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# Odontochronologies in male and female mandrills (*Mandrillus sphinx*) and the development of dental sexual dimorphism

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## Abstract

**Objectives:** We examine how dental sexual dimorphism develops in mandrills, an extremely sexually dimorphic primate. We aimed to (a) establish the chronology of dental development (odontochronology) in male and female mandrills, (b) understand interindividual and intersex variation in odontochronologies, and (c) determine how dental sexual dimorphism is achieved.

**Materials and Methods:** We prepared histological ground sections from the permanent teeth of four female and four male mandrills from the semi-free ranging colony at the Centre International de Recherches Médicales, Franceville, Gabon. We used the microscopic growth increments in the sections to create odontochronologies. We compared ages at crown initiation, crown formation times (CFT) and crown extension rates (CER) between individuals and sexes to assess interindividual and intersex variation.

**Results:** All mandrill teeth are sexually dimorphic in size. Dental sexual dimorphism in mandrills is achieved via sex differences in the duration of growth (bimaturism) and in growth rates. We also found interindividual and intersex variation in the ages at initiation and completion of crown formation.

**Discussion:** Our results show that the rate of ameloblast differentiation varies between individuals and that selection for both the age at tooth initiation and CER has occurred independently in males and females to ensure that the teeth develop at appropriate times relative to the growth of the sexually dimorphic jaws. They also show that canine dimorphism is achieved through differences in both CER and CFT, unlike extant great apes or *Cantius*. Given at least three mechanisms for achieving canine dimorphism, we need more information to trace the evolution of this trait in primates.

**KEYWORDS**

bimaturism, dental histology, extension rate, odontochronology, sexual dimorphism

## 1 | INTRODUCTION

Animals have finite resources to allocate to growth, maintenance and reproduction. Life history theory suggests that natural selection shapes the allocation of these resources to maximize fitness (Stearns, 1992). Selection pressures differ between the sexes, due to sexual selection. For example, developing sexually dimorphic characteristics is costly for the sex that does so—often the male among primates—and an understanding of how such characteristics develop can help us to understand the function and evolution of sexual dimorphism (Leigh, 1992, 1995; Pereira & Leigh, 2003; Setchell & Lee, 2004; Watts, 1985). Adult sexual dimorphism can arise through sex differences in the duration of growth (sexual bimaturism), sex differences in growth rates, or a combination of the two (Gavan & Swindler, 1966; Leigh, 1992; Shea, 1986). In this study, we examine how sexual dimorphism develops in teeth in an extremely sexually dimorphic primate, the mandrill (*Mandrillus sphinx)*, using dental histology to reconstruct dental development.

### 1.1 | Reconstructing dental development

The term odontochronology (Hogg, Hu, & Bromage, 2018; Hupková, Šáliová, Králík, & Malček, 2016) refers to the reconstruction of dental development in skeletal material using the incremental growth lines in histological ground sections of teeth, or, more recently, using synchrotron virtual histology (Smith & Tafforeau, 2008; Tafforeau & Smith, 2008). During tooth formation, the cells forming the enamel, the ameloblasts, and the cells forming dentine, the odontoblasts, leave a record of their temporal activity that is visible microscopically. We can use lines reflecting sub-daily, daily, and longer period biorhythms to reconstruct the duration of enamel and dentine formation, and determine the relative development of one tooth to another, or the overlap in their formation, using an irregular pattern of hypomineralized lines that form during periods of stress (Dean, 1987, 2000; Smith & Tafforeau, 2008). Odontochronologies permit the reconstruction of dental development in material for which no other information is known and have been widely used in biological anthropology to reconstruct dental development in humans (Boyde, 1963; Hupková, Dirks, Králik, & Račanská, 2015; Reid, Beynon, & Ramirez Rozzi, 1998), hominoids (Beynon, Dean, & Reid, 1991; Dirks & Bowman, 2007; Reid, Schwartz, Dean, Chandrasekera, & Dean, 1998; Smith et al., 2010), cercopithecoids (Dirks, Reid, Jolly, Phillips-Conroy, & Brett, 2002; Swindler & Beynon, 1993), and subfossil lemurs (Schwartz et al., 2005; Schwartz, Samonds, Godfrey, Jungers, & Simons, 2002), as well as Miocene fossil primates (Beynon, Dean, Leakey, Reid, & Walker, 1998; Le Cabec, Dean, & Begun, 2017; Nargolwalla, Begun, Dean, Reid, & Kordos, 2005; Nengo et al., 2017).

Tooth development begins in utero through cell signaling between the oral epithelium and ectomesenchyme derived from the neural crest in the developing oral cavity (Sharpe, 2001). Diphyodont mammals develop two sets of teeth. The first or primary set is formed from the dental lamina directly, an epithelial ingrowth into the developing oral cavity, and includes the deciduous teeth and the permanent molars. The epithelium differentiates into the bud, cap, and bell stages of tooth formation. The successional teeth, permanent incisors, canines, and premolars, form from an outgrowth of the epithelium of the developing primary teeth at the bell stage (reviewed in Whitlock & Richman, 2013).

