80	2.92	3.31	3.31	-0.67	0.11	-0.28
C_1	< 0.96	4.86	+ 3.90	3.70	4.21	4.21	-1.16	-0.14	-0.65
P_3	< 0.82	4.40	+ 3.58	4.72	5.30	5.30	0.32	1.48	0.90
P_4	< 1.04	4.09	+ 3.05	4.72	5.30	5.30	0.63	1.79	1.21
M^1	< 0.08	1.48	+ 1.40	1.87	2.48	2.18	0.39	1.00	0.69
M^2	1.40	3.68	2.28	3.70	4.72	4.21	0.02	1.04	0.53
M^3	3.38	5.46	2.08	7.90	8.98	8.44	2.44	3.52	2.98

Table 4: Crown initiation, completion and formation times for 2D8. '<' indicates teeth initiation ages and '+' crown formation time for worn teeth. Negative values for time from crown completion to gingival emergence indicate that gingival emergence started before crown formation was complete.

Male 2D8									
Tooth	Age at crown Initiation (years)	Age at crown completion (years)	Crown formation time	Age at gingival emergence		Mid-point age at gingival emergence (years)	Time between crown completion and gingival emergence (years)		Mean time between crown completion and gingival emergence (years)
				Last age when tooth was recorded absent	First age when tooth was recorded present		min	max	
I_1	< 0.38	3.10	+ 2.71	2.59	3.38	2.99	-0.51	0.28	-0.12
I_2	< 0.15	3.32	+ 3.17	2.59	3.38	2.99	-0.73	0.06	-0.34
C_1	0.75	7.18	6.43	3.43	8.51	5.97	-3.75	1.33	-1.21
P_3	0.36	6.31	5.95	3.43	5.20	6.29	-1.11	1.07	-0.02
P_4	< 2.20	4.44	+ 2.24	3.43	5.20	6.29	0.76	2.94	1.85
M_1	< 0.54	1.46	+ 0.92	0.62	1.88	1.25	-0.84	0.42	-0.21
M_2	< 1.44	3.18	+ 1.75	3.38	3.99	3.69	0.2	0.81	0.51
M_3	< 2.99	4.50	+ 1.51	5.20	7.38	6.29	0.7	2.88	1.79

Table 5: Crown initiation, completion and formation times for 17E2. '<' indicates teeth initiation ages and '+' crown formation time for worn teeth. Negative values for time from crown completion to gingival emergence indicate that gingival emergence started before crown formation was complete

Male 17E2									
Tooth	Age at crown Initiation (years)	Age at crown completion (years)	Crown formation time	Age at gingival emergence		Mid-point age at gingival emergence (years)	Time between crown completion and gingival emergence (years)		Mean time between crown completion and gingival emergence (years)
				Last age when tooth was recorded absent	First age when tooth was recorded present		min	max	
I_1	< 0.23	2.65	+ 2.42	2.68	3.09	2.89	0.03	0.44	0.24
I_2	< 0.40	3.37	+ 2.97	3.09	3.99	3.54	-0.28	0.62	0.17
C^1	+ 0.19	7.80	+ 7.99	4.91	6.13	5.52	-2.89	-1.67	-2.28
P^3	<1.26	4.76	+ 3.50	4.91	6.13	5.52	0.15	1.37	0.76
$P_4{}^4$	Tooth absent	Tooth absent	Tooth absent	4.91	6.13	5.52	Tooth absent	Tooth absent	Tooth absent
M_1	-0.21	1.29	1.51	1.23	2.06	1.65	-0.06	0.77	0.36
M^2	< 1.11	3.21	+ 2.09	3.99	4.91	4.45	0.78	1.7	1.24
M^3	2.78	4.70	1.92	6.13	7.21	6.67	1.43	2.51	1.97

Table 6: Crown initiation, completion and formation times for 5I2. '<' indicates teeth initiation ages and '+' crown formation time for worn teeth. Negative values for time from crown completion to gingival emergence indicate that gingival emergence started before crown formation was complete

Male 5I2									
Tooth	Age at crown Initiation (years)	Age at crown completion (years)	Crown formation time	Age at gingival emergence		Mid-point age at gingival emergence (years)	Time between crown completion and gingival emergence (years)		Mean time between crown completion and gingival emergence (years)
				Last age when tooth was recorded absent	First age when tooth was recorded present		min	max	
I_1	< 0.56	3.11	+ 2.55	2.48	3.39	2.94	-0.63	0.28	-0.18
I_2	< 0.36	3.32	+ 2.97	2.48	3.39	2.94	-0.84	0.07	-0.39
C_1	< 1.25	8.75	+ 7.49	5.44	6.58	6.01	-3.31	-2.17	-2.74
P_3	< 0.61	8.84	+ 8.23	6.58		6.58	-2.26		-2.26
P_4	< 1.60	4.34	+ 2.75	4.30	5.44	4.87	-0.04	1.1	0.53
M_1	-0.17	1.28	1.47	2.07		2.07	0.79		0.79
M_2	< 1.46	3.57	+ 2.11	4.30	5.44	4.87	0.73	1.87	1.30
M_3	< 3.47	6.33	+ 2.86	7.47	8.50	7.99	1.14	2.17	1.66

Table 7: Crown initiation, completion and formation times for HT12_15. '<' indicates teeth initiation ages and '+' crown formation time for worn teeth. Negative values for time from crown completion to gingival emergence indicate that gingival emergence started before crown formation was complete. The crowns of HT12_15's C_1, P_3 and M_3 were still developing at death

Male HT12_15									
Tooth	Age at crown Initiation (years)	Age at crown completion (years)	Crown formation time	Age at gingival emergence		Mid-point age at gingival emergence (years)	Time between crown completion and gingival emergence (years)		Mean time between crown completion and gingival emergence (years)
				Last age when tooth was recorded absent	First age when tooth was recorded present		min	max	
I_1	< 0.31	2.97	+ 2.66	2.78	3.98	3.38	-0.19	1.01	0.41
I_2	< 0.63	3.34	+ 2.71	3.04	4.23	3.64	-0.3	0.89	0.30
C_1	0.27	6.12	5.86	>6.12		>6.12	Alveolar eruption		Alveolar eruption
P_3	0.15	6.12	5.97	>6.12		>6.12	Alveolar eruption		Alveolar eruption
P_4	1.48	3.82	2.35	6.12	6.19	6.16	2.3	2.37	2.34
M_1	-0.21	1.81	2.02	1.52	3.07	2.30	-0.29	1.26	0.49
M_2	1.28	3.79	2.51	3.14	5.20	4.17	-0.65	1.41	0.38
M_3	4.39	6.08	1.68	4.09	8.33	6.21	-1.99	2.25	0.13

Appendix B.2: Sex-specific dental development calculations

Table 8: Cusp initiation, completion and formation times for female mandrills, used for female summary bar chart. Average crown formation time (CFT) is based on the average crown completion minus the earliest crown cusp initiation. Data from mandibular, well preserved and completely formed crowns. Gingival emergence based on published data (Setchell & Wickings, 2004a)

Tooth	Crown initiation (Age in years)	Crown completion (Age in years)	Crown formation time (Years)	Gingival emergence mandible left (Age in years, Setchell & Wickings, 2004a)		
				Midpoint	Min	Max
I_1	0.27	3.07	2.80	3.06	2.42	3.70
I_2	0.79	3.43	2.64	3.39	2.75	4.03
C_1	0.96	3.85	2.89	3.59	2,95	4.23
P_3	0.36	4.19	3.83	4.45	4.14	4.75
P_4	1.04	3.64	2.60	5.12	4.35	5.61
M_1	-0.06	1.29	1.35	2.13	1.52	2.74
M_2	1.30	3.49	2.19	3.70	3.16	4.23
M_3	3.24	5.59	2.35	6.78	4.83	8.73

Table 9: Cusp initiation, completion and formation times for male mandrills, used for male summary bar chart. Average crown formation time (CFT) is based on the average crown completion minus the earliest crown cusp initiation. Data from mandibular, well preserved and completely formed crowns. Gingival emergence based on published data (Setchell & Wickings, 2004a)

