Faster growth corresponds with shallower linear hypoplastic defects in great ape canines

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3 **Abstract**

4 Deeper or more ‘severe’ linear enamel hypoplasia (LEH) defects are hypothesized to reflect
5 more severe stress during development, but it is not yet clear how depth is influenced by intrinsic
6 enamel growth patterns. Recent work documented inter- and intraspecific differences in LEH
7 defect depth in extant great apes, with mountain gorillas having shallower defects than other
8 taxa, and females having deeper defects than males. Here, we assess the correspondence of inter-
9 and intraspecific defect depth and intrinsic aspects of enamel growth: enamel extension rates,
10 outer enamel striae of Retzius angles, and linear enamel thickness. Thin sections of great ape
11 canines ($n = 40$) from *Gorilla beringei beringei*, *Gorilla gorilla gorilla*, *Pan troglodytes*, and
12 *Pongo* spp. were analyzed. Enamel extension rates were calculated within deciles of enamel-
13 dentine junction length. Linear enamel thickness and the angle of intersection between striae of
14 Retzius and the outer enamel surface were measured in the imbricational enamel. Mountain
15 gorillas have faster enamel extension rates and shallower striae angles than the other taxa
16 examined. Mountain gorillas have thinner imbricational enamel than western lowland gorillas
17 and orangutans, but not chimpanzees. In the combined-taxon sample, females exhibit larger
18 striae angles and thicker imbricational enamel than males. Enamel extension rates are highly
19 negatively correlated with striae angles and LEH defect depth. Enamel growth variation
20 corresponds with documented inter- and intraspecific differences in LEH defect depth in great
21 ape canines. Mountain gorillas have shallower striae angles and faster extension rates than other
22 taxa, which might explain their shallow LEH defect morphology and the underestimation of their
23 LEH prevalence in previous studies. These results suggest that stressors of similar magnitude and

timing might produce defects of different depths in one species or sex vs. another, which has implications for interpretations of stress histories in hominins with variable enamel growth patterns.

1. Introduction

Linear enamel hypoplasia (LEH) is known as a nonspecific indicator of physiological stress during dental development (Goodman and Rose, 1990). LEH defects occur on the outer enamel surface as localized reductions in enamel thickness. As they are caused by systemic stressors, they manifest in all concurrently forming teeth (Berten, 1895). Such defects are exceedingly common in great apes (e.g., Hannibal and Guatelli-Steinberg, 2005; Guatelli-Steinberg, 2012) and, to a lesser extent, early hominins (e.g., White, 1978; Guatelli-Steinberg, 2004). Defect severity is hypothesized to reflect the magnitude of the stressor that disrupted growth and led to enamel defect formation (Skinner and Hopwood, 2004; Skinner and Skinner, 2017; Skinner, 2019). Experimental studies in non-primate mammals demonstrate a link between higher, intermittent doses of administered fluoride and deeper and wider surface defects (Kierdorf et al., 2004, Suckling and Thurley, 1984). However, comparable data on stress-related correlates of enamel depth variation do not exist in primate models.

Previous work indicates that variation in enamel growth patterns and geometry of internal growth increments may influence LEH defect depth (Hillson and Bond, 1997; Guatelli-Steinberg, 2004, 2008; Witzel et al., 2006, 2008; Guatelli-Steinberg et al., 2012a, 2017; McGrath et al., 2018). While stress severity might also influence defect dimensions, the potential for variation in enamel growth patterns to shape and constrain defect dimensions complicates direct inference of stress severity from surface depths alone. Furthermore, defect depth variation can

affect how well defects are defined on the enamel surface, leading to an underestimation of both defect prevalence (Guatelli-Steinberg et al., 2012; McGrath et al., 2018) and the duration of enamel growth disruption that a defect represents (Guatelli-Steinberg, 2008). It has been suggested that the lower prevalence and shorter estimated durations of stress episodes represented by LEH defects in *Paranthropus* vs. *Australopithecus* is a consequence of faster enamel extension rates in the former genus (Guatelli-Steinberg, 2008), but defect depths are yet to be reported in these taxa. Skinner (2019) reported the first defect depths in hominins, *Australopithecus africanus* and *Homo naledi*, both of which show a bimodal pattern of semiannual stress events. Further studies in these and other hominin taxa could incorporate internal growth information (where available) to more fully evaluate the roles that enamel growth variation vs. stress severity play in determining defect dimensions.

The present study was designed to assess the degree to which differences in canine enamel growth patterns mirror documented differences in LEH defect depth among extant great apes (*Gorilla beringei beringei*, *Gorilla gorilla gorilla*, *Pan troglodytes*, *Pongo* spp.). We measure growth variables that have been hypothesized to influence defect depth, including enamel extension rates, the angle of intersection between striae of Retzius and the outer enamel surface, and linear enamel thickness. We test the relationships among these variables to assess how well they correspond to differences in LEH defect depths among species and sexes previously reported in a larger sample of the same taxa (McGrath et al., 2018). Associations between defect depth and specific enamel growth variables would suggest that these variables should be factored into analyses of LEH prevalence and defect dimensions in fossil hominins, especially in analyses focusing on the severity and/or duration of stress episodes (e.g., Skinner, 2019).

1.1. Canine development and LEH

Teeth preserve a permanent record of their incremental growth in the form of short- and long-period incremental lines (Boyde, 1964). Short-period lines reflect daily fluctuations in enamel secretion. Termed cross-striations, they record the circadian rhythm of enamel-secreting cells or ameloblasts (Boyde, 1989, 1990; Smith, 2006). Long-period lines, or striae of Retzius (Retzius, 1837), record episodic disturbances in enamel formation that occur with a regular periodicity in all permanent teeth of an individual (FitzGerald, 1998). Striae of Retzius periodicity ranges from 5–11 days in extant great apes (Schwartz et al., 2001; Smith et al., 2010). The first striae are laid down over the dentine horn and do not reach the outer enamel surface (Beynon and Wood, 1987). Once maximum cusp height is attained, occupying roughly 5–20% of total crown height in ape canines (Schwartz and Dean, 2001), growth continues down the crown toward the cervix as ameloblasts differentiate along the enamel-dentine junction, or EDJ (Boyde, 1964, 1989; Shellis 1984). These layers are laid down in a tile-like manner in the lateral and cervical regions of the crown, or the imbricational enamel (Pickerill, 1913; Beynon and Dean, 1987). It is in the imbricational enamel that striae of Retzius reach the outer enamel surface and form perikymata (Preiswerk, 1895; Pickerill, 1913; Risnes, 1985, 1998). LEH defects occur among perikymata grooves, which allows for the calculation of the approximate developmental timing of growth disruptions (Reid and Dean, 2000). This paper focuses on the most common type of LEH—furrow-form defects—rather than pit-form or plane-form defects (Berten, 1895), which can have more complex formation processes and are better understood via histological analysis (Witzel et al., 2008).

The majority of research on enamel defects in great apes has focused on canines due to their long periods of growth and ‘windows of vulnerability’ to stress (Vrijenhoek, 2004; Guatelli-Steinberg et al., 2012a). Compared to postcanine teeth, a greater proportion of canine crowns is made up of imbricational enamel, where defects are visible on the enamel surface (Hillson and Bond, 1997). Permanent canines start to mineralize shortly after birth in great apes, and they, along with the third molars, are the last teeth to complete formation (Dean and Wood, 1981; Beynon et al., 1991; Reid et al., 1998; Schwartz and Dean, 2001), fully emerging into the mouth by around 11 years of age in wild chimpanzees (Machanda et al., 2015). Early radiological studies did not report significant differences in the age at first mineralization, total period of crown formation, or age of gingival emergence among *Pan*, *Gorilla*, or *Pongo* (Dean and Wood, 1981). Schwartz and Dean (2001) provided the first study of the ontogeny of canine dimorphism in known-sex great ape samples. They found that within species, males achieve their tall canines primarily through extending the duration of crown formation compared to females. Differences between taxa can be explained by differences in both the duration and rates of enamel secretion (Schwartz et al., 2001), but it is not yet clear how enamel extension rates contribute to this variation. The current study provides the first histological data on canine development in Virunga mountain gorillas (*G. b. beringei*), a population that lives at an ecological extreme in terms of elevation, relies on an almost entirely folivorous diet, and demonstrates accelerated somatic growth, brain growth, and life history patterns compared to other great apes, including western lowland gorillas (Watts and Pusey, 1993; Taylor, 1997; Breuer et al., 2007; McFarlin et al., 2013; Stoinski et al., 2013; Galbany et al., 2017).