In both sets of teeth, a cell signaling center known as the enamel knot regulates epithelial cell division in such a way as to form the future shape of the enamel dentine junction (EDJ) (Jernvall, Åberg, Kettunen, Keränen, & Thesleff, 1998; Simmer et al., 2010; Thesleff, Keranen, & Jernvall, 2001; Vaahtokari, Åberg, Jernvall, Keränen, & Thesleff, 1996). Cell signaling interactions between ectomesenchyme and the epithelial layer induce differentiation of odontoblasts and ameloblasts. As ameloblasts differentiate from the future dentine horn toward the tooth cervix, the EDJ increases in size until the outline of the crown overlying the dentine surface is complete. The rate of ameloblast differentiation is regulated by a complex system of signaling between epithelial and ectomesenchymal cells, controlled by microRNA posttranscriptional gene expression (Jin, Wang, Cheng, Zhao, & Li, 2017) and is quantified in ground sections as the crown extension rate (CER). This is measured as the distance formed along the EDJ per day (μm/day). Histologists measure the distance between two points along the EDJ because they work on two-dimensional surfaces in ground sections, but of course, the ameloblasts actually differentiate over a three-dimensional surface. Variation in extension rate along a transect may therefore represent adjustments to maintaining appropriate rates of growth locally while creating a complex morphology along the three-dimensional surface. Once ameloblasts differentiate, they secrete a thin layer of aprismatic enamel matrix from their distal flat surfaces but quickly develop a secretory structure known as the Tomes' process (Line & Novaes, 2005).

Ameloblast and odontoblast cellular activity occurs in a regular repeated periodic pattern, regulated by circadian clock genes (Lacruz et al., 2012; Zheng et al., 2014; Zheng, Papagerakis, Schnell, Hoogerwerf, & Papagerakis, 2011). Constrictions and bulges along the prism representing a periodic change in enamel matrix secretion are visible in ground sections as paired dark and light bands known as cross striations and have a daily periodicity in primates (Antoine, Hillson, & Dean, 2009; Bromage, 1991; FitzGerald, 1998; Smith, 2006). Equivalent daily lines in dentine are called von Ebner lines (Dean, 1995, 2000). Measuring the distance between daily lines permits quantification of the daily secretion rate (DSR) for enamel and dentine. Longer period lines, or striae of Retzius, have a fixed number of days between them, known as the Retzius interval (RI), and mark the forming front of enamel at successive times during crown formation (Asper, 1917; Retzius, 1837). Equivalent lines in dentine are known as Andresen lines (Dean, 1995; Dean & Scandrett, 1996). Bromage et al. (2009) have hypothesized that the long period rhythm, which they term the Havers-Hallberg

oscillation (HHO), operates on ameloblast and odontoblast activity secondarily to its primary function of regulating cell proliferation rates. This oscillatory rhythm is hypothesized to operate via hypothalamic nuclei integrated by the circadian master clock, the suprachiasmatic nucleus (SCN). This activity regulates bone lamellae formation as well as hormonally mediated life history traits, body mass, and metabolic rate via the pituitary gland (Bromage, Hogg, Lacruz, & Hou, 2012). Determination of the RI, therefore, gives information about relative growth rates between species, with lower numbers indicating relatively faster growth and higher numbers indicating slower growth.

Boughner and Hallgrimsson (2008) also consider the role of the SCN in coordinating the growth of the dentition and the mandible. They discuss the developmental integration of these two separate functional modules, and whether they share a genetic developmental pathway. They argue that it is most likely that dental and mandibular development are regulated separately by local peripheral cellular clocks but that these in turn are regulated by the SCN. There is evidence for a peripheral clock regulating bone volume and a circadian oscillator regulating bone mineralization (reviewed in Zheng et al., 2014). Boughner and Hallgrimsson (2008) argue that there is strong selection for the separate peripheral clocks regulating development of the teeth and jaws to do so in a coordinated fashion. If both jaw and tooth formation are regulated via coordinated peripheral clocks, we expect similar mechanisms to regulate overall skeletal growth, with peripheral clocks regulating the bone formation underlying both jaw and crown rump length (CRL), perhaps via the mechanisms outlined by Bromage et al. (2009) and Bromage and Janal (2014).

A further set of lines used in the construction of odontochronologies are hypomineralized areas along the forming front of enamel and dentine that appear microscopically as accentuated lines among the normal long period Retzius and Andresen lines (Dirks et al., 2002; Rose, 1977; Rose, Armelagos, & Lallo, 1978; Schwartz, Reid, Dean, & Zihlman, 2006). These lines, or calciotraumatic bands (Kierdorf & Kierdorf, 1997), occur at times of physiological stress, potentially due to increased cortisol disrupting ameloblast sodium and potassium balance (reviewed in Temple, 2019) and are thought to form in enamel when the secretory activity of the Tomes' process is disrupted. The duration and intensity of the stress appear to affect the appearance of the line, while the same event appears to affect ameloblast activity differentially, dependent on the age of the cell; that is, the length of time that an ameloblast has been secreting enamel matrix. Younger ameloblasts closer to the EDJ appear to be able to recover secretory activity more effectively than older cells closer to the enamel surface and the end of their secretory lifespan (Witzel, Kierdorf, Schultz, & Kierdorf, 2008). The most important of these accentuated lines forms at birth, and is known as the neonatal line (Jakobsen, 1975; Schour, 1936), and permits determination of the ages of subsequent events in dental development. These accentuated lines can also be used to determine the duration of crown formation or crown formation time (CFT) and the CER (Dean, 1998; Risnes, 1986).