Tooth	Crown initiation (Age in years)	Crown completion (Age in years)	Crown formation time (Years)	Gingival emergence mandible left (Age in years, Setchell & Wickings, 2004a)		
				Midpoint	Min	Max
I_1	0.23	2.91	2.68	3.38	2.78	3.98
I_2	0.35	3.34	2.99	3.58	3.04	4.13
C_1	0.27	8.75	8.48	5.10	3.66	6.53
P_3	0.15	8.84	8.69	5.18	4.15	6.19
P_4	1.48	4.08	2.60	5.00	3.81	6.19
M_1	-0.21	1.42	1.63	2.23	1.68	2.79
M_2	1.11	3.68	2.57	4.18	3.14	5.20
M_3	3.26	6.33	3.07	5.70	4.09	7.31

Appendix B.3: Daily increment measurements in the crowns of the mandrills

Table 10: Overview of daily increment measurements in the crowns of the mandrills. I used daily increment measurements to calculate crown formation times. Maxillary teeth indicated with *. The enamel of 5I2 and 17E2's canines were too damaged to make measurements, hence measurement are made in dentine and excluded from the means

Tooth	Value	HT12_15	5I2	17E2	2D8	PB	16L	5D3A
I_1	Mean	3.9	3.8	3.8	3.8	3.9	4.5	3.9
	Median	3.9	3.8	3.8	3.8	3.9	4.5	3.9
	Range	2.8-4.4	3.0-4.2	3.3-4.4	3.4-4.2	3.2-4.7	3.6-5.1	3.5-4.3
I_2	Mean	4.3,	3.7	3.6	4.1	3.9	3.7	4.0
	Median	4.4	3.6	3.6	4.0	3.8	3.7	3.9
	Range	3.4-4.8	3.1-4.3	3.1-4.0	3.4-5.6	3.6-4.4	2.9-4.3	3.5-4.9
C	Mean	3.8	3.4	3.1*	3.4	3.8	4.3	3.8
	Median	3.9	3.7	2.9*	3.3	3.64	4.4	3.8
	Range	2.9-4.3	3.0-3.8	2.7-3.9*	3.3-3.6	3.3-4.3	3.6-4.8	3.1-4.6
P_3	Mean	4.1	4.5	3.5*	3.5,	3.6,	3.9	3.5
	Median	4.1	4.6	3.5*	3.5	3.5	3.9	3.5
	Range	3.6-4.5	3.6-5.1	2.8-3.9*	3.2-3.8	3.6-4.4	3.0-4.7	3.0-4.4
P_4	Mean	3.7	4.1	Tooth absent	4.3	3.7	4.4	4.2
	Median	3.7	3.9		4.3	3.939	4.6	4.3,
	Range	3.8-4.0	3.3-5.1		4.2-4.3	3.0-4.2	3.5-5.1	3.1-5.0
M_1	Mean	4.1	3.5	4.2	3.9	4.0*	3.6	4.1
	Median	4.1	3.6	4.2	4.0	3.9*	3.6	4.2
	Range	3.8-4.5	2.6-3.8	3.2-4.7	3.5-4.2	3.6-4.4*	3.4-3.8	3.4-4.5
M_2	Mean	3.7	4.2	3.6	4.3	3.7*	4.5	3.6
	Median	3.7	4.1	3.7	4.7	3.4*	4.6	3.6
	Range	2.9-4.2	3.8-5.9	3.2-4.3	3.4-4.9	2.9-4.1*	3.9-5.0	2.8-4.3
M_3	Mean	3.44	3.4	3.9	4.2	4.1*	3.9	3.7
	Median	3.37	3.4	3.9	4.2	4.0*	3.9	3.6
	Range	2.5-4.3	2.8-3.9	2.9-4.6	3.8-4.7	4.0-4.1*	3.0-4.5	3.3-4.4
Mean per individual		3.9	3.9	3.8	4.0	3.8	4.1	3.9
Mean per sex		3.9				3.9		

Appendix B.4: Photographs unerupted M_3 in male HT12_15

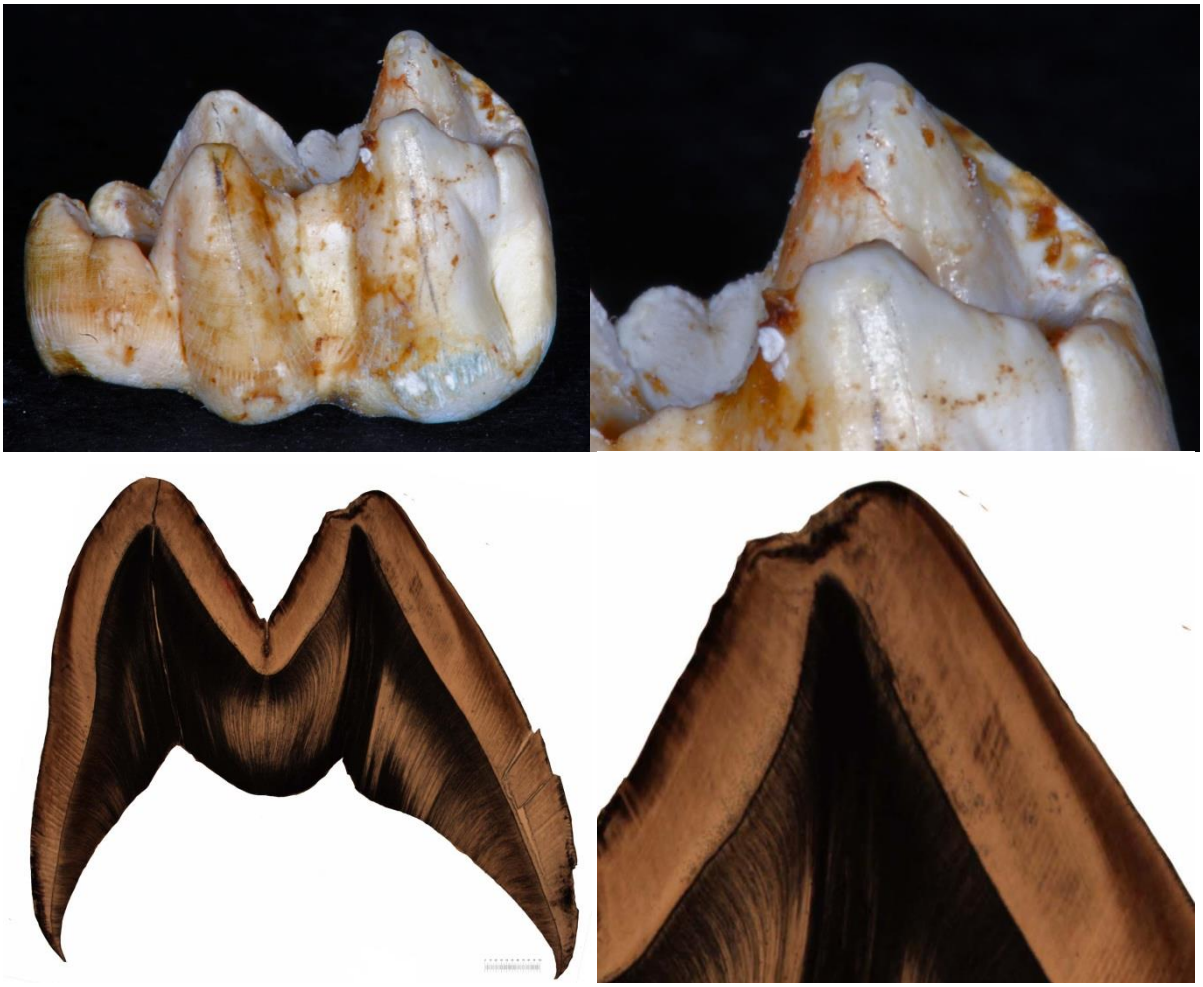

Figure 1: Un-erupted M_3 in male HT12_15. This male was the only individual from our sample with un-erupted teeth and therefore the only individual with completely unworn cusps. The M_3 and un-erupted P_3 showed small indentations on the tips of their cuspal enamel. Macrophotos courtesy of Janet Howarth, Medical Photographer Dental Hospital, Newcastle upon Tyne.

Appendix B.5 CIRMF records of gingival emergence

Table 11: CIRMF records of gingival emergence for 5D3A. I collated information on when teeth were observed to be present and absent. In the tables, 0 indicated the age at which a tooth was not noted as present, 1 when a tooth was noted as present, and 'point' when a tip of the cusp was noted as visible through the gingiva. Gingival emergence must have started between the last observed 0 and first observed 1. Ambiguities in the CIRMF records are in red.