1.2. Enamel extension rates

Enamel extension rates (EER) refer to the rate at which ameloblasts differentiate down the EDJ (Shellis, 1984). Boyde (1964, 1989) first described the relationship between enamel extension rates and the angle of striae of Retzius in relation to the EDJ. Shellis (1984) developed a method for estimating enamel extension rates based on Boyde's (1964, 1989) model of enamel growth by calculating the distance over which ameloblasts differentiate each day. He established in modern humans that extension rates are highest at the cusp tip, fall to a relatively constant level in the midcrown, and then drop off even further at the cervix (Shellis, 1984). Like Boyde (1964, 1989) predicted, where the intersection of striae and the EDJ are more acute, a greater number of ameloblasts are differentiated throughout the course of the day, and thus extension rates are higher (Shellis, 1984).

Some studies have categorized the pace of hominoid dental development as being 'fast' or 'slow' (e.g., Martin, 1985). However, it is important to recognize that there is no sharp distinction; instead there is a continuum of secretion rates, which vary down the tooth crown and across the thickness of enamel (Beynon et al., 1991). Other studies have focused on assessing the relationship between crown formation times and enamel extension rates in modern humans and hominins (Dean, 2009; Guatelli-Steinberg et al., 2012b). They suggest that enamel extension rates and crown formation times can vary independently, emphasizing the need for detailed histologic studies of more hominoid taxa. Schwartz et al. (2001; see also Schwartz and Dean, 2001) found some differences in canine growth rates between species, but they emphasized that differences in crown formation time explain canine sexual dimorphism in great apes. The current study reports enamel extension rates in great ape canines, and assesses the relationship between enamel extension rates and LEH defect depths previously reported by McGrath et al. (2018).

1.3. Striae of Retzius angles

Recent work suggests that Virunga mountain gorillas have shallower LEH defects than other great apes (McGrath et al., 2018), which may have led to underestimation of LEH prevalence in previous studies (Hannibal and Guatelli-Steinberg, 2005; Guatelli-Steinberg et al., 2012a). Guatelli-Steinberg et al. (2012) hypothesized that mountain gorillas might have fewer defects compared to other great apes as a result of their 1) dedicated folivory and reduced seasonal food-related stress, and/or 2) shallower defect morphology, which might have caused defects to be overlooked using qualitative methods. They suggest that shallow defects might result from shallow striae of Retzius angles, or the angle at which long-period growth lines meet the outer enamel surface (OES; Fig. 1; Hillson and Bond, 1997; Guatelli-Steinberg et al., 2012a). Guatelli-Steinberg et al. (2012) provided the first data on outer enamel striae angles in great apes, reporting that defects are most likely to occur in crown regions with larger striae angles, which is generally in the midcrown. Guatelli-Steinberg et al. (2012a) found no significant differences in outer enamel striae angles among *G. gorilla*, *Pan*, and *Pongo*, corresponding with nonsignificant differences in defect depth among these taxa reported by McGrath et al. (2018). However, Guatelli-Steinberg et al. (2017) found that *G. gorilla* exhibits shallower angles at the EDJ (called enamel forming front angles, or EFF angles) than *Pan* or *Pongo*, suggesting that striae of Retzius angles at the EDJ may vary independently of striae angles at the OES in *G. gorilla*.

Other work has also focused on measuring the angle at which striae of Retzius extend from the EDJ (i.e., angle ‘D’ in Shellis, 1984; see also Shellis, 1998; Hogg and Walker, 2011; Guatelli-Steinberg et al., 2017). These studies tested whether striae angles at the EDJ correlate with body size (Shellis, 1998), encephalization quotient (Hogg and Walker, 2011), degree of

folivory, and periodicity (Guatelli-Steinberg et al., 2017). Boyde (1964, 1989) was the first to point out that extension rate is reflected by striae angles at the EDJ, with slow extension rates associated with larger striae angles, and rapid extension rates associated with shallower striae angles. However, this model does not capture the local variation in daily secretion and extension rates, which vary both down the crown and throughout the enamel thickness (Schwartz et al., 2001; Smith et al., 2006b). The relationship between striae angles at the EDJ and the outer enamel surface has not been tested, nor is this the focus of the current study. Rather, the current study measures angles at the outer enamel surface because they underlie LEH defects and are thus hypothesized to influence LEH defect morphology. Striae are known to diverge as they course through the thickness of imbricational enamel (Beynon et al., 1991), so it is unknown to what extent outer enamel striae angles reflect enamel extension rates at the EDJ, and whether other variables like enamel thickness, periodicity and/or daily secretion rates might also influence striae angles and thus defect depths at the OES.

1.4. Linear enamel thickness

Most enamel thickness research measures the area of enamel relative to tooth size in postcanine teeth to address questions about diet and phylogenetic relationships among extinct and extant primates (e.g., Martin, 1985; Shellis et al., 1998; Schwartz, 2000). Less research has focused on characterizing enamel thickness in anterior teeth, but it is an important variable to consider in this context because it places a constraint on the maximum potential depth of a surface defect (i.e., a defect cannot be deeper than the enamel thickness). It similarly shapes the gross morphology of the tooth crown (Beynon et al., 1991). Linear enamel thickness has been measured in the canines of a number of hominoid species, including western lowland gorillas,

chimpanzees, and orangutans (Schwartz et al., 2001). Schwartz et al. (2001) found that females have significantly thicker enamel, particularly in the more sexually dimorphic *Gorilla* and *Pongo*, which the authors attribute to faster daily enamel secretion rates near the enamel-dentine junction. Interspecifically, they found that canines mirror postcanine teeth with *Pan* having thinner enamel than *Gorilla*, and *Gorilla* having thinner enamel than *Pongo*. These differences may relate to variation in daily secretion rates toward the outer enamel surface, especially in the cusp (Schwartz et al., 2001), as well as differences in the duration of the secretory period of ameloblasts in *Pongo* compared to the other taxa (Beynon et al., 1991). Enamel thickness values have not been reported for mountain gorillas, but as dedicated folivores, they are expected to exhibit thin enamel, and the same sex differences reported for other sexually dimorphic great apes.

1.5. Specific objectives

We use histological methods to assess the relationship between inter- and intraspecific enamel growth variation and LEH defect morphology in four extant great ape taxa (*G. b. beringei*, *G. g. gorilla*, *P. troglodytes*, *Pongo* spp.). Our goals are to:

(1) Test whether groups previously shown to have shallow LEH defects (i.e., mountain gorillas compared to other taxa, and males compared to females among great apes) have canine crowns that grow faster in height compared to other groups. This is done by measuring enamel extension rates, or the rate at which enamel-secreting cells differentiate down the EDJ.

(2) Test whether shallower outer enamel striae angles occur in faster-growing crowns (i.e., those with faster enamel secretion rates), as striae angles below the OES are understood to reflect the geometric relationship between extension rates and defect depth.

(3) Test for differences in imbricational linear enamel thickness that might contribute to the documented variation in LEH defect depth. Enamel thickness provides a threshold for defect depth, and we therefore expect to find thicker imbricational enamel in females and in non-mountain gorilla taxa with deeper LEH defects.

(4) Assess the relationships among these variables and defect depth to determine which best corresponds with the documented differences in defect depth. Depths come from a previous study of the same taxa (McGrath et al., 2018) as paired histological and depth data are available only for the mountain gorillas in the current study.