### 1.2 | Previous histological studies of the development of dental sexual dimorphism in primates

Previous histological studies documenting the processes underlying the development of dental sexual dimorphism in primates have focused on canines. Schwartz and Dean (2001) studied canine dimorphism in *Pan*, *Gorilla*, and *Pongo*, concluding that it arises from bimaturism, with males taking longer to form canines than females but forming them at similar rates. Schwartz, Miller, and Gunnell (2005) examined the developmental basis of canine dimorphism in a mixed sample of maxillary and mandibular canines from several species of the Eocene adapiform *Cantius*. In contrast to the apes, canine dimorphism in *Cantius* was primarily achieved by differences in CER. The authors suggested that selection for dimorphic canines has occurred at least twice in primate evolution and that it has been achieved by different mechanisms—sex differences in duration of development in apes, and sex differences in rate of development in *Cantius*. There are no other purely histological studies of the development of canine dimorphism in other primates, but Guatelli-Steinberg et al. (2009) combined dental histology with perikymata counts and packing patterns to examine rate and duration differences in canine development between the sexes in a sample of platyrrhines and catarrhines. They concluded that the primary mechanism for canine sexual dimorphism in both groups is bimaturism but that there was a secondary contribution of rate differences to canine dimorphism in *Cercocebus* and *Papio*.

Unlike growth of the length and mass of the body, in which there is a fixed starting point, teeth initiate at different ages in a constrained sequence that permits eruption at the appropriate time for their function in food processing. For sexually dimorphic teeth like canines, eruption is timed so that male weaponry reaches its maximum height at the age at which it is most likely to contribute to reproductive success (Leigh, Setchell, & Buchanan, 2005). A histological study of dental development in *Theropithecus gelada* was not specifically designed to address sexual dimorphism, but showed an earlier initiation of the male weaponry complex in males than in females (Swindler & Beynon, 1993). When the mechanism for achieving dimorphism is bimaturism, the larger tooth requires a longer time in which to develop, requiring either an earlier age at initiation of crown formation, or a later age at completion, or a combination of the two. Therefore, a complete odontochronology, in which the ages at initiation and completion of crown formation are determined, may add to our understanding of how dimorphism occurs.

### 1.3 | Study species and aims

Our study focuses on a highly sexually dimorphic cercopithecine, the mandrill. Mandrills live in large, multi-male, multi-female groups, have a polygynandrous mating system, and exhibit the greatest sexual dimorphism of any living primate. Males are 3.4 times the body mass of females (Setchell et al., 2001), have exaggerated secondary sexual adornments, including brightly colored skin on the face, rump and genitalia, and possess long upper canine teeth (Leigh et al., 2005;

Setchell & Dixson, 2002). Adult male and female skulls show extreme sexual dimorphism (Figure 1). Adult sexual dimorphism is reflected in patterns of growth and development: while females reach adult CRL at 6 years and body mass at 7 years, males do not attain adult body mass, CRL and appearance until 9–10 years (Setchell et al., 2001; Setchell & Dixson, 2002). Differences between males and females are linked to sex differences in reproductive strategy and reproductive scheduling across the lifetime (Leigh et al., 2008; Setchell et al., 2005). Moreover, while male rank changes across the lifetime, and males fight viciously, inflicting serious injury on one another (Setchell et al., 2006), female ranks are stable and female offspring inherit their mother's rank (Setchell et al., 2008).

Dimorphism in male canine height in mandrills is attributed to bimaturism through differential age at onset and duration of eruption between males and females (Leigh et al., 2005). Dimorphism in CRL is also primarily achieved through bimaturism (Setchell, Lee, Wickings, & Dixson, 2001). Body mass dimorphism is achieved through both bimaturism and differences in growth rate (Setchell, Lee, Wickings, & Dixson, 2001). Changes in body mass occur in response to changes in numerous tissues, each with its own cell types containing circadian clock genes (Schibler, 2017), and we would expect a more complex pattern of increase than bimaturism alone.

Consistent with increases in overall body length, shape differences in facial growth between male and female drills (*Mandrillus leucophaeus*), the mandrill's congener, are primarily due to differences in duration and a late divergence of growth trajectories between the sexes (O'Higgins & Collard, 2002). Bimaturism creates a more prognathic muzzle and larger maxilla in males than females, while the divergence in trajectories also contributes to shape differences.

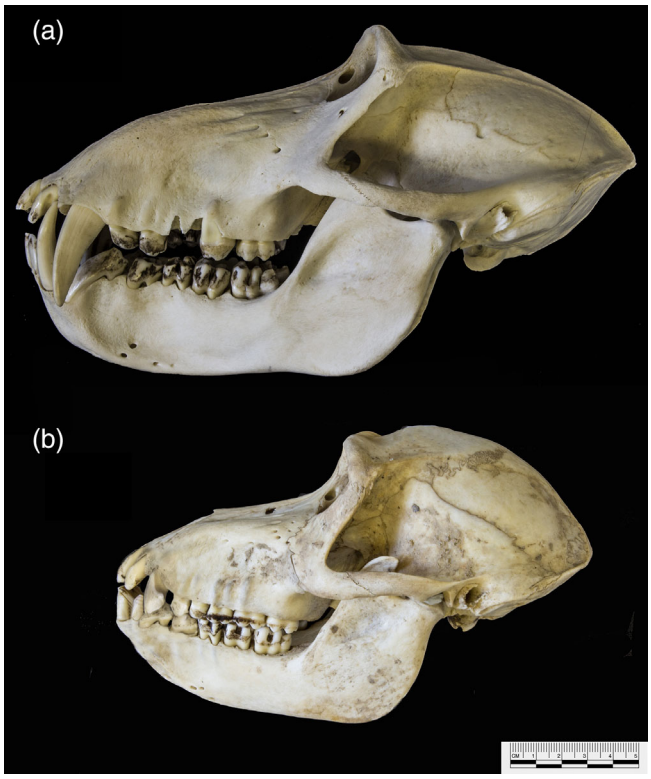



**FIGURE 1** Skulls of male (a) and female (b) mandrills from the CIRMF colony, illustrating the degree of sexual dimorphism in size

Previous studies have examined the sequences and timing of dental eruption in the CIRMF mandrills (Setchell & Wickings, 2004) and sex differences in canine eruption (Leigh et al., 2005). Eruption of the mandibular first molars, incisors, canines, and third premolars is earlier in females than in males while eruption of the fourth premolars and second molars occurs at similar ages in both sexes. The third molar erupts later in females than in males (Setchell & Wickings, 2004). There are no existing detailed odontochronologies of mandrills.