5D3A mandible permanent right quadrant								
Age (yr)	I_1	I_2	C_1	P_3	P_4	M_1	M_2	M_3
0.16	0	0	0	0	0	0	0	0
2.27	0	0	0	0	0	1	0	0
3.05	1	1	1	0	0	1	0	0
3.66	1	1	0	0	0	1	1	0
4.10	1	1	1	0	0	1	1	0
4.87	1	1	1	1	1	1	1	0
5.90	1	1	1	1	1	1	1	0
7.05	1	1	1	1	1	1	1	1
5D3A mandible permanent left quadrant								
Age (yr)	I_1	I_2	C_1	P_3	P_4	M_1	M_2	M_3
0.16	0	0	0	0	0	0	0	0
2.27	0	0	0	0	0	1	0	0
3.05	1	1	0	0	0	1	0	0
3.66	1	1	0	0	0	1	1	0
4.10	1	1	1	0	0	1	1	0
4.87	1	1	1	1	point	1	1	0
5.90	1	1	1	1	1	1	1	0
7.05	1	1	1	1	1	1	1	1

Table 1: CIRMF records of gingival emergence for 16L. I collated information on when teeth were observed to be present and absent. In the tables, 0 indicated the age at which a tooth was not noted as present, 1 when a tooth was noted as present, and 'point' when a tip of the cusp was noted as visible through the gingiva. Gingival emergence must have started between the last observed 0 and first observed 1. Ambiguities in the CIRMF records are in red.

16L mandible permanent right quadrant								
Age (yr)	I_1	I_2	C_1	P_3	P_4	M_1	M_2	M_3
0.08	0	0	0	0	0	0	0	0
1.56	0	0	0	0	0	0	0	0
1.96	0	0	0	0	0	1	0	0
2.86	0	0	0	0	0	1	0	0
3.79	1	1	0	0	0	1	1	0
4.95	1	1	1	1	1	1	1	0
6.03	1	1	1	1	1	1	1	0
6.96	1	1	1	1	1	1	0	0
8.04	1	1	1	1	1	1	1	1
16L mandible permanent left quadrant								
Age (yr)	I_1	I_2	**C**	P_3	P_4	M_1	M_2	M_3
0.08	0	0	0	0	0	0	0	0
1.56	0	0	0	0	0	0	0	0
1.96	0	0	0	0	0	1	0	0
2.86	0	0	0	0	0	1	0	0
3.79	1	1	0	0	0	1	1	0
4.95	1	1	1	1	1	1	1	0
6.03	1	1	1	1	1	1	1	0
6.96	1	1	1	1	1	1	0	0
8.04	1	1	1	1	1	1	1	1

Table 2: CIRMF records of gingival emergence for PB. I collated information on when teeth were observed to be present and absent. In the tables, 0 indicated the age at which a tooth was not noted as present, 1 when a tooth was noted as present, and 'point' when a tip of the cusp was noted as visible through the gingiva. Gingival emergence must have started between the last observed 0 and first observed 1. Ambiguities in the CIRMF records are in red.

PB mandible permanent right quadrant								
Age (yr)	I_1	I_2	**C**	P_3	P_4	M_1	M_2	M_3
1.87	0	0	0	0	0	Point	0	0
2.48	0	0	0	0	0	1	0	0
2.92	0	0	0	0	0	1	0	0
3.70	1	1	0	0	0	1	0	0
4.72	1	1	1	0	0	1	1	0
5.88	1	1	1	1	1	1	1	0
7.01	1	1	0	0	0	1	1	X
7.90	1	1	1	1	1	1	1	point
8.98	1	1	1	1	1	1	1	1
PB mandible permanent left quadrant								
Age (yr)	I_1	I_2	**C**	P_3	P_4	M_1	M_2	M_3
1.87	0	0	0	0	0	Point	0	0
2.48	0	0	0	0	0	1	0	0
2.92	0	0	0	0	0	1	0	0
3.70	1	1	0	0	0	1	0	0
4.72	1	1	1	0	1	1	1	0
5.88	1	1	1	1	1	1	1	0
7.01	1	1	0	0	0	1	1	0
7.90	1	1	1	1	1	1	1	Point
8.98	1	1	1	1	1	1	1	1

PB maxilla permanent right quadrant								
Age (yr)	I_1	I_2	**C**	P_3	P_4	M_1	M_2	M_3
1.87	0	0	0	0	0	0	0	0
2.48	0	0	0	0	0	1	0	0
2.92	0	0	0	0	0	1	0	0
3.70	1	0	0	0	0	1	0	0
4.72	1	1	1	0	0	1	1	0
5.88	1	1	1	1	1	1	1	0
7.01	1	1	0	0	0	1	1	0
7.90	1	1	1	1	1	1	1	0
8.98	1	1	1	1	1	1	1	1
PB maxilla permanent left quadrant								
Age (yr)	I_1	I_2	**C**	P_3	P_4	M_1	M_2	M_3
1.87	0	0	0	0	0	0	0	0
2.48	0	0	0	0	0	1	0	0
2.92	0	0	0	0	0	1	0	0
3.70	1	0	0	0	0	1	0	0
4.72	1	1	1	0	0	1	1	0
5.88	1	1	1	1	1	1	1	0
7.01	1	1	0	0	0	1	1	0
7.90	1	1	1	1	1	1	1	0
8.98	1	1	1	1	1	1	1	1

Table 3: CIRMF records of gingival emergence for 2D8. I collated information on when teeth were observed to be present and absent. In the tables, 0 indicated the age at which a tooth was not noted as present, 1 when a tooth was noted as present, and 'point' when a tip of the cusp was noted as visible through the gingiva. Gingival emergence must have started between the last observed 0 and first observed 1. Ambiguities in the CIRMF records are in red.

2D8 mandible permanent right quadrant								
Age (yr)	I_1	I_2	C	P_3	P_4	M_1	M_2	M_3
0.62	0	0	0	0	0	0	0	0
1.88	0	0	0	0	0	1	0	0
2.59	0	0	0	0	0	1	0	0
3.38	1	1	0	0	0	1	0	0
3.99	1	1	0	0	0	1	1	0
3.43	1	1	0	0	0	1	1	0
5.20	0	0	1	0	0	1	1	0
7.38	1	1	0?	1	1	1	1	1
8.51	1	1	1	1	1	1	1	0
9.39	1	1	1	1	1	1	1	1
10.48	lost	1	1	1	1	1	1	1
2D8 mandible permanent left quadrant								
Age (yr)	I_1	I_2	C	P_3	P_4	M_1	M_2	M_3
0.62	0	0	0	0	0	0	0	0
1.88	0	0	0	0	0	1	0	0
2.59	0	0	0	0	0	1	0	0
3.38	1	1	0	0	0	1	0	0
3.99	1	1	0	0	0	1	1	0
3.43	1	1	0	0	0	1	1	0
5.20	0	0	1	1	1	1	1	0
7.38	1	1	0?	1	1	1	1	1
8.51	1	1	1	1	1	1	1	0
9.39	1	1	1	1	1	1	1	1

Table 4: CIRMF records of gingival emergence for 17E2. I collated information on when teeth were observed to be present and absent. In the tables, 0 indicated the age at which a tooth was not noted as present, 1 when a tooth was noted as present, and 'point' when a tip of the cusp was noted as visible through the gingiva. Gingival emergence must have started between the last observed 0 and first observed 1. Ambiguities in the CIRMF records are in red.