2. Materials and methods

2.1. Sample

The sample includes histological thin sections of 40 permanent mandibular canines of known sex (Table 1; Supplementary Online Material [SOM] Table S1). The Virunga mountain gorilla (*G. b. beringei*) specimens are from the Mountain Gorilla Skeletal Project (MGSP) collection in Rwanda (McFarlin et al., 2009). Mountain gorilla canine thin sections were prepared in the Hard Tissue Biology Lab at The George Washington University using a Buehler Isomet 1000 Precision saw and Buehler Ecomet 4000 grinding and polishing machine. Canines were embedded in a methyl methacrylate resin and sectioned along the midline axial plane through the cusp tip and the entire buccal aspect of each crown, i.e., ideally capturing the first- to last-formed enamel. Sections were lapped to a final thickness of approximately 100 μm , as close as possible to the tip of the dentine horn and the pulpal horn. They were then polished using 1 μm diamond suspension liquid on polishing cloths, mounted to plastic slides and cover slipped for imaging. Western lowland gorilla (*G. g. gorilla*), chimpanzee (*P. troglodytes*), and orangutan

(*Pongo* spp.) specimens were sourced as prepared histological thin sections from the Newcastle Collection (NCL), The Royal College of Surgeons (RCS), and the Anthropological Institute and Museum at the University of Zürich (UZH).

2.2. Image collection and preparation

Digital photomontages were created on one of three microscope setups. Canines from the NCL collection were imaged using a Leica EZ4 microscope, digital camera, and LAS EZ software (1 pixel = 1.28 μm resolution; Leica Microsystems, Wetzlar, Germany). Specimens from the RCS and UZH were imaged using Motic BA310 microscope and Moticam2 digital camera/software (1 pixel = 1.26 μm resolution; Motic, Richmond, Canada). MGSP canines were imaged using Zeiss AxioImager microscope, Optronics MicroFire CCD camera, and StereoInvestigator software (1 pixel = 0.74 μm resolution; MBF Bioscience, Williston, VT, USA). In all cases, transmitted light was used to collect overlapping images along the labial side of canine crowns. With the first two setups, it was necessary to align adjacent image fields using Photoshop CC2015 software (Adobe, Inc., San Jose, CA, USA). Images were ‘photomerged’ using the reposition function without the blend option selected. Photo pairs that did not successfully automerge in the software were aligned by hand. As the Virtual Slice tool in StereoInvestigator automatically creates photomontages, the mountain gorilla specimens did not require further image alignment.

Full resolution photomontages were viewed and measured at 150–300% zoom in Adobe Photoshop CC2015. The best-preserved canines of those available were selected for this study. Some level of wear was unavoidable given the need to optimize sample size, but we were particularly careful to select the least worn specimens when calculating enamel extension rates,

thus further reducing the sample size for that analysis. Enamel extension rates were calculated down the entire EDJ, whereas linear enamel thickness and outer enamel striae angle measurements were collected at three equidistant locations within the midcrown (middle 3/5ths of crown height; described below). Thus, small deviations in the location of the dentine horn would have a relatively smaller effect on the latter analyses. Crown height reconstructions were performed for incomplete specimens following Saunders et al. (2007): where the outer enamel surface was worn or chipped, lines were extended until they met, and an arc was drawn to estimate the location of the cusp tip. This method has been demonstrated to reliably reconstruct cusp tips with different degrees of wear (<2% error; Saunders et al., 2007). Some studies suggest that this method is more subjective and produces higher error compared to more recently-developed polynomial regression-based methods to reconstruct worn cusps (Modesto-Mata et al., 2017), but for our purposes of estimating EDJ length and locating crown regions along the EDJ, the former method suffices.

Photomontages of canine crowns were aligned along a horizontal reference axis between the dentine horn, or estimated location of the dentine horn in cases of slight section obliquity or wear, and the cervix. The linear distance between the dentine horn and cervix along this horizontal reference axis was then divided into three equally-spaced regions of the labial enamel: 1) cuspal third, 2) midcrown, and 3) cervical third. Within each of these crown regions, linear enamel thickness and outer enamel striae angles were collected within 750 μm windows of crown height, situated to avoid major LEH defects and accentuated lines while constraining measurements to a relatively small area (Fig. 2). Enamel extension rates were measured in deciles along the EDJ to track changes in growth rates down the crown following the second method used by Guatelli-Steinberg et al. (2012b; see Fig. 4 and description below). Additional

images of daily cross striations were opportunistically collected at higher magnification (1 pixel = 0.32 μm resolution) to assess striae of Retzius periodicity.

2.3. Measurement protocol

Linear enamel thickness was calculated by dragging the measurement tool in Adobe Photoshop CC 2015 orthogonally from a tangent of the enamel-dentine junction to the outer enamel surface, defined as the edge of enamel (i.e., not including calculus or other obscurities; Fig. 1). This pathway roughly follows the secretory axes of ameloblasts, but we note that linear enamel thickness was not collected along the length of individual enamel prisms. Outer enamel striae of Retzius angles were measured using the angle tool. The first angle arm was aligned with the outer enamel surface, and then the second arm was aligned with the stria of Retzius being measured. The smaller of the two possible angles was measured. The second arm was dragged to align with the course of an individual stria 350 μm into the enamel thickness to make measurements more easily repeatable. We acknowledge that the full complexity of stria morphology is not captured by 2D measurements, but the data presented here are both comparable with the existing literature (e.g., Guatelli-Steinberg et al., 2012a) and standardized in way that makes the measurements replicable for future researchers. Our decision to measure stria angles 350 μm into the enamel thickness was made as to avoid the potential ‘tail’ end of the striae as they approach the outer enamel surface, thus capturing the angle that best represents the majority of the enamel thickness. This tail can occur especially where striae are ‘S-shaped’ (Shellis and Dean, 1998). Three measurements were collected in each crown location and averaged for analysis: for linear enamel thickness, these were spaced evenly throughout the 750 μm windows of crown height described above. For outer enamel striae angles, separate striae

were measured each time, avoiding accentuated lines when necessary. We used Adobe Photoshop CC2015 to collect these measurements, but NIH-developed freeware ImageJ (Schneider et al., 2012) is a suitable substitute.

Enamel extension rates, or the rate at which ameloblasts differentiate along the EDJ, were calculated for deciles of EDJ length (one value per decile). We first measured the curvilinear length of the EDJ from the dentine horn, or the first-formed enamel, to the last-formed enamel at the cervix. The EDJ was then divided into 10 segments or deciles, and markers were placed on closely-associated striae of Retzius marking the boundaries between the deciles (Fig. 2). In cases where decile divisions fell between successive striae of Retzius, the nearest stria was selected as the boundary. The number of striae were counted within each decile (including the first dividing stria) and multiplied by the periodicity of the individual to determine the number of days represented in that decile of the imbricational crown. Once the number of days of enamel growth was determined for each decile, we divided by the length of that segment of the EDJ, or 1/10 total EDJ length, to determine the daily rate of enamel extension (Guatelli-Steinberg et al., 2012b). This was done for a subsample ($n = 16$) of the best-preserved canine thin sections in the sample (Table 1; SOM Table S2). One male mountain gorilla specimen included in this analysis, GP.075, died just before or around the time of crown completion. While we suspect that it had actually completed the crown before death (SOM Fig. S1; SOM Table S3), a small amount of diagenesis affected particularly the enamel of the cervix. Therefore, dentine lines were used to estimate the time lost, which was minimal (Boyde, 1990).