Our study has three aims:

1 to establish odontochronologies of dental development in male and female mandrills
2 to understand interindividual and intersex variation in odontochronologies
3 to determine how sexual dimorphism is achieved developmentally in canines and the other teeth

We divide the teeth based on whether they form part of sexually dimorphic male weaponry (the canine-$P_3$ honing complex) or whether they function in food processing, as selection will have operated differently on these two functional units. We consider the food processing teeth as either successional (incisors, fourth premolar) or primary (molars). We derive hypotheses and associated predictions from what we know about canine dimorphism in hominids, *Cantius*, *Cercocebus*, *Papio*, CRL and body mass ontogeny in mandrills, size differences between male and female teeth in other cercopithecoids, and studies of other papionins showing differences in initiation of the male weaponry complex (Table 1). The hypotheses are not mutually exclusive and some of them give rise to the same predictions.

## 2 | MATERIALS AND METHODS

Our sample comprised permanent teeth from four female and four male naturally deceased mandrills from a semi-free ranging colony at the Centre International de Recherches Médicales de Franceville (CIRMF), Gabon (Table 2). CIRMF established the colony in 1983 and maintains three groups of mandrills in large, naturally rain-forested enclosures (2, 3.5, and 6.5 ha). The mandrills eat a natural diet, supplemented by daily provision of monkey chow and seasonal fruits. Water is always available from a stream, which runs through the enclosures.

When animals die, the animal technicians collect the remains and place them in punctured plastic bags for controlled decomposition with identification for later reference. Staff monitor the state of decomposition occasionally and collect the skeleton once all the soft tissue is gone. They clean the material with a dilute solution of bleach or salt in water, store it in a dilute solution of alcohol in water for 2–3 months, then allow it to dry. Occasionally teeth are missing although the staff make every effort to keep all the remains together.

**TABLE 1** Hypotheses and derived predictions for how dental sexual dimorphism occurs in mandrills (*Mandrillus sphinx*)

| Hypotheses | Predictions |
|---|---|
| 1. Male mandrill teeth are larger than are females' teeth, as in other cercopithecoids. | EDJ length is longer in males than in females. |
| 2. Dental sexual dimorphism occurs via bimaturism, as it does in hominid canines. | CFT is longer in males than in females. |
| 3. Dental sexual dimorphism occurs via rate differences, as it does in *Cantius* canines. | CER is higher in males than in females. |
| 4. Dental sexual dimorphism occurs, primarily via bimaturism but with some differences in rate along crown height, as it does in *Papio* and *Cercocebus* canines. | CFT is longer in males than in females but there may also be a higher CER in males at some points along the EDJ. |
| 5. Dental sexual dimorphism occurs via both bimaturism and rate differences, as it does in body mass dimorphism. | CFT is longer and CER is higher in males than in females. |
| 6. Dental sexual dimorphism occurs, via bimaturism, as it does in CRL. | CFT is longer in males than in females. |
| 7. Teeth involved in food processing that erupt earlier in one sex than another initiate earlier, form at a faster rate, or have a shorter duration of crown formation than those that erupt later. | $I_1$, $I_2$, and $M_1$ initiate earlier, have higher CER, or have shorter CFT in females than in males. $M_3$ will initiate earlier, have a higher CER, or a shorter CFT in males than in females. |
| 8. Teeth involved in food processing that erupt at the same age in both sexes have earlier ages at initiation or a faster CER in males than in females due to the presumed differences in size. | $P_4$ and $M_2$ initiate earlier or have faster CER in males than in females. |
| 9. Teeth involved in the male weaponry complex have earlier ages at initiation in males than in females, as in *Papio*, *Theropithecus*, and *Macaca*. | Canines and the $P_3$ initiate earlier in males than in females. |

Before sectioning the teeth, we photographed each individual skull and CT scanned them at Hull-York Medical School. The youngest individual in the sample was a male with developing teeth (HT12-15) for whom no other information was available (Table 2) and we imaged the developing teeth using a cone beam CT scan at the Dental Hospital in Newcastle upon Tyne. One female (HT12-13) contributed only a maxillary canine for comparison of CER with a male.

We sampled at least one of each tooth type, using mandibular teeth from the same quadrant when possible. Because reconstructing the entire odontochronology required us to match each tooth to the next to develop, if a mandibular tooth from one quadrant was damaged, we used the contralateral tooth. In a few cases, if both mandibular teeth were missing or were too damaged, we used the corresponding maxillary tooth instead.