17E2 mandible permanent right quadrant								
Age (yr)	I_1	I_2	C	P_3	P_4	M_1	M_2	M_3
0.06	0	0	0	0	0	0	0	0
0.64	0	0	0	0	0	0	0	0
1.23	0	0	0	0	0	0	0	0
2.06	0	0	0	0	0	1	0	0
2.68	0	0	0	0	0	1	0	0
3.09	1	0	0	0	0	1	0	0
3.99	1	1	0	0	0	1	0	0
4.91	1	1	0	0	0	1	1	0
6.13	1	1	1	1	1	1	1	0
7.21	1	1	1	1	1	1	1	1
17E2 mandible permanent left quadrant								
Age (yr)	I_1	I_2	C	P_3	P_4	M_1	M_2	M_3
0.06	0	0	0	0	0	0	0	0
0.64	0	0	0	0	0	0	0	0
1.23	0	0	0	0	0	0	0	0
2.06	0	0	0	0	0	1	0	0
2.68	0	0	0	0	0	1	0	0
3.09	1	0	0	0	0	1	0	0
3.99	1	1	0	0	0	1	0	0
4.91	1	1	0	0	0	1	1	0
6.13	1	1	1	1	1	1	1	0
7.21	1	1	1	1	1	1	1	1

17E2 maxilla permanent right quadrant								
Age (yr)	I_1	I_2	C	P_3	P_4	M_1	M_2	M_3
0.06	0	0	0	0	0	0	0	0
0.64	0	0	0	0	0	0	0	0
1.23	0	0	0	0	0	0	0	0
2.06	0	0	0	0	0	1	0	0
2.68	0	0	0	0	0	1	0	0
3.09	1	0	0	0	0	1	0	0
3.99	1	1	0	0	0	1	0	0
4.91	1	1	0	1	1	1	1	0
6.13	1	1	0	1	1	1	1	0
7.21	1	1	1	1	1	1	1	1
8.08	1	1	1	1	1	1	1	1
17E2 maxilla permanent left quadrant								
Age (yr)	I_1	I_2	C	P_3	P_4	M_1	M_2	M_3
0.06	0	0	0	0	0	0	0	0
0.64	0	0	0	0	0	0	0	0
1.23	0	0	0	0	0	0	0	0
2.06	0	0	0	0	0	1	0	0
2.68	0	0	0	0	0	1	0	0
3.09	1	0	0	0	0	1	0	0
3.99	1	1	0	0	0	1	0	0
4.91	1	1	0	1	1	1	1	0
6.13	1	1	0	1	1	1	1	0
7.21	1	1	1	1	1	1	1	1
8.08	1	1	1	1	1	1	1	1

Table 5: CIRMF records of gingival emergence for 5I2. I collated information on when teeth were observed to be present and absent. In the tables, 0 indicated the age at which a tooth was not noted as present, 1 when a tooth was noted as present, and 'point' when a tip of the cusp was noted as visible through the gingiva. Gingival emergence must have started between the last observed 0 and first observed 1. Ambiguities in the CIRMF records are in red.

5I2 mandible permanent right quadrant								
Age (yr)	I_1	I_2	C	P_3	P_4	M_1	M_2	M_3
1.22	0	0	0	0	0	0	0	0
2.07	0	0	0	0	0	point	0	0
2.48	0	0	0	0	0	1	0	0
3.39	1	1	0	0	0	1	0	0
4.30	1	1	0	0	0	1	0	0
5.44	1	1	0	0	1	1	1	0
6.58	1	1	1	0	0	1	1	0
7.47	1	1	1	1	1	1	1	0
8.50	1	1	1	1	1	1	1	1
9.02	1	1	1	1	1	1	1	1
5I2 mandible permanent left quadrant								
Age (yr)	I_1	I_2	C	P_3	P_4	M_1	M_2	M_3
1.22	0	0	0	0	0	0	0	0
2.07	0	0	0	0	0	point	0	0
2.48	0	0	0	0	0	1	0	0
3.39	1	1	0	0	0	1	0	0
4.30	0	0	0	0	0	1	0	0
5.44	1	1	0	0	1	1	1	0
6.58	1	1	1	point	0	1	1	0
7.47	1	1	1	1	1	1	1	0
8.50	1	1	1	1	1	1	1	1
9.02	1	1	1	1	1	1	1	1

Appendix B.6 Eruption data HT12_15

Table 6: Mandrill HT12_15 eruption data. There were no observational data for HT12_15. However, I know which teeth were erupted, in eruption and not yet in eruption when he died at the age of 6.12 (age at death calculated using dental histology). Additional information is from published values (Setchell & Wickings 2014).

Tooth	Mid-point	Min	Max	Description	Developmental stage (Moorrees et al., 1963)	Developmental stage (Demirjian et al., 1973).
I_1	3.38	2.78	3.98	Crown and root complete, in occlusion with visible wear.	Stage 14	Stage H
I_2	3.63	3.04	4.23	Crown and root complete, in occlusion with visible wear.	Stage 6	Stage H
C_1	>6.12			Erupting through the alveolus, crown 3/4 complete	Stage 5	Stage C
P_3	>6.12			Erupting through the alveolus, crown 3/4 complete	Stage 5	Stage C
P_4	6.12-6.19 (max Setchell & Wickings 2004)			Crown complete in crypt, root 3/4 complete	Stage 11	Stage F
M_1	2.29	1.52	3.07	Crown and root complete, in occlusion with visible wear	Stage 14	Stage H
M_2	4.18	3.14	5.20	Crown and root complete, in occlusion with no visible wear	Stage 14	Stage H
M_3	6.21	4.09	8.33	Crown complete in crypt	Stage 6	Stage D

Appendix B.7 Data used for sex-specific dental development bar chart

Table 7: Data used for female sex-specific dental development bar chart. Data excluded from the summaries are in grey. For initiation I chose the earliest initiation per tooth, excluding maxillary teeth. For age at completion I calculated the mean, excluding data from maxillary teeth (PB M_1, M_2 and M_3)

Females – age at crown initiation (years)				
Tooth	**5D3A**	**PB**	**16L**	**Value used (earliest initiation**
I_1	0.56	0.71	0.27	0.27
I_2	1.25	0.79	0.86	0.79
C	2.26	0.96	1.09	0.96
P_3	0.90	0.82	0.36	0.36
P_4	1.65	1.04	1.74	1.04
M_1	-0.06	0.08 (M^1)	0.23	-0.06
M_2	1.57	1.4 (M^2)	1.30	1.30
M_3	3.24	3.38 (M^3)	3.89	3.24
Females – age at crown completion (years)				
Tooth	**5D3A**	**PB**	**16L**	**Value used (mean)**
I_1	2.88	3.16	3.17	3.07
I_2	3.36	3.59	3.33	3.43
C_1	3.35	4.86	3.34	3.85
P_3	4.83	4.4	3.33	4.19
P_4	2.99	4.09	3.83	3.64
M_1	1.09	1.48 (M^1)	1.49	1.29
M_2	3.47	3.68 (M^2)	3.51	3.49
M_3	4.77	5.46 (M^3)	6.42	5.59

Table 8: Data used for male sex-specific dental development bar chart. Data excluded from the summaries are in grey. For initiation I chose the earliest initiation per tooth, excluding maxillary teeth. For age at completion I calculated the mean, excluding data from maxillary teeth (5I2's M^1 17E2's M^1, P^3, Canine) or teeth that were still developing (HT12_15: C, P_3, M_3).

Males - age at crown initiation (years)					
Tooth	**2D8***	**HT12_15**	**5I2**	**17E2**	**Value used (earliest initiation)**
I_1	0.38	0.31	0.56	0.23	0.23
I_2	0.15	0.63	0.35	0.40	0.35
C_1	0.75	0.27	1.25	0.48 (C^1)	0.27
P_3	0.36	0.15	0.61	1.27 (P^3)	0.15
P_4	2.20	1.48	1.59	Tooth absent	1.48
M_1	0.54	-0.21	-0.19	-0.19	-0.21
M_2	1.44	1.28	1.46	1.11	1.11
M_3	2.99	4.39	3.47	3.26	3.26
Males - age at crown completion (years)					
Tooth	**2D8***	**HT12_15**	**5I2**	**17E2**	**Value used (Mean)**
I_1	3.10	2.97	3.11	2.65	2.91
I_2	3.32	3.34	3.32	3.37	3.34
C_1	7.18	6.12 (developing)	8.75	8.48 (C^1)	8.75
P_3	6.31	6.12 (developing)	8.84	4.77 (P^3)	8.84
P_4	4.44	3.82	4.35	Tooth absent	4.08
M_1	1.46	1.81	1.28	1.19	1.42
M_2	3.19	3.80	3.57	3.20 (M^2)	3.68
M_3	4.50	6.07 (developing)	6.33	5.15 (M^3)	6.33
Initiation and completion ages of 2D8 excluded since its positioning was uncertain due to absence of neonatal line and open roots, and is based on the values of the other males.					

Appendix B.8 Extension rates of male and female

Tabel 9: Extension rates of male and female $I_{1.}$. CFT= Crown formation time in years. EER= Enamel extension rate in µm.