Periodicities were independently determined by counting the number of cross striations visible between successive striae of Retzius in at least three crown locations for all specimens (SOM Table S2). In some specimens, it was difficult to assign a specific periodicity visually, so

an additional method was used: the length of daily cross striations were measured along a single prism, usually two or three at a time, at least ten times in total, to get an average daily secretion rate for that crown location. We then measured the spacing of associated striae of Retzius at least ten times, so that the mean striae of Retzius spacing could be divided by the mean cross striation spacing to estimate periodicity mathematically (SOM Table 2). Total crown formation times were calculated by adding the formation times of each decile together. Striae do not reach the outer enamel surface in the cuspal region, and due to decussation cross striations are often hard to visualize along an entire enamel prism, so this can hinder attempts to calculate cuspal formation time (Schwartz and Dean, 2001). Additionally, we lacked consistent high magnification images of the cusp in several *G. gorilla*, *Pongo*, and *Pan* specimens. Therefore, in specimens with unclear cross striations, or partially reconstructed cusp tips ($n = 8$), we measured the length of enamel prisms from the dentine horn to the outer enamel surface and divided by the average cuspal daily secretion rate for each species as reported in the literature for western lowland gorillas, chimpanzees, and orangutans (Schwartz et al., 2001). We were able to directly calculate cuspal daily secretion rates for each mountain gorilla thin section by 1) counting individual cross striations, and/or 2) measuring the length of individual cross striations throughout the inner, middle, and outer cuspal enamel and multiplying by the curvilinear length of an individual prism coursing from the dentine horn to the cusp tip. While calculating crown formation times was not a major goal of this research, we report the data as their calculation was necessary to determine enamel extension rates for the first decile(s), or before striae reach the outer enamel surface in the imbricational enamel.

Defect depths are derived from a larger sample of canine replicas of the same great ape taxa (McGrath et al., 2018; SOM Table S4). In that study, epoxy replicas were imaged using a

Sensofar PLu Neox white-light confocal profiler (Sensofar, Barcelona, Spain). Defects were visually identified, matched for presence on the antimere when available, and scanned to create high resolution digital elevation models of individual defects (see example in Fig. 3). ImageJ software (Schneider et al., 2012) was used to extract 2D transects of points in order to measure maximum defect depth ($n = 255$ defects).

Interobserver error was assessed by comparing the percentage difference in cuspal formation times and imbricational striae counts made independently by two coauthors ($n = 4$ specimens). The mean difference in cuspal formation times between the two observers is 3.1% (range = 1.1–6.2%). The mean difference in imbricational striae counts is 1.6% (range = 0.5–3.3%). Intraobserver error was assessed by comparing the linear enamel thickness and outer enamel striae angle measurements of the first author with repeated measurements collected one to two years apart ($n = 10$ specimens). The mean difference in linear enamel thickness measurements is 0.6% (range = 0.1–1.1%), with an absolute mean difference of 3.5 μm (range = 0.6–10.3 μm). The mean difference in striae angle measurements is 3.7% (range = 0.4–8.5%), with a mean absolute difference of 1.0° (range = 0.4–1.9°).

2.4. Statistical analyses

We used separate linear models to examine outer enamel striae angles and linear enamel thickness by species and sex at each of the three crown locations, with the interaction of species and sex as a fixed explanatory variable. The interaction between species and sex was not significant, so it was dropped from the final models. Separate models were run for each of the three crown regions (i.e., cuspal third, midcrown, cervical third). Assumptions of normality and homogeneity of variance were visually assessed using residual diagnostic plots; linear enamel

thickness and striae angles were normal, so no transformation was necessary. Although species designations were available for many (but not all) individuals in the *Pongo* spp. sample, the results did not differ whether they were grouped by species or genus, so we maintained the larger sample size of the latter. Differences between multiple levels of significant fixed effects were examined using Tukey's post hoc tests. Significance values were adjusted to compensate for multiple comparisons using the false discovery rate method (Benjamini and Hockberg, 1995).

No statistical tests were conducted to examine whether there are intra- or interspecific differences in enamel extension rates; the sample sizes were too small given that repeated measurements were collected for each individual in deciles of EDJ length. To assess the relationships between each of the three enamel growth variables (i.e., enamel extension rates, outer enamel striae of Retzius angles, and linear enamel thickness) and defect depth, we conducted a pairwise correlation analysis using the Pearson method. Data density differed among each of the variables: linear enamel thickness and striae angles were calculated for the full sample of thin sections in this study ($n = 40$), but enamel extension rates were only calculated for 16 individuals. Therefore, we used sex- and species-specific means of enamel extension rates in this analysis. We also included median defect depths reported in McGrath et al. (2018) for a larger sample of great ape canine replicas of mostly non-overlapping individuals (SOM Table S4). Three of the four mountain gorilla specimens included in this study were also included in McGrath et al. (2018; SOM Table S4), but it was not possible to examine defect depths for most histological specimens analyzed here because original teeth were not available for replication via dental impressions, and vice versa. As defect depths were measured within the middle 3/5ths of the crown in McGrath et al. (2018), we averaged the enamel extension rates within the middle six deciles to make the data most comparable. Only midcrown values for linear enamel thickness

and striae angles were included in this analysis for the same reason. These data were natural logged prior to analysis. All statistical analyses were performed in R v. 0.99.903 (R Core Team, 2016).

3. Results

Table 2 summarizes the canine growth variables assessed in this study. These include the curvilinear EDJ lengths, canine crown formation times, striae of Retzius periodicity, and the number of imbricational striae. Though no statistical tests were performed for this part of the analysis, several patterns are apparent. Male western lowland gorillas have the longest EDJ lengths, while male chimpanzees have the highest number of imbricational striae. Females of all species, especially mountain gorillas, chimpanzees, and orangutans, have similar EDJ lengths. However, chimpanzees have a higher number of imbricational striae compared to the other two taxa, overlapping in this trait with western lowland gorillas. Orangutan males have the longest crown formation times of 10–11 years, while female mountain gorillas have the shortest of under 4.5 years. Orangutans also show a higher periodicity than is currently reported for extant great apes: the two males analyzed here have a 12-day periodicity. Based on our measurements, one individual might even have a 13-day periodicity (SOM Table S2), but we use the more conservative 12-day periodicity here. To further evaluate the possibility of a 13-day periodicity, other thin sections from this individual should be analyzed as they might have cross striations that are easier to visualize.

Table 3 and Figure 3 show the mean and range of enamel extension rates in a subsample of especially well-preserved individuals included in this study ($n = 16$). While the sample sizes were too small to conduct statistical tests, the range of values among mountain gorillas and other

species of the same sex do not overlap in the midcrown, or the middle six deciles, where LEH defects are most commonly visible. Males have faster mean enamel extension rates overall compared to females in all taxa. However, mountain gorillas are the only species with no overlap between males and females in mean extension rates in the midcrown. Female mountain gorillas and chimpanzees have higher mean enamel extension rates in the cusp (first decile) compared to males of the same species. In contrast to the pattern that has been described for modern humans, with enamel extension rates slowing down toward the end of enamel secretion, extension rates in these taxa either remain stable or increase in the last deciles. Male mountain gorillas are the exception to this pattern, but it is possible that their last deciles do not reflect normal growth patterns as one individual died around the time of crown completion.

3.1. Sex and species differences in outer enamel striae angles

Species and sex are significant predictors of outer enamel striae angles in the cuspal region (species: $F_{3,36} = 8.13$, $p < 0.001$), the midcrown (species: $F_{3,36} = 8.39$, $p < 0.001$; sex: $F_{1,36} = 14.58$, $p < 0.001$), and the cervical region (species: $F_{3,36} = 10.10$, $p < 0.001$; sex: $F_{1,36} = 24.51$, $p < 0.001$), with the exception of the cusp, where sex does not significantly predict striae angles (sex: $F_{1,36} = 0.32$, $p = 0.56$). Results are described in Figure 4 and Tables 4 and 5. Mountain gorillas have significantly shallower outer enamel striae angles at the three crown locations than all other taxa examined. Western lowland gorillas and chimpanzees differ significantly in the midcrown, whereas chimpanzees and orangutans differ in the cervix. Western lowland gorillas have shallower angles than orangutans in the cervix and midcrown. Females in the combined sample have larger outer enamel striae angles at the cervix and midcrown, but not in the cusp. Figure 4 shows striae angles by species and sex in the midcrown region.