We prepared histological ground sections from the teeth using standard protocols developed at Newcastle University's School of Dental Sciences (Beynon et al., 1991, 1998; Dirks et al., 2002; Reid, Schwartz, et al., 1998). After extraction, we coated the teeth with cyanoacrylate to prevent breakage, then cut thick sections of 180–200 μm on a Micro Slice II slow speed annular saw just outside the optimum plane through the cusp tips and dentine horn. We then mounted the thick sections on glass slides and lapped them on a Logitech PM2 with 3 μm aluminium oxide powder to a final thickness of ~100 μm, ensuring that we reached the optimum section plane. We mounted the sections with cover slips using Histomount® mounting medium.

We analyzed the sections using an Olympus BX51 microscope mounted with a Q-Imaging Micropublisher 3.3 RTV camera and Improvision Openlab 5.0.2 image analysis software. We used the 20× and 40× objectives to measure daily increments and created photomontages from the 20× micrographs in Adobe Photoshop CS5 to measure length along prisms and the EDJ. We used 10× montages to identify and mark accentuated lines.

We calculated the CFT and CER using a method described by Risnes (1986), similar to that used by Boyde (1963), and elaborated by Dean and colleagues (Birch & Dean, 2013, 2014; Dean, 1998; Guatelli-Steinberg, Floyd, Dean, & Reid, 2012; Reid, Schwartz, et al., 1998). In the successional teeth, we first identified an accentuated line intersecting a prism path that initiated as close to the dentine horn as possible. We measured the distance from the EDJ to the accentuated line, following the prism path rather than measuring in a straight line. Although it is impossible to accurately follow a single prism in a two-dimensional plane due to prism decussation in three dimensions (Risnes, 1986), it is possible to follow the general direction of the prisms as they undulate. This method ensured that we could calculate the complete CFT for teeth with some cuspal wear, but in which the dentine horn had not been breached. In worn teeth in which the dentine horn was no longer visible, we chose a point on the worn occlusal surface that intersected an accentuated line and followed a prism from this point to the EDJ to calculate a minimum CFT for that tooth.

When calculating total molar formation time, we used matching accentuated lines in multiple cusps and moved from one cusp to another when necessary due to taphonomic or preparation damage. We calculated total CFT beginning with the first cusp to initiate and working from cusp to cusp to the final cusp to complete. In many cases, we were only able to match one mesial or distal cusp to the other due to section quality and these CFT estimates represent a minimum value as they only represent two of the four cusps.

We calculated the mean DSR by measuring the length of a minimum of 10 sets of cross striations visible along the prism path and dividing this length by the number of days represented. We then divided the distance along the prism path from the EDJ to the accentuated line by the mean DSR. This yielded the number of days of crown formation from the dentine horn to the accentuated line. We then followed the accentuated line from its intersection with the prism path back to the EDJ. The area

**TABLE 2** Sample used in the analysis

| 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), $RM^2$(m), $RM^3$(d), $RM_3$(end) | $RM^3$ |
| 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), $RM_3$(m, end) | $RM_3$ |
| HT12-13 | Female | Unknown | Unknown | Unknown | $RC^1$ | None |
| 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 | $RI_1$, $RI_2$, $LC^1$, $LP^3$, $LM_1$(prd, 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), $LP_3$, $LP_4$, $LM_1$(d), $RM_2$(m), $LM_3$(m) | $LM_3$ |
| HT12-15 | Male | Unknown | Unknown | *6.1* | $RI_1$, $RI_2$, $RC_1$, $RP_3$, $RP_4$(i), $RM_1$(d), $RM_2$(m), $RM_3$(m, d) | $RC_1$, $RP_3$, $RM_3$ |

*Note:* L and R indicate left and right, (m) or (d) indicate mesial or distal cusps, (i) indicates incomplete crown, (prd) indicates protoconid, (med) indicates metaconid, (hyd) indicates hypoconid, (end) indicates entoconid, italicized value indicates age at death calculated histologically.

between this line and the EDJ represents all the enamel formed along the prism path during those days. We calculated the CER in successional teeth by measuring along the EDJ from the intersection of the prism path at the dentine horn to the intersection of the accentuated line and dividing it by the number of days it took to form. We next followed another prism path from the intersection of the accentuated line at the EDJ to another accentuated line that had formed after the first one and repeated the procedure, adding the duration of crown formation along this segment to the previously determined duration. In this way, we worked our way from the first enamel formation at the dentine horn to the cervix of the crown, determining CFT and CER simultaneously. Some canine crowns with very thin enamel had taphonomic damage so we used the coronal dentine to determine CFT and CER using daily increments (von Ebner lines) measured along the dentine tubule and measurements made along the root surface.

To determine CER and cusp specific formation time in the molars, we used a slightly different method. To calculate cusp specific CFT and CER, each cusp must be free from damage with increments visible from the dentine horn to the cervix. Because of section quality, we could not calculate cusp specific CFT and CER for all four major cusps in every molar. We confined our analysis to those cusps for which two males and two females were usable, the protoconid and entoconid of $M_1$, the metaconid of $M_2$, and the entoconid of $M_3$. The $M_1$ and the $M_2$ were worn, so we started at the tooth cervix, and measured 500 μm intervals along the EDJ toward the occlusal surface. At each marked interval, we followed a prism path to the striae that intersected the previous marked point and calculated the number of days from the EDJ to the stria by measuring cross striations. We then divided 500 μm by that number of days to determine CER. We worked our way up the crown in this way until we came to the occlusal edge of the EDJ. The $M_3$ entoconid had an intact dentine horn in all four sections so we reversed the process and started at the dentine horn, measuring 500 μm intervals toward the cervix.