5D3A		16L		PB		2D8		17_E2		5I2		HT12_15	
CFT	EER	CFT	EER	CFT	EER	CFT	EER	CFT	EER	CFT	EER	CFT	EER
0,28	11,3	0,06	28,7	0,06	22,4	0,12	17,8	0,11	22,4	0,06	32,3	0,18	24,9
0,37	15,7	0,15	17,2	0,13	13,3	0,18	19,3	0,13	15,8	0,2	21,6	0,3	16,3
0,43	12,4	0,36	16,0	0,18	12,5	0,27	12,2	0,17	18,3	0,42	19,1	0,46	20,5
0,51	10,6	0,45	17,1	0,33	9,9	0,43	12,6	0,2	22,2	0,62	12,3	0,54	15,8
0,6	15,3	0,51	15,5	0,47	11,0	0,62	13,2	0,22	20,0	0,79	10,5	0,6	17,1
0,66	14,7	0,56	11,8	0,55	8,5	0,69	10,9	0,28	21,2	0,93	12,2	0,88	18,7
0,78	15,9	0,7	11,9	0,58	14,8	0,7	14,1	0,35	19,9	1,12	11,6	1,07	13,3
0,87	9,7	0,83	14,1	0,65	7,7	0,74	10,7	0,4	17,8	1,14	7,6	1,22	11,7
0,98	12,1	1,08	12,2	0,7	8,0	0,76	10,7	0,42	10,8	1,27	11,8	1,3	18,7
1,06	10,9	1,17	12,6	0,75	10,8	0,82	12,2	0,48	11,6	1,3	9,7	1,34	15,6
1,14	7,9	1,29	12,2	0,77	10,1	0,89	13,7	0,51	10,0	1,46	12,5	1,41	14,6
1,23	9,9	1,32	8,7	0,79	10,0	0,91	9,1	0,6	19,3	1,59	12,4	1,48	18,8
1,33	11,9	1,47	10,7	0,83	12,2	0,99	12,2	0,62	17,7	1,71	13,8	1,51	12,2
1,53	11,8	1,5	9,5	0,89	10,2	1,07	10,4	0,66	21,1	1,87	10,5	1,53	15,4
1,59	8,8	1,63	11,8	0,94	8,4	1,17	14,5	0,68	14,9	1,97	12,2	1,55	15,7
1,69	12,6	1,72	10,0	0,98	8,4	1,21	13,3	0,71	10,0	2,01	13,5	1,81	14,6
1,71	12,2	1,82	9,5	1,03	11,4	1,31	9,6	0,73	15,3	2,09	12,7	1,88	13,4
1,85	10,9	1,93	9,8	1,08	8,0	1,36	9,5	0,75	18,8	2,3	13,1	1,99	14,8
1,94	13,8	2,04	9,9	1,14	10,9	1,4	11,4	0,79	16,4	2,41	11,0	2,14	10,9
1,97	13,0	2,23	10,8	1,17	10,5	1,63	11,5	0,86	15,3	2,49	18,2	2,29	12,7
2,11	15,6	2,27	8,4	1,2	9,6	1,68	11,5	0,91	17,4	2,55	12,2	2,44	13,6

2,33	10,8	1,23	9,4	1,91	10,4	0,98	15,8
2,4	13,5	1,33	13,1	1,98	11,8	1	16,1
2,55	9,7	1,36	14,3	2,04	11,4	1,06	16,7
2,67	10,0	1,41	11,2	2,13	10,7	1,1	21,6
2,74	13,3	1,58	10,9	2,18	8,6	1,11	24,2
2,8	13,9	1,65	11,0	2,28	12,1	1,14	16,1
2,85	14,6	1,82	11,3	2,35	11,9	1,16	15,1
2,88	13,6	1,89	12,8	2,42	12,1	1,18	19,9
2,9	7,9	1,94	12,8	2,56	13,9	1,2	26,9
		2	12,7	2,65	14,2	1,3	15,6
		2,04	13,4	2,69	19,9	1,33	11,5
		2,07	11,7	2,72	12,8	1,36	15,0
		2,23	12,7			1,4	15,4
		2,3	11,9			1,48	15,4
		2,45	13,8			1,55	16,9
		2,55	13,5			1,69	14,1
		2,62	12,0			1,76	11,8
		3,19	13,2			1,77	12,0
		3,31	17,0			1,84	14,2
						1,85	10,3
						1,89	11,2
						2,01	16,2
						2,17	16,5
						2,22	20,0
						2,27	17,4
						2,38	22,7
						2,44	21,6

2,49	14,1
2,53	14,5
2,6	8,9
2,65	16,0

2,47	9,2
2,48	10,6
2,49	20,6

Table 10 Extension rates of male and female I_2. CFT= Crown formation time in years. EER= Enamel extension rate in µm.

5D3A		16L		PB		2D8		17_E2		5I2		HT12_15	
CFT	EER	CFT	EER	CFT	EER	cft	EER	CFT	EER	CFT	EER	CFT	EER
0,19	18,9	0,07	20,0	0,18	11,8	0,14	12,3	0,06	21,5	0,31	12,3	0,25	18,8
0,31	14,9	0,10	13,3	0,24	13,6	0,42	9,2	0,22	21,6	0,54	16,5	0,48	11,3
0,43	14,4	0,14	12,6	0,33	9,9	0,50	8,7	0,24	21,4	0,74	12,3	0,62	12,3
0,50	9,5	0,16	14,2	0,40	7,7	0,61	6,5	0,37	16,9	0,98	9,2	0,78	15,8
0,58	8,3	0,20	18,8	0,51	14,0	0,71	6,1	0,39	19,4	1,14	15,0	0,98	15,2
0,64	12,1	0,28	17,6	0,60	13,4	0,78	9,8	0,41	16,4	1,35	9,9	1,09	13,3
0,75	9,0	0,31	16,7	0,62	12,1	0,91	5,5	0,44	10,3	1,50	9,9	1,17	16,1
0,77	7,3	0,49	13,4	0,66	6,6	1,19	8,5	0,49	18,5	1,70	11,7	1,39	12,9
0,98	12,4	0,58	10,4	0,78	8,4	1,29	9,0	0,59	16,0	1,84	14,6	1,52	12,9
1,03	10,6	0,69	13,6	0,83	10,6	1,39	8,0	0,70	16,1	2,04	12,2	1,68	16,1
1,06	14,4	0,73	8,6	0,87	10,0	1,50	8,9	0,72	13,5	2,31	10,4	1,83	16,3
1,25	12,9	0,87	11,6	0,90	13,9	1,65	7,5	0,86	13,4	2,47	16,7	1,99	14,1
1,27	12,7	0,90	8,3	1,04	10,9	1,74	10,7	0,90	14,0	2,57	13,6	2,05	10,3
1,40	14,9	1,03	13,1	1,22	8,5	1,82	11,3	0,92	12,9	2,79	11,6	2,25	15,2
1,47	12,2	1,12	7,7	1,31	7,8	1,91	14,1	1,02	16,8	2,95	16,2	2,43	12,4
1,54	12,2	1,21	11,7	1,50	8,8	1,96	10,1	1,12	16,1	2,98	4,1	2,51	13,4
1,59	14,2	1,44	8,8	1,62	7,2	2,00	13,0	1,29	12,6			2,54	17,9
1,78	12,1	1,76	8,5	1,77	8,0	2,03	12,6	1,43	13,8			2,61	17,7
1,90	13,8	1,98	9,5	1,84	9,2	2,05	19,6	1,50	14,4			2,67	27,8
1,98	12,2	2,13	12,6	2,04	10,7	2,07	20,7	1,57	12,8			2,71	15,0

	2,23	9,7	2,19	10,0	2,10	11,9	1,59	10,2
	2,28	6,9	2,31	11,0	2,12	11,1	1,62	11,3
	2,39	13,0	2,49	10,5	2,18	14,3	1,76	14,0
	2,43	9,4	2,65	12,0	2,21	11,8	1,95	13,3
	2,47	11,1	2,76	11,0	2,23	18,0	2,14	13,4
			2,85	10,7	2,26	16,1	2,29	13,0
			2,96	10,0	2,29	18,5	2,45	13,4
					2,31	9,3	2,61	15,3
					2,37	9,4	2,65	13,1
					2,42	12,2	2,71	14,1
					2,49	10,8	2,83	11,5
					2,60	10,7	2,91	20,6
					2,72	13,0	2,95	29,2
					2,81	10,4	2,96	19,7
					2,90	10,9		
					2,96	11,4		
					3,05	18,5		
					3,11	14,8		
					3,17	17,3		