3.2. Sex and species differences in linear enamel thickness

Both species and sex are significant predictors of linear enamel thickness in the cuspal region (species: $F_{3,36} = 19.68$, $p < 0.001$; sex: $F_{1,36} = 6.49$, $p = 0.021$), the midcrown (species: $F_{3,36} = 21.94$, $p < 0.001$; sex: $F_{1,36} = 13.75$, $p < 0.001$), and the cervical region (species: $F_{3,36} = 12.87$, $p < 0.001$; sex: $F_{1,36} = 17.91$, $p < 0.001$). Inter- and intraspecific differences in linear enamel thickness are summarized in Figure 5 and Table 6. Mountain gorillas have significantly thinner enamel than western lowland gorillas, except in the cuspal region. Chimpanzees and mountain gorillas do not differ in linear enamel thickness, nor do chimpanzees differ from western lowland gorillas. Orangutans have significantly thicker enamel than all of the other taxa examined. In the combined taxon sample, females have significantly thicker enamel than males at all three crown locations. Figure 5 shows linear enamel thickness broken down by species and sex at the midcrown region.

Table 4 provides a summary of the linear enamel thickness and outer enamel striae angle measurements, including the range and mean values for the three crown regions evaluated. Female orangutans have the thickest enamel, falling outside the range of all other species, while mountain gorilla males have the thinnest enamel. In most species, enamel thickness decreases from the cusp to the cervix. Female orangutans also have the largest striae angles, while male mountain gorillas have the most acute striae angles. In most species, outer enamel striae angles are the largest in the midcrown, except mountain gorillas, which show larger angles in the cusp.

3.3. Relationships among enamel growth variables and defect depth

The three enamel growth variables (i.e., enamel extension rates, outer enamel striae angles, and linear enamel thickness) are correlated with each other. Coefficients of determination and significance levels are reported in Table 7. There are also significant correlations among all pairs of enamel growth variables and species/sex median defect depths established in a prior study, with a strong negative correlation between defect depth and enamel extension rate. This indicates that higher extension rates are related to shallower defect depths on the outer enamel surface, as in mountain gorillas compared to other species, or males compared to females. Though the effect size is not as large, both outer enamel striae angles and linear enamel thickness are positively correlated with defect depth, meaning larger angles and thicker enamel are related to deeper defects on the outer enamel surface. However, it is also the case that a sizeable proportion of the variation in defect depth is not explained by these variables as demonstrated by the R^2 values in Table 7. For example, only 66% of the variation in defect depth is explained by enamel extension rates despite the strong negative correlation between these variables.

4. Discussion

The purpose of this study is to assess the extent to which species- and sex-related variation in canine enamel growth influences LEH defect morphology at the outer enamel surface among extant great apes. Mountain gorillas were previously characterized as having fewer defects than other great apes (e.g., Guatelli-Steinberg et al., 2012a). However, recent work demonstrates that mountain gorillas have significantly shallower defects than other taxa, which might have led to their underestimation in past studies (McGrath et al., 2018). Mountain gorilla canine enamel growth patterns have not been described previously, and this study demonstrates that they have thinner linear enamel, faster enamel extension rates, and shallower outer enamel

striae angles compared to other great apes, which may explain their shallow LEH defects on the outer enamel surface. Our results suggest that outer enamel striae angles broadly reflect enamel extension rates at the EDJ, building upon the work of Boyde (1964, 1989) and Shellis (1984), which demonstrated the relationship between extension rates and striae angles at the EDJ. However, it is important to note that localized variation in enamel secretion and extension rates influence striae angles throughout the enamel thickness, and that striae angles should not be used to reconstruct extension rates alone (Smith et al., 2006b). Future work should assess the relationships among these variables at a finer scale, including the localized changes in extension and secretion rates around individual defects. The pattern of faster extension rates, shallower outer enamel striae angles, and thinner enamel in mountain gorillas compared to other great apes is also observed between males and females in this sample, perhaps reflecting broader relationships between defect depth and these enamel growth variables.

4.1. Species differences in canine growth

Despite having used a different method to measure linear enamel thickness, our results fit well with what Schwartz et al. (2001) reported for great apes: *Pongo* spp. has the thickest enamel, followed by *G. gorilla*, and *P. troglodytes*. In the combined sex sample, mountain gorillas do not have thinner enamel than chimpanzees, but it is clear from the plots that male mountain gorillas in particular stand out as having the thinnest enamel in the sample (Fig. 5). Mountain gorillas have significantly thinner enamel than western lowland gorillas, except in the cuspal enamel. This might relate to differences in daily secretion rates (Schwartz et al., 2001), and/or differences in the secretory lifespan of ameloblasts in those areas (Beynon et al., 1991). Western lowland gorillas have longer total crown formation times than mountain gorillas (Table

2). They also have slower enamel extension rates than mountain gorillas in the midcrown, where defects are most likely to be macroscopically visible. Our data suggest that mountain gorillas maintain a high enamel extension rate from the cuspal to cervical regions, rather than exhibiting a slowing of extension rate throughout the lateral and cervical regions like the other taxa. Overall, great ape canines do not follow the modern human pattern reported by Shellis (1984), characterized by high initial extension rates followed by a steady, intermediate rate before dropping off at the cervix. Instead, individuals in our sample often show an increase in extension rate towards the end of canine crown development (Fig. 3).

Our results underscore earlier observations that striae angles change down the crown (Shellis, 1984; Smith et al., 2006b; Witzel et al., 2006; Guatelli-Steinberg et al., 2012a). In the majority of our sample, outer enamel striae angles are shallowest toward the cervix, largest in the midcrown, and shallow again toward the cusp. Male gorillas of both species are the only exception to this pattern. Great ape outer enamel striae angles vary in ways that are consistent with previously reported LEH defect depths, with mountain gorillas having the shallowest angles and the shallowest defects in the sample (McGrath et al., 2018). Outer enamel striae angles also reflect enamel extension rates at the EDJ: faster extension rates correspond to more acute striae angles at the outer enamel surface in mountain gorillas, while slower rates correspond to more obtuse angles in the other taxa (Fig. 4). Western lowland gorillas, *Pongo*, and *Pan* have similarly slow extension rates, but *Pongo* has thicker enamel, and more obtuse striae angles (Figs. 3 and 4). These results suggest that there is a close relationship between outer enamel striae angles and extension rates, but other factors like daily secretion rates might also affect striae angles where there are significant differences in the sample (Smith et al., 2006b). The results presented here suggest that outer enamel striae angles might be able to be used as a rough proxy for local

enamel extension rates in cases where the latter cannot be readily quantified (e.g., due to time constraints, sample preservation, poor image/magnification resolution). However, particularly when interested in fine scale changes throughout the crown, it is important to take daily secretion rates into consideration as striae angles, even at the EDJ, do not capture extension rates reliably enough to reconstruct crown formation times (Smith et al., 2006b).

We were not able to statistically test for differences in enamel extension rates due to limitations in sample size, but the correlation between enamel extension rates and defect depth is the highest of all pairwise comparisons (Table 7). Western lowland gorillas, chimpanzees, and orangutans do not appear to differ in enamel extension rates, especially in the middle six deciles of crown height. McGrath et al. (2018) measured defect depth in the middle 3/5ths of canine crowns of a larger sample of (mostly) non-overlapping individuals in these same taxa and found no significant differences. Mountain gorillas, however, exhibited significantly shallower defects, mirrored by their higher extension rates found in the current study. If the relationship between surface defect depth and extension rates holds true among a broader comparative sample (e.g., *Paranthropus* vs. *Australopithecus*; Guatelli-Steinberg, 2004, 2008), median defect depths at the population-level might be used as a proxy to infer important growth information about fossil taxa, i.e., approximate growth rates that can only currently be gleaned through histological analyses.