We tested hypothesis 1, that male teeth are larger than female teeth, by comparing the lengths of the EDJ between the sexes for each tooth type. We suggest that EDJ length is a useful indicator of sexual dimorphism because, unlike simple measurements of length and breadth, it accounts for subtle differences in the both size and shape of the tooth and reflects the length of the inner enamel epithelium as it differentiates into ameloblasts. EDJ length, however, does not take account of enamel thickness, which varies between males and females in hominoids, in which female canines have thicker enamel than males (Schwartz, Reid, & Dean, 2001). This appears to be true for mandrills as well, but quantification of these differences is beyond the scope of this article.

We reconstructed odontochronology in each mandrill by matching the pattern of accentuated lines between teeth. We could assign an age to these accentuated lines in dentitions that included a neonatal line in the first molar by calculating the time between birth and the formation of the accentuated line itself using the normal daily and long period incremental lines. We then determined the age at initiation and completion of each crown by calculating the time between these events and accentuated lines for which we knew the age of formation.

For dentitions in which the first molar was too worn to retain a neonatal line, we used the date of death from the CIRMF records and worked from the incomplete root forming at death back to the last accentuated line, continuing until we reached the age at the formation of the worn occlusal surface of the first molar. In some cases, matching accentuated lines were found in the roots rather than the crowns and we used incremental lines in dentine rather than enamel to match them. In these cases, lines found in the roots of earlier forming teeth could be matched to accentuated lines in the enamel of later forming teeth. In this way, we were able to match teeth that lacked overlap in crown formation. We also matched accentuated lines in dentine in cases in which matching was ambiguous in enamel. One specimen, male 2D8, had neither a neonatal line nor incomplete roots. For this specimen, we calculated CFT and CER and used these data in calculating individual and sex specific crown extension rates but did not include his individual odontochronology.

To explore the differences between individuals and between the sexes in CFT and CER, and test hypotheses 2–8 (Table 1), we plotted

CER for the crowns of mandibular teeth and a single maxillary canine from each sex at each point measured along the EDJ. The preferred method for this comparison is to align the teeth to the onset of growth at the dentine horn and make measurements to the crown cervix. Because most of the teeth were worn, we were unable to do this. With the underlying assumption that the maximum EDJ length between individuals in any given tooth in each sex was the least worn tooth, we aligned the cervices of the teeth separately by sex. This underlying assumption may be violated when teeth differ significantly in size between individuals within a sex, but provides an estimate of differences in our sample. To create this "calibrated" EDJ length, we subtracted the cumulative EDJ length between each point where CER was calculated from the maximum length at the cervix for each sex. We used the male and female cervices separately because the EDJ was longer in males than in females in all cases, no matter what the degree of wear (Table 3). In teeth for which all the individuals had an intact dentine horn, the $C^1$ and the $M_3$ entoconid, we aligned the measurements from the dentine horn (i.e., we use the actual EDJ length for these teeth). We then used LOESS curve smoothing in SPSS, a form of locally weighted polynomial regression, to compare extension rates among and between the sexes. Not all individuals contributed to each tooth type, as they did not all contribute mandibular teeth.

## 3 | RESULTS

### 3.1 | Interindividual variation in odontochronologies of mandrill teeth

We found individual differences in the ages at which crowns completed, although it was impossible to gauge differences among individuals in the age at initiation of worn teeth. Among females, PB stands out for the late age at completion of her $I_2$, $C_1$, and $P_4$ (Figure 2). With the exception of the $M_3$ entoconid, female PB's teeth were larger than the other females' and her $C_1$ was double rooted.

There are also individual differences in the degree of overlap in crown formation between subsequently forming molars. While the formation of the $M_1$ and $M_2$ overlapped in four of the six animals in our sample, the completion of the mesial cusps of $M_1$ and the initiation of the mesial cusps of $M_2$ did not overlap in female 53DA (Figure 2). Due to section quality, we do not know whether the completion of the distal cusps of $M_1$ and the mesial cusps of $M_2$ overlap, but the end of the formation of the metaconid and hypoconid of $M_1$ and the initiation of the mesial cusps of the $M_2$ do not overlap in male 5I2 (Figure 3). The degree of overlap between the completion of the second molar crown and the initiation of the third molar crown varies among the females, with $M_2$ and $M_3$ mesial cusp formation overlapping in female 53DA, $M^2$ and $M^3$ distal cusp formation overlapping in female PB, and no overlap in $M_2$ mesial and $M_3$ distal cusp formation in female 16 L. This variation may be due to the cusps used in the analysis. However, although second and third molar formation overlap in three of the four males (2D8, 17E2, and 5I2), this is not the case for male HT12-15. HT12-15 lacks overlap between the mesial cusps of $M_2$ and both the mesial and distal cusps of $M_3$. The $M_2$ mesial and $M_3$ distal cusps overlap in male 2D8, suggesting that the variation in the degree of overlap between molar crown formation is not due to the cusps chosen, but that interindividual variation is a feature of mandrill dental development.

Tables S1 and S2 provide details of the variables we measured for each individual.