Table 11 Extension rates of male and female C_1. CFT= Crown formation time in years. EER= Enamel extension rate in µm. A single C^1 indicated with *

16L		PB		2D8		17_E2*		5I2		HT12_15	
CFT	EER	CFT	EER	cft	EER	cft	EER	CFT	DER	CFT	EER
0,06	16,8	0,28	16,3	CFT	EER	0,20	20,4	0,38	17,0	0,21	21,6
0,25	11,2	0,37	11,7	0,87	15,6	0,49	10,3	0,57	11,4	0,23	14,0
0,34	12,3	0,51	11,1	1,16	10,5	0,94	10,9	0,62	12,9	0,25	13,7
0,45	11,2	0,53	16,3	1,46	10,4	1,32	11,9	0,93	12,0	0,38	15,6
0,48	12,2	0,70	9,9	1,71	12,2	2,02	11,9	1,33	11,8	0,46	16,0
0,61	9,6	0,93	9,9	1,85	9,5	2,73	13,5	1,60	9,3	0,60	14,2
0,65	7,5	1,15	8,6	1,99	18,3	3,50	12,8	2,24	11,8	0,72	17,1
0,77	12,4	1,26	9,8	2,39	13,3	3,80	16,7	2,44	13,6	0,85	14,0
0,87	8,2	1,41	8,8	3,00	14,3	4,12	20,1	3,04	10,4	0,96	13,9
0,98	8,0	1,48	7,9	3,65	15,2	4,53	16,0	3,21	12,8	1,01	14,7
1,22	8,4	1,62	8,5	4,51	12,9	4,86	19,4	3,52	10,1	1,10	16,7
1,39	8,3	1,65	7,1	4,90	11,4	5,22	12,2	4,07	14,4	1,23	15,6
1,51	8,0	1,69	5,7	5,02	17,3	6,00	22,9	4,84	12,5	1,29	20,1
1,54	7,1	1,76	9,1	5,35	18,5	6,51	24,2	5,97	13,2	1,36	11,9
1,78	8,4	2,08	6,6	5,71	9,3	6,98	26,6	6,19	17,0	1,40	15,9
1,94	9,3	2,27	9,3	6,31	18,8	7,14	29,8	7,21	12,0	1,44	14,0
2,00	8,5	2,46	8,3	6,43	18,3	7,46	25,0	7,50	22,3	1,58	8,1
2,13	15,6	2,62	10,1			7,86	36,6			1,68	12,8
2,19	15,3	2,82	7,7			7,99	23,1			1,79	7,9
2,25	8,3	2,94	9,1							1,92	9,0
		3,14	7,4							2,03	11,8
		3,30	8,9							2,13	11,8
		3,45	9,5							2,27	15,9
		3,58	9,9							2,42	8,0
		3,75	9,2							2,55	12,2

3,90	9,6
3,99	14,5
4,17	10,9
4,29	16,5
4,39	11,7

2,64	15,5
2,89	14,7
3,09	10,6
3,28	11,7
3,53	13,7
3,82	14,5
3,89	12,0
4,27	16,0
4,41	14,6
4,56	15,7
4,64	15,7
4,68	16,0
4,81	14,2
4,89	18,9
4,95	16,9
5,08	16,3
5,28	13,1
5,37	18,9
5,45	20,9
5,57	17,2
5,66	18,1
5,72	12,3
5,77	12,5
5,81	13,7
5,85	20,9

Table 12 Extension rates of male and female P_3. CFT= Crown formation time in years. EER= Enamel extension rate in µm. A single C^1 indicated with *.

16L		PB		2D8		17_E2*		5I2		HT12_15	
CFT	EER	CFT	EER	CFT	EER	CFT	EER	CFT	EER	CFT	EER
0,04	23,2	0,11	12,1	1,21	11,6	0,03	35,0	0,14	13,6	0,31	6,9
0,20	7,6	0,57	7,1	1,56	7,1	0,27	15,3	0,24	9,6	0,45	8,6
0,45	9,6	0,90	5,9	1,77	8,2	0,42	14,0	0,31	18,7	0,57	8,3
0,54	10,0	0,98	7,2	2,03	7,4	0,52	7,1	0,38	13,6	0,74	8,5
0,62	7,5	1,15	5,2	2,24	9,1	0,54	6,2	0,46	12,2	0,85	9,8
0,78	4,0	1,37	6,0	2,34	12,0	0,61	6,7	0,52	12,3	1,02	12,3
0,96	3,6	1,55	4,4	2,62	9,3	0,69	7,6	0,60	11,0	1,16	10,1
1,14	3,7	1,63	6,6	2,82	6,9	0,73	8,7	0,66	8,7	1,25	15,6
1,35	6,6	1,74	6,2	2,97	7,6	0,75	11,7	0,75	12,0	1,41	8,0
1,56	5,0	1,96	5,0	3,24	6,6	0,90	12,7	0,90	9,9	1,46	9,0
1,89	5,4	2,18	4,5	3,37	10,9	1,29	8,0	1,00	8,1	1,54	8,9
2,07	6,4	2,33	5,3	3,56	14,0	1,44	7,5	1,08	7,1	1,67	8,4
2,23	7,6	2,48	4,1	3,98	9,6	1,64	15,4	1,20	13,0	1,75	7,9
2,46	5,2	2,62	5,5	4,17	12,7	2,05	10,0	1,44	5,4	1,82	10,5
2,57	5,6	2,67	4,9	4,64	10,6	2,13	12,6	1,62	4,0	1,92	8,5
2,63	10,0	2,80	5,9	5,00	13,0	2,18	9,2	1,71	6,2	1,98	8,9
2,72	10,6	2,91	6,5	5,35	16,0	2,30	13,4	1,90	4,6	2,16	9,8
2,77	7,6	3,07	6,6			2,39	6,7	2,09	4,8	2,28	15,4
2,87	8,8	3,19	6,3			2,68	13,3	2,23	6,0	2,31	15,8
2,97	7,3	3,39	22,4			2,96	7,5	2,56	5,8	2,43	16,7
		3,56	2,9			3,22	7,5	2,80	4,6	2,56	16,8
		3,58	3,1			3,42	14,6	2,98	6,5	2,62	19,0
						3,46	2,4	3,12	6,7	2,90	7,5

3,21	6,3	3,07	6,7
3,31	6,6	3,13	10,9
3,41	7,3	3,24	10,7
3,57	10,8	3,38	8,8
3,76	10,5	3,56	8,5
3,92	10,7	3,66	9,1
4,03	7,1	3,76	13,2
4,11	13,7	3,93	10,9
4,25	8,2	4,01	10,8
4,42	10,5	4,15	9,5
4,58	8,1	4,36	9,7
4,72	10,9	4,62	8,6
4,87	11,5	4,73	10,1
4,93	13,8	4,93	6,4
5,03	14,6	5,02	7,0
5,14	12,2	5,28	7,8
5,25	16,9	5,44	12,4
5,36	12,7	5,59	13,9
5,50	10,7	5,76	8,1
5,59	11,4	5,89	10,7
5,86	12,7	5,96	12,9
5,96	12,8		
6,10	17,4		
6,36	13,1		
6,52	15,7		
6,69	14,6		
6,76	18,0		

6,95	9,2
6,99	14,2
7,11	20,5
7,26	13,4
7,34	14,0
7,59	13,8
7,76	12,3
7,87	11,4
7,95	13,3
8,05	22,7
8,20	23,8

Table 13 Extension rates of male and female P_4. CFT= Crown formation time in years. EER= Enamel extension rate in µm.