4.2. Sex differences in canine growth

Canine dimorphism is linked to several behavioral and ecological factors, including sexual selection, body size dimorphism, phylogeny, predation pressure, and more (reviewed in Plavcan and van Schaik, 1993). Mountain gorillas have a higher degree of body size dimorphism

551 compared to western lowland gorillas (Taylor, 1997), but according to our EDJ lengths and
552 canine crown heights (SOM Table S3), male western lowland gorillas have larger canines than
553 male mountain gorillas. However, it is not yet clear to what extent dental development follows
554 the trajectory of somatic growth. Comparative ontogenetic data on body size dimorphism suggest
555 that different mechanisms underlie comparable levels of adult dimorphism in great apes (Leigh
556 and Shea, 1995). While males of some taxa might acquire a larger size through extending the
557 duration of growth, others accomplish the same through increasing the rate (for similar findings
558 in dental development, see Smith, 2016; Schwartz and Dean, 2001). Our data support this
559 hypothesis in that similar-looking canines can grow differently (Guatelli-Steinberg et al., 2009),
560 even among closely related taxa. Male western lowland gorillas have slower extension rates than
561 male mountain gorillas, but they have taller canines (SOM Table S3), which western lowlands
562 accomplish by growing their crowns for a longer duration. This fits well with recent data from
563 living mountain gorillas suggests that they reach maximum body size at earlier ages compared to
564 western lowland gorillas (Galbany et al., 2017). In terms of reproductive and social systems,
565 research suggests that species living in single-male groups should have higher levels of
566 dimorphism compared to those living in multi-male groups (Harvey, 1978). Our data support this
567 idea given that western lowland gorilla groups are almost exclusively single-male, while
568 mountain gorillas live in multimale groups about 40% of the time (Robbins and Robbins, 2018).

569 Extension rates are calculated by multiplying periodicity by the number of striae of
570 Retzius in each decile, information which at this time can only be readily gleaned from
571 histological investigation or by using synchrotron computed microtomography. This study
572 suggests that the range of periodicity for extant great apes is broader than previously reported by
573 Schwartz and Dean (2001) and Smith (2016), with *Pongo* males exhibiting periodicities of 12,

and possibly even 13 (SOM Table S2). However, fossil *Pongo* specimens have already been reported to exhibit periodicities of 12 (Smith, 2016). *Pongo* enamel extension rates are similar to those of western lowland gorillas and chimpanzees, but *Pongo* males have comparatively prolonged crown formation times, more than one year beyond what has been previously reported for any extant ape (11.0 in this study vs. 9.6 years in Schwartz and Dean, 2001). The lifespan of individual ameloblasts is also expected to be longer in *Pongo* compared to other taxa as evidenced by their relatively thick enamel (Beynon et al., 1991). It is not particularly surprising that *Pongo* males exhibit extended canine crown development given that they have the slowest life histories of the great apes, including the longest interbirth intervals and a prolonged period of dependency as marked by the latest weaning ages of any mammal (Knott, 1998, 2001; Smith et al., 2017; van Noordwijk et al., 2018). However, it is worth noting that female orangutans do not exhibit a similarly prolonged period of canine crown formation compared to other taxa. Female canine growth patterns are hypothesized to provide a ‘template’ for species canine morphology, and thus better reflect the life history of the species, due to the fact that male canine growth is influenced by sexual selection (Zingesser and Phoenix, 1978; Leigh et al., 2008; Guatelli-Steinberg et al., 2009). The longer the period of canine formation, the longer the ‘window of vulnerability’ to stress, and potential for defect formation (Vrijenhoek, 2004; Guatelli-Steinberg et al., 2012a).

Females have thicker enamel in the combined sex sample with little overlap between males and females except in *Pan*, the least sexually dimorphic taxon in this study (Fig. 5). Female mountain gorilla linear enamel thickness measurements fall within the range of both sexes of western lowland and chimpanzee values, well above the range for male mountain gorillas. In order to create a canine of a similar crown height and intermediately-thick enamel

compared to the other taxa, female mountain gorillas have accelerated enamel extension rates in their imbricational enamel. They also exhibit shallower outer enamel striae angles throughout the crown compared to females of other species. Females have thicker enamel than males, which is more resistant to wear, and might allow for longer use by females that have longer lifespans than males in many primate species (Smith et al., 2006a; Clutton-Brock and Isvaran, 2007; Bronikowski et al., 2011; Pampush et al., 2013; Austad and Fischer, 2016).

Schwartz and Dean (2001) attributed the intraspecific difference in crown height primarily to differences in the duration canine crown formation between males and females. They found that *G. gorilla* and *Pongo* males grow their canines for 3–4 years longer than females of the same taxon, while *Pan* males only grow their canines for about one year longer than females, mirroring documented differences in canine crown height. Our results suggest that enamel extension rates also play an important role in determining canine height in great apes: female western lowland and mountain gorillas have similar crown heights, but different crown formation times and extension rates (Tables 2 and 3). Male great apes have higher mean extension rates than females overall, but not in every decile, and there is considerable overlap except in mountain gorillas (Table 3). Larger sample sizes would allow statistical testing of the hypothesis that higher extension rates in males contributes to canine dimorphism in great apes, in addition to the documented difference in the duration of canine crown growth (Schwartz and Dean, 2001).

4.3. Inter-individual variation in canine growth patterns

Individuals of the same sex-class with lower periodicities have higher imbricational striae of Retzius counts than conspecific individuals with higher periodicities, ultimately producing

crowns of similar height in roughly the same amount of time (as was described by Reid and Ferrell, 2006). This pattern holds true for all sex-classes that demonstrate variation in periodicity in this sample except western lowland gorilla females; they showed the largest amount of variation in crown formation times, and the female with a higher periodicity grew her canine for a longer duration. In *Pongo*, one female has a periodicity of 10 and 194 imbricational striae, while another has a periodicity of nine and 217 imbricational striae, yet they formed their canine crowns in 6.1 and 6.2 years, respectively. The latter individual has a longer EDJ length, our proxy for canine crown height, of 15.5 mm vs. 14.2 in the other individual (Table 2). This same pattern is evident in *Pan* males, where one individual has a periodicity of six, an imbricational striae count of 398, and a canine crown formation time of 7.2 years, while a male with a periodicity of eight has only 304 imbricational striae, but formed its canine in 7.1 years. Again, the individual with a longer crown formation time has a longer EDJ length at 22.5 vs. 19.1 mm in the other individual. Larger sample sizes will allow for statistical testing of this relationship, and potentially offer insight into the evolution of these traits over time.

4.4. Enamel growth variation and defect depth

Enamel extension rates have a strong negative correlation with previously-reported LEH defect depths (Table 7). This holds true despite the fact that enamel extension rates are measured at the EDJ, while defects are measured at the outer enamel surface in a mostly non-overlapping sample of the same taxa. As described by Boyde (1964, 1989), variation in extension rates has a profound effect on the geometry of the crown. However, 34% of the variation in defect depth was not explained by enamel extension rates based on this model. Outer enamel striae angles are moderately correlated with enamel extension rates and defect depth, but again, a sizeable

proportion of the variation in defect depth is unexplained by this variable alone. Daily secretion rates, which vary within and down the crown, are also known to influence striae angle morphology and might explain some of the variation not captured in the model (Smith et al., 2006b). Linear enamel thickness is positively correlated with defect depth, but not as strongly as the other two variables. Enamel thickness sets a threshold for defect depth, but it is influenced by factors other than enamel extension rate, such as daily secretion rate (Beynon et al., 1991). The extent to which defect depth is explained by all three variables together is not yet clear; larger sample sizes of measurements derived from the same individuals will allow further testing of these relationships in the future.