**TABLE 3** Measures of dental development for all members of a single sex for each mandibular tooth type and the maxillary canine in female (F) and male (M) mandrills (*Mandrillus sphinx*)

| | Maximum CFT (years) | | Maximum EDJ length (mm) | |
|---|---|---|---|---|
| Tooth type | F | M | F | M |
| $I_1$ | >2.9 | >2.7 | >13.4 | >15.3 |
| $I_2$ | >2.8 | >3.0 | >11.0 | >16.3 |
| $C_1$ | >3.9 | >7.5 | >15.8 | >35.4 |
| $C^1$ | >3.3 | >8.0 | 18.2 | >53.4 |
| $P_3$ | >3.9 | >8.2 | >8.8 | >32.5 |
| $P_4$ | >3.0 | >2.8 | >8.5 | >10.4 |
| $M_1$ | >1.4 | >2.0 | | |
| Protoconid | >1.2 | >1.4 | >5.0 | >5.5 |
| Entoconid | 0.9 | >1.2 | 4.2 | >5.0 |
| $M_2$ | >2.2 | 2.5 | | |
| Metaconid | >1.4 | >1.8 | >6.0 | >8.0 |
| $M_3$ | 2.5 | >2.9 | | |
| Entoconid | 1.7 | 1.5 | 7.0 | 7.8 |

*Note*: Values for worn teeth are preceded by the "greater than" sign (>).

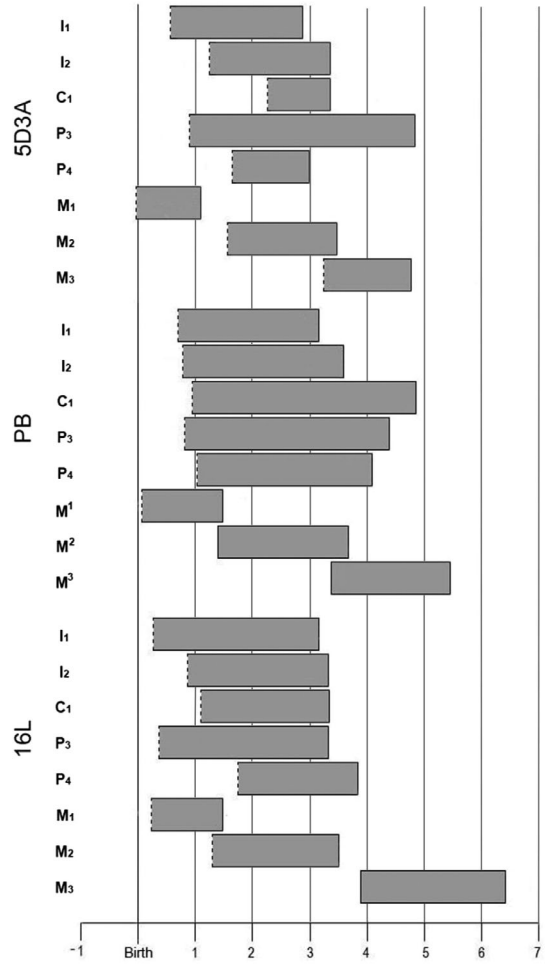



**FIGURE 2** Bar charts illustrating mandibular crown odontochronologies in three female mandrills. Gray bars indicate age at initiation and completion of crown formation. Dotted lines at the beginning of the bars indicate that the tooth had initiated before this age and wear had progressed beyond the dentine horn

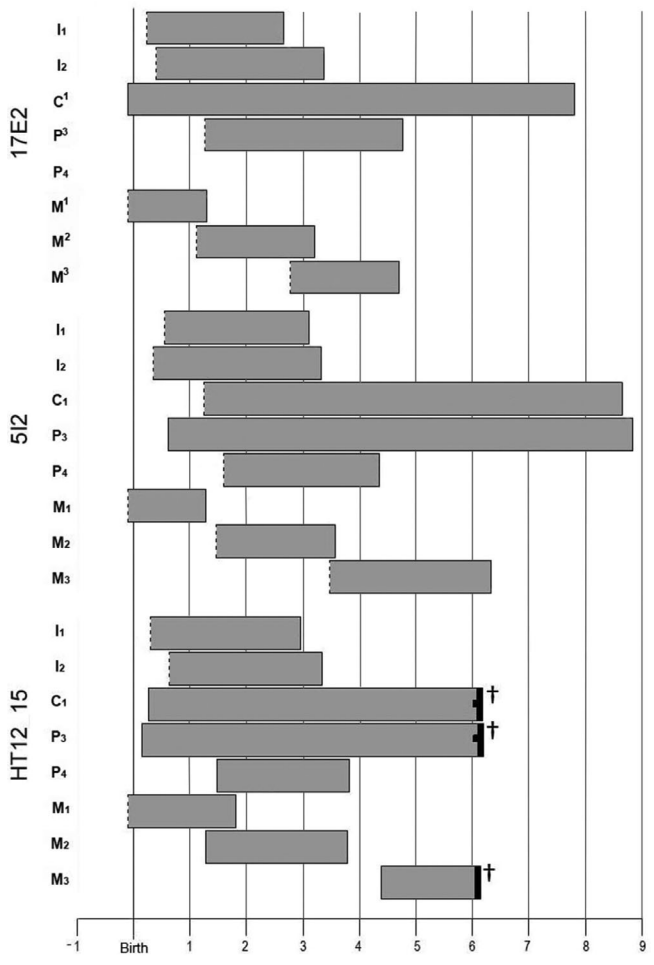



**FIGURE 3** Bar charts illustrating mandibular crown odontochronologies in three male mandrills. Gray bars indicate age at initiation and completion of crown formation. Dotted lines at the beginning of the bars indicate that the tooth initiated before this age and wear had progressed beyond the dentine horn. Crosses indicate age at death for incomplete tooth crowns

## 3.2 | Intersexual variation in the sequence of crown formation

Males in our sample appear to initiate the first molar earlier than females, although it is impossible to know definitively due to the small sample size. Female 53DA was the only female whose $M_1$ retained a neonatal line, which formed 2 days after initiation. The other two females' first molars were too worn to retain a neonatal line. Three of the four males showed neonatal lines in their $M_1$, which formed 62–72 days after initiation. These differences between individuals could be due to the cusp used, as 53DA's neonatal line was visible in the mesial cusps and the males' neonatal lines were visible in the distal cusps. However, a neonatal line was visible in male 5I2's metaconid with 62 days of prenatal crown formation, suggesting that an earlier age at initiation of the first molar in males than in females is a feature of mandrill dental development. Additionally, the $M_1$ completes at similar ages in both males and females (Figures 2 and 3), and the larger crowns of males may require an earlier age at initiation in order to complete and erupt at similar ages (Setchell & Wickings, 2004).