5D3A		16L		PB		2D8		5I2		HT12_15	
CFT	EER	CFT	EER	CFT	EER	CFT	EER	CFT	EER	CFT	EER
0,15	15,9	0,14	20,2	0,28	16,2	0,11	22,8	0,02	18,7	0,06	56,5
0,26	4,5	0,26	14,7	0,30	15,2	0,34	15,0	0,12	14,5	0,12	38,9
0,39	5,7	0,30	6,7	0,44	11,8	0,57	11,6	0,16	11,5	0,24	16,7
0,45	15,7	0,37	16,0	0,57	7,9	0,67	11,4	0,18	11,8	0,34	24,4
0,56	8,3	0,40	6,2	0,60	11,3	0,77	11,2	0,23	15,4	0,65	11,9
0,61	5,1	0,48	8,0	0,73	8,7	0,79	11,0	0,25	13,9	0,74	8,2
0,65	6,3	0,52	10,4	0,77	8,6	0,82	10,9	0,81	9,7	0,79	9,5
0,76	10,3	0,55	10,9	0,89	8,4	0,85	14,9	1,18	11,1	0,96	6,7
0,82	12,6	0,59	14,1	0,98	8,6	0,87	8,2	1,24	7,7	1,14	6,2
0,84	6,7	0,67	10,4	1,02	7,0	0,91	9,7	1,27	8,2	1,20	6,8
0,92	10,2	0,69	9,6	1,10	5,7	0,96	11,9	1,37	8,0	1,37	6,8
0,95	10,2	0,70	14,1	1,46	4,0	1,02	5,8	1,63	8,3	1,55	6,9
1,00	10,5	0,75	7,0	1,49	6,3	1,04	7,4	1,65	9,9	1,79	8,1
1,05	14,4	0,76	8,6	1,59	4,3	1,07	7,9	1,89	6,2	1,90	6,8
1,11	11,6	0,93	8,8	1,67	5,9	1,09	13,6	2,09	7,5	2,09	8,8
1,24	10,8	1,00	6,5	1,69	8,7	1,11	6,8	2,40	6,3	2,17	7,9
1,27	10,7	1,06	8,0	1,77	5,6	1,15	7,9	2,61	8,6	2,25	9,3
1,32	9,9	1,26	6,8	1,87	6,8	1,17	11,2	2,75	9,9	2,31	9,6
		1,37	8,9	1,99	4,7	1,26	7,3	2,81	15,5	2,35	19,8
		1,41	9,5	2,08	4,6	1,31	9,1	2,83	13,3		
		1,53	9,2	2,20	6,8	1,34	9,2	2,86	12,1		
		1,65	8,3	2,28	10,5	1,38	7,2	3,05	9,1		
		1,75	6,6	2,40	7,8	1,49	8,4				

1,90	4,7	2,61	8,1	1,80	9,6
1,99	5,8	2,69	11,5	1,94	12,8
2,05	8,5	2,77	10,0	2,06	9,8
2,09	19,4	2,79	19,4	2,19	11,1
				2,24	12,4

Table 14 Extension rates of male and female M_1. CFT= Crown formation time in years. EER= Enamel extension rate in µm.

16L		PB		2D8		17_E2		5I2		HT12_15	
CFT	EER	CFT	EER	CFT	EER	CFT	EER	CFT	EER	CFT	EER
0,27	17,6	0,11	30,9	0,03	31,2	0,19	34,1	0,19	34,1	0,22	20,5
0,40	14,1	0,18	17,6	0,06	36,8	0,30	14,2	0,48	8,6	0,45	12,7
0,48	7,8	0,27	8,8	0,09	18,8	0,42	9,7	0,50	15,5	0,47	11,9
0,57	11,5	0,36	7,2	0,18	13,8	0,53	7,0	0,66	10,6	0,66	6,4
0,62	9,1	0,39	8,1	0,23	10,8	0,58	11,8	0,91	9,5	0,79	4,3
0,68	7,1	0,52	6,7	0,26	15,0	0,61	7,6	1,00	9,2	0,94	6,3
0,85	7,3	0,56	8,2	0,34	8,7	0,64	8,2	1,25	8,3	1,07	5,5
0,97	6,2	0,59	6,6	0,44	11,5	0,69	9,6	1,28	12,9	1,22	6,7
1,09	7,1	0,80	5,2	0,53	9,1	0,72	7,9	1,30	13,7	1,41	7,4
1,20	7,4	0,86	5,9	0,56	16,6	0,79	14,1	1,34	10,4	1,60	7,2
1,26	5,5	0,87	8,0	0,61	4,7	0,83	13,8	1,40	13,1	1,68	5,7
		0,90	9,6	0,65	11,1	0,85	9,4	1,44	14,9	1,80	5,0
		0,98	6,3	0,70	11,1	0,88	10,9	1,48	4,8	1,91	7,0
		1,27	6,2	0,83	8,7	0,91	11,1			1,99	8,0
		1,37	12,0	0,90	11,9	0,93	11,0			2,02	13,0
		1,41	19,3	0,92	6,1						

Table 15: Extension rates of male and female M_2. CFT= Crown formation time in years. EER= Enamel extension rate in µm. A single M^2 indicated with *.

5D3A		16L		PB*		2D8		5I2		HT12_15	
CFT	EER	CFT	EER	CFT	EER	CFT	EER	CFT	EER	CFT	EER
0,28	16,5	0,32	11,8	0,37	18,8	0,03	21,1	0,37	19,8	0,06	29,7
0,33	9,2	0,36	13,2	0,41	22,7	0,04	16,1	0,50	12,8	0,45	26,9
0,48	10,9	0,55	12,9	0,48	18,8	0,19	24,6	0,63	11,0	0,80	14,5
0,57	8,0	0,58	9,8	0,55	6,2	0,35	12,0	0,68	9,4	0,93	8,0
0,66	10,6	0,73	7,7	0,58	13,3	0,39	8,8	0,78	6,1	1,00	9,0
0,68	10,1	0,87	7,8	0,66	10,3	0,41	14,1	0,84	9,0	1,16	8,7
0,71	9,8	0,98	8,0	0,70	6,7	0,44	12,0	0,89	6,9	1,37	9,6
0,84	7,5	1,05	9,6	0,73	5,3	0,52	12,2	0,92	7,9	1,57	6,1
0,93	8,4	1,12	8,3	0,75	10,0	0,57	8,1	0,98	9,3	1,84	6,4
0,95	7,5	1,18	7,5	0,77	10,6	0,59	13,8	1,03	7,9	1,93	8,4
1,10	8,5	1,22	8,3	0,79	7,8	0,64	8,4	1,05	7,6	2,18	8,5
1,20	11,8	1,26	10,4	0,81	8,1	0,67	10,4	1,13	7,1	2,24	8,1
1,27	13,3	1,29	6,8	0,84	6,6	0,74	11,0	1,38	7,3	2,46	10,7
1,42	8,4	1,36	5,9	0,88	5,3	0,79	7,8	1,53	6,8	2,51	10,3
1,45	7,9	1,46	8,4	0,90	7,0	0,80	8,9	1,56	5,7		
1,49	9,9	1,56	7,2	0,93	7,5	0,82	9,7	1,75	6,5		
1,52	9,5	1,71	6,9	0,90	7,0	0,84	9,2	1,95	7,7		
1,67	10,5	1,79	6,8	0,93	7,5	0,85	8,0	2,11	12,6		
1,71	8,2	1,83	6,7	0,97	11,3	0,87	11,0				
1,74	8,0	1,96	7,2	1,04	5,1	0,88	8,2				
1,84	10,2	2,09	11,0	1,08	7,4	0,94	10,8				
1,88	7,4	2,17	9,2	1,14	6,4	0,99	8,2				
		2,20	26,5	1,15	6,7	1,06	7,2				

1,17	11,5	1,11	8,0
1,20	5,9	1,16	8,0
1,22	8,2	1,24	7,0
1,25	5,7	1,29	8,1
1,29	4,6	1,48	9,2
1,31	5,3	1,61	10,8
1,36	5,3	1,70	9,9
1,38	9,6	1,75	7,7
1,42	9,3		
1,46	5,8		
1,53	6,2		
1,68	5,8		
1,91	6,7		
1,97	8,2		
2,07	8,4		
2,11	13,5		

Table 16 Extension rates of male and female M_3. CFT= Crown formation time in years. EER= Enamel extension rate in µm. A single M^3 indicated with *