5. Conclusions

We suggest that sex- and species-specific enamel growth patterns are reflected in the morphology of the outer enamel surface, namely the depth of LEH defects. The final shape of the crown is heavily influenced by ameloblast secretory activity (Beynon et al., 1991; Witzel et al., 2006, 2008), and this variation should be taken into consideration when interpreting outer enamel surface morphology. The three variables investigated here, enamel extension rates, outer enamel striae angles, and linear enamel thickness, were all shown to shape LEH defect morphology at the population level. However, a fair amount of the variation in LEH defect depth remains unexplained by these factors. Stress severity warrants continued study as a possible explanatory factor for variation in defect depth (e.g., wild-captured apes have deeper defects than wild individuals; McGrath et al., 2018), as do other enamel growth variables not included in this study.

Regarding the influence of enamel growth on LEH morphology, enamel extension rates best predict the sex and species-specific patterns in defect depth, followed closely by outer enamel striae angles, which are likely to reflect the same biological mechanism (Boyde, 1964, 1989). While we find sex differences in enamel extension rates, thicker linear enamel might also contribute to the deeper surface defects in females compared to males in great apes. If these relationships hold true among a larger and more diverse sample, important information about enamel growth variation could be gleaned on the basis of median defect depths using nondestructive imaging methods alone. Future work aims to incorporate a more diverse sample of extant great apes, including the more frugivorous Bwindi mountain gorillas and grauer gorillas, with the goal of assessing the variation of these traits among closely related, yet differently-adapted, taxa with associated life history, climate, and health records. An implication of this work is that stressors of a similar magnitude and duration might produce defects of different depths in different species or sexes due to variation in enamel growth patterns. Given the documented differences in enamel growth among modern humans and extinct hominins, the relationships among these variables should be considered when interpreting the stress experiences of fossil or archaeological samples that cannot be sectioned.

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Figure captions

Figure 1. Relationships among enamel growth variables and linear enamel hypoplasia defect depth, shown with photomontages of male mountain gorilla (GP033, left overview and middle close-up) and female western lowland gorilla (A64.41; right close-up) mandibular canine thin sections. Mountain gorillas have shallow LEH defects (McGrath et al., 2018), and exhibit the traits shown on the left compared to more frugivorous apes as represented on the right. In the combined taxon sample, females have deeper LEH defects, as well as thicker enamel, larger striae angles (SA), and slower extension rates (EER).

Figure 2. Female western lowland gorilla (RCS G67.17) canine thin section photomontage. The labial enamel is shown with the cusp toward the right of the image. To calculate enamel extension rates (EER), the enamel-dentine junction (EDJ) was divided into ten segments of equal length. Striae of Retzius were then traced from the EDJ to the outer enamel surface to create the deciles (labeled d1-d10). Stria angle and linear enamel thickness measurements were collected within 750 μm windows at three equidistant crown locations (cervical third, midcrown, cuspal third) located along a horizontal reference axis between the dentine horn and cervix. In the lower

image, the fifth decile is shown. Striae of Retzius are labeled with dots both internally and at the surface so that an average extension rate value can be calculated for this decile (total number of striae within the decile x periodicity / EDJ length of that decile = EER).

Figure 3. Female (top) and male (bottom) canine enamel extension rates by decile of EDJ length (decile 1 = cusp tip; decile 10 = cervix; $n = 16$). Right: Linear enamel hypoplasia defect depths in the same taxa (sexes combined), measured on digital elevation models of defects imaged using confocal profilometry (adapted from McGrath et al., 2018: Fig. 6, $n = 255$ defects). In the middle 3/5ths of crown height, where defects were measured (deciles 3–8), there is an inverse relationship between enamel extension rates and defect depth.

Figure 4. Striae angles measured below the outer enamel surface (OES) of the midcrown region by species and sex. Using a linear model, *G. b. beringei* ($n = 4$) has significantly shallower striae angles ($*p < 0.05$; $**p < 0.01$; $***p < 0.001$) than *G. g. gorilla* ($n = 17$), *P. troglodytes* ($n = 9$), and *Pongo* spp. ($n = 10$). *G. g. gorilla* has shallower angles than *P. troglodytes* and *Pongo* spp. There are no differences between *P. troglodytes* and *Pongo* spp. Females have significantly larger striae angles than males in the pooled sample ($p < 0.001$).

Figure 5. Linear enamel thickness in the midcrown region by species and sex. Using a linear model, we found significant differences ($**p < 0.01$; $***p < 0.001$) between *G. b. beringei* ($n = 4$) and *G. g. gorilla* ($n = 17$), and between *Pongo* spp. ($n = 10$) and all three other taxa, including *P. troglodytes* ($n = 9$). There is no difference between *G. b. beringei* and *P. troglodytes*, nor

939 between *G. g. gorilla* and *P. troglodytes*. Females have significantly thicker enamel in the pooled
940 sample ($p < 0.001$).

941

A: *G. b. beringei*
 B: *G. g. gorilla*
 C: *P. troglodytes*
 D: *Pongo spp.*

Outer enamel stria angle (°)

40

30

20

F

M

F

M

F

M

F

M

G.b. beringei

G. g. gorilla

P. troglodytes

Pongo spp.

Table 1

Composition of permanent mandibular canine histological thin section sample.

Taxon	Sex	Source	<i>n</i> (EER)	<i>n</i> (LET, SRA)
<i>Gorilla beringei</i>	F	MGSP	2	2
<i>beringei</i>	M		2	2
<i>Gorilla gorilla</i>	F	NCL, RCS, UZH	2	12
<i>gorilla</i>	M		2	5
<i>Pan troglodytes</i>	F	NCL, RCS, UZH	2	4
	M		2	5
<i>Pongo</i> spp.	F	NCL, RCS, UZH	2	5
	M		2	5
Total	F		8	23
	M		8	17

Abbreviations: F = female; M = male; LET = linear enamel thickness analysis; SRA = striae of Retzius angles analysis; EER = enamel extension rates analysis; MSGP = Mountain Gorilla Skeletal Project, Musanze, Rwanda; NCL = Newcastle Collection, The George Washington University, Washington D.C.; RCS = The Royal College of Surgeons, London, UK; UZH = Anthropological Institute and Museum, University of Zürich, Switzerland.

Table 2Summary of canine growth variables.^a

Species	Sex	<i>n</i>	EDJ Length (range in mm)	CFT (range in years)	Periodicity (days)	Number of imbricational striae
<i>G. b.</i>	F	2	14.6–15.7	4.26–4.38	7–8	181–200
<i>beringei</i>	M	2	23.4*–26.2	4.78*–6.16	6–7	269*–301
<i>G. g.</i>	F	2	16.0–18.2	5.90–6.47	8–9	246–251
<i>gorilla</i>	M	2	28.5–31.8	8.52*–9.88	10	311–339
<i>P.</i>	F	2	15.3–15.6	6.09–6.19*	8	241–277
<i>troglodytes</i>	M	2	19.1–22.5	7.10–7.23	6–8	304–398
<i>Pongo</i> spp.	F	2	14.2–15.5	6.08–6.19	9–10	194–217
	M	2	27.7–29.0	10.08–11.02	12	290–317

^a N.B. GP.075 male mountain gorilla died around the time of canine crown completion, and two other specimens have partially worn cusps, so estimates marked with an asterisk (*) may be underrepresentative of the final form.