16L		PB*		2D8		17_E2		5I2		HT12_15	
CFT	EER	CFT	EER	CFT	EER	CFT	EER	CFT	EER	CFT	EER
0,24	35,8	0,04	47,0	0,21	21,3	0,18	29,6	0,10	25,5	0,08	52,1
0,31	14,0	0,06	29,9	0,32	10,1	0,27	19,0	0,31	23,2	0,32	23,2
0,36	8,2	0,07	39,6	0,39	14,1	0,32	19,1	0,48	10,3	0,53	8,6
0,39	15,4	0,18	22,1	0,48	11,5	0,35	11,9	0,79	10,8	0,56	14,6
0,45	9,6	0,23	17,1	0,59	9,0	0,40	15,2	0,81	11,8	0,78	9,3
0,58	9,9	0,25	8,1	0,63	7,6	0,45	10,0	1,14	8,5	0,84	13,3
0,67	6,2	0,27	8,9	0,69	8,8	0,56	10,3	1,34	8,8	1,06	8,6
0,76	7,0	0,34	12,4	0,75	7,8	0,60	15,1	1,70	6,6	1,30	9,1
0,89	7,5	0,38	16,5	0,88	14,8	0,67	6,3	1,79	6,4	1,37	6,3
1,01	4,3	0,41	8,0	0,96	7,4	0,73	9,6	1,88	7,4	1,44	8,5
1,09	6,4	0,48	4,7	1,01	9,3	0,83	8,9	1,96	8,6	1,52	9,5
1,13	5,3	0,52	5,4	1,11	8,8	0,91	7,5	2,07	7,4	1,61	8,0
1,27	6,6	0,56	7,9	1,19	6,1	0,93	4,3	2,27	10,9	1,68	7,9
1,35	3,8	0,62	8,6	1,27	7,9	0,95	12,7	2,37	14,3		
1,79	5,2	0,65	6,4	1,35	14,1	0,96	5,5	2,45	6,7		
1,89	6,6	0,70	10,0	1,48	8,3	1,00	12,0				
1,98	5,8	0,79	5,4	1,51	4,3	1,04	7,2				
2,05	6,1	0,84	6,3			1,08	6,7				
2,16	6,1	0,91	6,9			1,14	4,7				
2,21	8,2	0,93	8,1			1,16	8,0				
2,36	7,8	0,96	6,9			1,22	6,6				
2,49	6,4	0,98	5,3			1,27	5,1				
2,53	12,57668	1,04	11,2			1,33	8,7				

1,07	5,0
1,12	4,2
1,14	8,7
1,20	13,1
1,28	4,1
1,31	7,7
1,33	8,5

1,44	7,9
1,50	4,7
1,53	7,1
1,60	7,4
1,65	5,2
1,70	4,5
1,72	10,4
1,75	10,1
1,81	10,0
1,87	4,7
1,93	9,9

COMPARATIVE STUDY OF DENTAL DEVELOPMENT IN AFRICAN PAPIONINS

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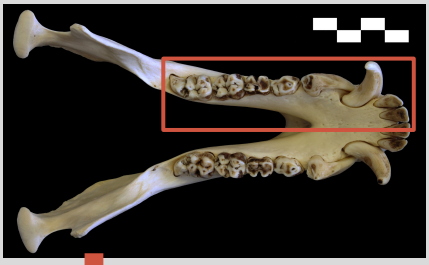
AIM

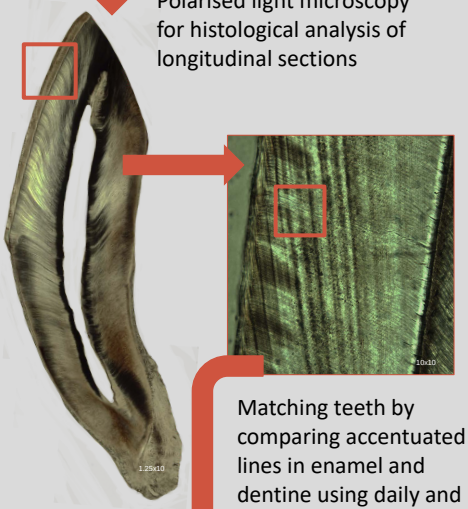
To understand variation in dental development among African papionins and its relationship to feeding ecology.

METHODS



One quadrant of mandibular dentition

Polarised light microscopy for histological analysis of longitudinal sections

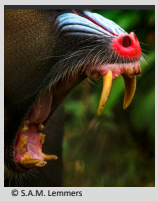


Matching teeth by comparing accentuated lines in enamel and dentine using daily and longer period growth increments [1,2,3]

Calibration of development to age using neonatal line in M1 (forms at birth), open roots in developing dentitions and the daily and longer period increments [1,2,3]

MANDRILLS

3 female & 4 male semi-free-ranging *Mandrillus sphinx* from Gabon, individual eruption ages (**E**), and published mean eruption ages [4]



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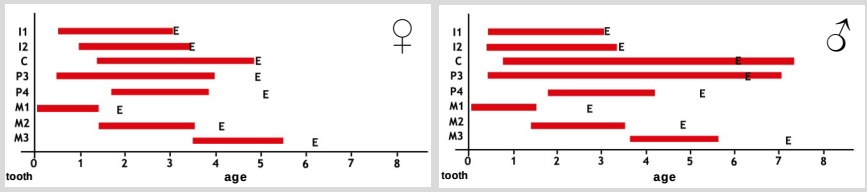
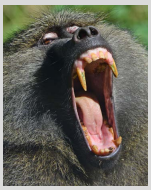


Incisors erupt when little root has formed
Male canines and P3s erupt during crown formation
Strong individual morphological variation among females

BABOONS

2 females: *Papio anubis-hamadryas* hybrids [2], 3 males: 2 *Papio h. anubis,* 1 *anubis-hamadryas* hybrid from Awash National Park, Ethiopia, published mean eruption ages (**E**) [5]



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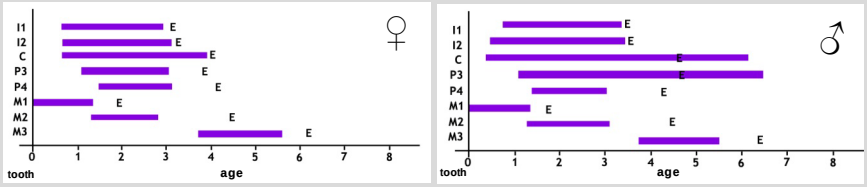
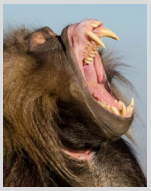


Male canines and P3s erupt when crowns are still forming, similar to mandrills
Lower incisors erupt with little root formation, but more than in mandrills and mangabeys

GELADAS

Published histological and eruption ages (**E**) for *Theropithecus gelada* [6]



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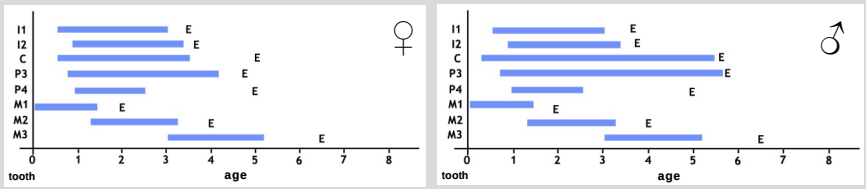
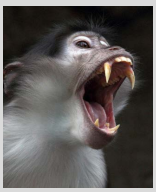


Incisors erupt with more root than in the other 3 species
Male canines and P3s erupt after completion of crown formation
Less difference in eruption ages between sexes than in other 3 species

MANGABEYS

Mangabeys: 2 female *Cercocebus atys* from UCL anatomical collection. Mean eruption ages (**E**) for 27 females from Yerkes Regional Primate centre, USA



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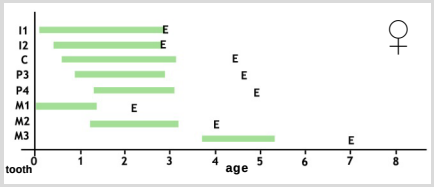

Incisors erupt when little root has formed, similar to mandrills
Anterior teeth and premolars initiate in a stepwise fashion

M1 and incisor initiation are maximum ages for all four species due to age related wear.

DISCUSSION

- Differences in diet may explain differences in root development at eruption: mandrills and mangabeys consume hard fruits and show extreme tooth wear of the anterior dentition [7]. Geladas mainly consume grass.
- Results suggest that amount of root formed during eruption is not uniform across species and root length is not a crucial factor in the eruption process [8,9].
- Difference in prenatal enamel formation in M1 between the sexes could indicate earlier start of dental formation for males in highly sexual dimorphic species.
- Results suggest *Mandrillus* and *Cercocebus* differ from the other African papionins, supporting genetic evidence for their sister group relationship within this tribe [10].

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Special thanks to Pamela Walton, Hard Tissue Lab, Newcastle University, for preparing the thin sections used in this study and to the Leverhulme Trust for funding this project

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