Table 3

Mean and range enamel extension rates (μm per day) by decile (cusp [1] to cervix [10]).^a

Species	Sex	D1	D2	D3	D4	D5	D6	D7	D8	D9	D10	AV
<i>G. b. beringei</i>	F	18.0	17.1	11.3	10.1	10.2	9.0	6.9	8.3	8.1	7.7	10.7
		(15.6–20.4)	(13.2–20.9)	(11.0–11.6)	(8.6–11.6)	(10.0–10.4)	(8.0–9.9)	(6.5–7.3)	(8.0–8.6)	(8.0–8.2)	(7.0–8.4)	
	M	15.0	13.4	12.6	12.8	12.8	12.7	12.4	12.6	11.8	10.8	12.7
		(14.8–15.1)	(12.9–13.9)	(12.2–12.9)	(11.7–13.9)	(12.1–13.4)	(11.0–14.4)	(11.3–13.4)	(11.7–13.4)	(11.7–11.8)	(8.5–13.0)	
<i>G. g. gorilla</i>	F	15.2	10.4	7.2	8.0	6.6	6.1	6.1	6.9	7.6	8.3	8.2
		(14.7–15.7)	(7.9–14.0)	(7.1–7.2)	(7.4–8.4)	(5.6–7.5)	(5.7–6.5)	(6.1)	(6.3–7.4)	(6.1–9.1)	(7.5–9.1)	
	M	16.7	7.6	6.6	7.8	8.1	9.0	9.3	8.8	9.5	11.0	9.4
		(16.7)	(6.6–8.6)	(6.2–6.9)	(7.4–8.1)	(6.9–9.2)	(8.2–9.8)	(8.9–9.6)	(8.1–9.4)	(7.3–11.8)	(9.2–12.7)	
<i>P. troglodytes</i>	F	14.0	9.6	5.4	5.9	5.4	5.8	5.9	6.1	8.3	8.3	7.5
		(14.0)	(7.4–11.8)	(4.2–6.6)	(5.6–6.2)	(5.3–5.5)	(5.6–5.9)	(5.8–5.9)	(5.6–6.5)	(7.5–9.1)	(7.5–9.1)	
	M	10.8	9.7	6.3	6.4	6.9	7.3	7.9	8.3	10.1	11.9	8.6
		(9.5–12.0)	(6.8–12.6)	(5.6–7.0)	(5.4–7.4)	(6.6–7.1)	(7.1–7.5)	(6.5–9.4)	(6.1–10.4)	(7.7–12.5)	(10.4–13.4)	
<i>Pongo</i> spp.	F	12.4	9.7	7.2	5.5	6.1	6.0	5.7	6.7	5.9	6.2	7.1
		(11.6–13.2)	(6.9–12.4)	(7.2)	(5.2–5.7)	(5.2–6.9)	(5.7–6.4)	(5.2–6.2)	(5.7–7.8)	(5.5–6.4)	(6.2)	
	M	15.5	8.3	6.2	6.9	7.2	7.4	7.0	6.1	6.9	8.4	8.0
		(12.7–18.2)	(7.2–9.3)	(6.1–6.4)	(6.4–7.3)	(6.6–7.8)	(6.3–8.6)	(5.4–8.6)	(5.1–7.1)	(6.7–7.0)	(7.5–9.3)	

^a Mean and range of enamel extension rates ($\mu\text{m}/\text{day}$) by decile of EDJ length, a proxy for crown height. The final AV column lists mean values across the crown.

Table 4

Summary of linear enamel thickness (LET) and OES striae angle (SA) measurements, including mean values and ranges in parentheses.

Species	Sex	<i>n</i>	LET cervix (μm)	LET midcrown (μm)	LET cusp (μm)	SA cervix ($^{\circ}$)	SA midcrown ($^{\circ}$)	SA cusp ($^{\circ}$)
<i>G. b.</i>	F	2	500	565	679	21.0	24.0	20.2
<i>beringei</i>			(485–514)	(562–568)	(673–685)	(20.5–21.5)	(23.1–24.9)	(18.4–22.1)
	M	2	368	423	491	15.4	18.5	21.1
			(320–415)	(387–460)	(460–522)	(15.3–15.4)	(17.7–19.3)	(18.9–23.3)
<i>G. g.</i>	F	12	573	645	669	27.5	32.9	27.8
<i>gorilla</i>			(474–652)	(565–785)	(557–839)	(19.3–33.1)	(25.8–38.6)	(24.2–34.4)
	M	5	460	551	593	20.1	23.3	29.6
			(323–541)	(481–591)	(530–650)	(15.1–27.0)	(19.5–28.1)	(25.3–33.3)
<i>P.</i>	F	4	492	564	671	29.5	35.8	32.5
<i>troglodytes</i>			(419–568)	(521–608)	(596–803)	(24.9–31.9)	(34.1–38.4)	(27.5–37.7)
	M	5	499	524	599	23.7	33.2	32.5
			(441–531)	(433–607)	(555–640)	(18.8–28.3)	(25.7–45.7)	(24.2–44.0)
<i>Pongo</i> spp.	F	5	660	817	996	38.8	38.1	31.5
			(640–705)	(687–926)	(651–1258)	(30.2–49.6)	(30.5–45.5)	(26.1–38.9)
	M	5	578	718	897	27.9	32.9	32.5

(513–619)	(597–812)	(744–1089)	(18.4–39.0)	(25.8–44.7)	(28.3–36.4)
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Table 5

Summary of ANOVA results for OES striae angles by species and sex.^a

Group comparison	Cervical third	Midcrown	Cuspal third
<i>G. b. beringei</i> vs. <i>G. g. gorilla</i>	$p = \mathbf{0.044}$	$p = \mathbf{0.019}$	$p = \mathbf{0.005}$
<i>G. b. beringei</i> vs. <i>P. troglodytes</i>	$p = \mathbf{0.011}$	$p < \mathbf{0.001}$	$p < \mathbf{0.001}$
<i>G. b. beringei</i> vs. <i>Pongo</i> spp.	$p < \mathbf{0.001}$	$p < \mathbf{0.001}$	$p < \mathbf{0.001}$
<i>G. g. gorilla</i> vs. <i>P. troglodytes</i>	$p = 0.248$	$p = \mathbf{0.010}$	$p = 0.075$
<i>G. g. gorilla</i> vs. <i>Pongo</i> spp.	$p < \mathbf{0.001}$	$p = \mathbf{0.004}$	$p = 0.083$
<i>P. troglodytes</i> vs. <i>Pongo</i> spp.	$p = \mathbf{0.011}$	$p = 0.739$	$p = 0.883$
Females vs. males	$p < \mathbf{0.001}$	$p < \mathbf{0.001}$	$p = 0.561$

Abbreviations: OES = outer enamel surface.

^a Sample sizes are listed in Table 1. Interspecific comparisons are based on Tukey's post hoc tests with a significance threshold of $p < 0.05$ (in boldface). Significance levels were adjusted using the false discovery rate method to account for multiple comparisons.

Table 6

Summary of ANOVA results for linear enamel thickness by species and sex.^a

Group comparison	Cervical third	Midcrown	Cuspal third
<i>G. b. beringei</i> vs. <i>G. g. gorilla</i>	$p = 0.011$	$p = 0.013$	$p = 0.517$
<i>G. b. beringei</i> vs. <i>P. troglodytes</i>	$p = 0.079$	$p = 0.223$	$p = 0.516$
<i>G. b. beringei</i> vs. <i>Pongo</i> spp.	$p < 0.001$	$p < 0.001$	$p < 0.001$
<i>G. g. gorilla</i> vs. <i>P. troglodytes</i>	$p = 0.299$	$p = 0.079$	$p = 0.943$
<i>G. g. gorilla</i> vs. <i>Pongo</i> spp.	$p < 0.001$	$p < 0.001$	$p < 0.001$
<i>P. troglodytes</i> vs. <i>Pongo</i> spp.	$p < 0.001$	$p < 0.001$	$p < 0.001$
Females vs. males	$p < 0.001$	$p < 0.001$	$p = 0.021$

^a Sample sizes are listed in Table 1. Interspecific comparisons are based on Tukey's post hoc tests with a significance threshold of $p < 0.05$ (in boldface). Significance levels were adjusted using false discovery rate method to account for multiple comparisons.

Table 7

Pairwise correlation analysis of enamel growth variables and defect depth.

Variables	R²	<i>p</i>
LET - SA	0.20	$p = 0.004$
LET - EER	0.30	$p < 0.001$
SA - EER	0.57	$p < 0.001$
LET - Depth	0.29	$p < 0.001$
SA - Depth	0.42	$p < 0.001$
EER - Depth	0.66	$p < 0.001$

Abbreviations: LET = linear enamel thickness; SA = striae of Retzius angles (measured below OES); EER = enamel extension rates.