Despite occlusal wear, our male and female odontochronologies provide evidence that canines and the sectorial $P_3$ initiate earlier and complete later in males than in females and that the $P_3$ may be the first mandibular permanent tooth to initiate after the first molar in males (Figures 2 and 3). In male 17E2, only the $C^1$ and $P^3$ were available and the $C^1$ had a neonatal line, indicating that it initiated before birth (Figure 3).

## 3.3 | Interindividual and intersexual variation in the duration and rate of crown formation and the development of sexually dimorphic teeth

CFT appears to be similar in the successional food processing teeth in male and female mandrills, the $I_1$, $I_2$, and $P_4$, although the EDJ is longer in males than in females (Table 3). Dimorphism in these teeth appears to be achieved by a higher CER in males than in females. CER varies considerably among all individuals of both sexes as the EDJ elongates during development, indicating considerable

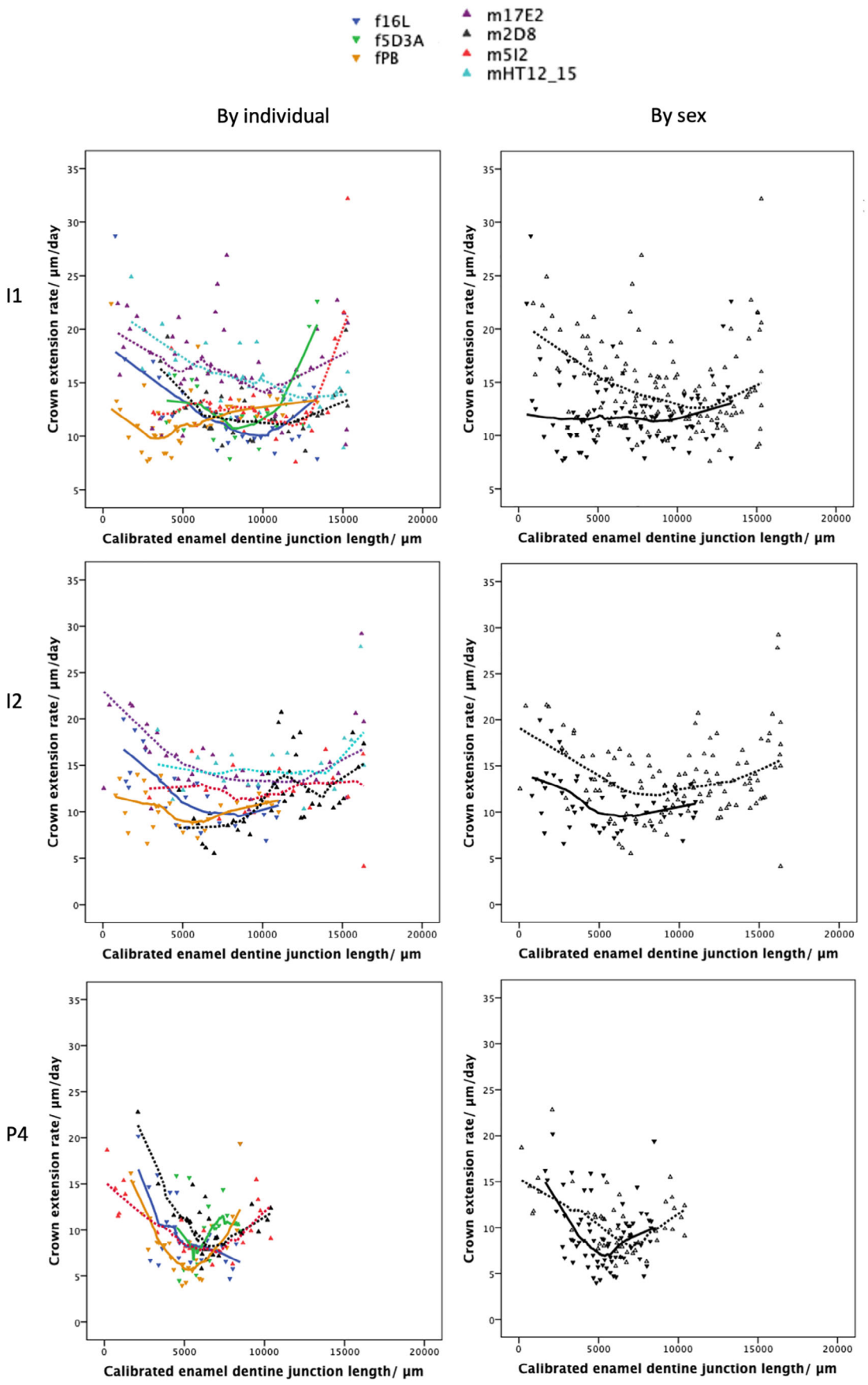
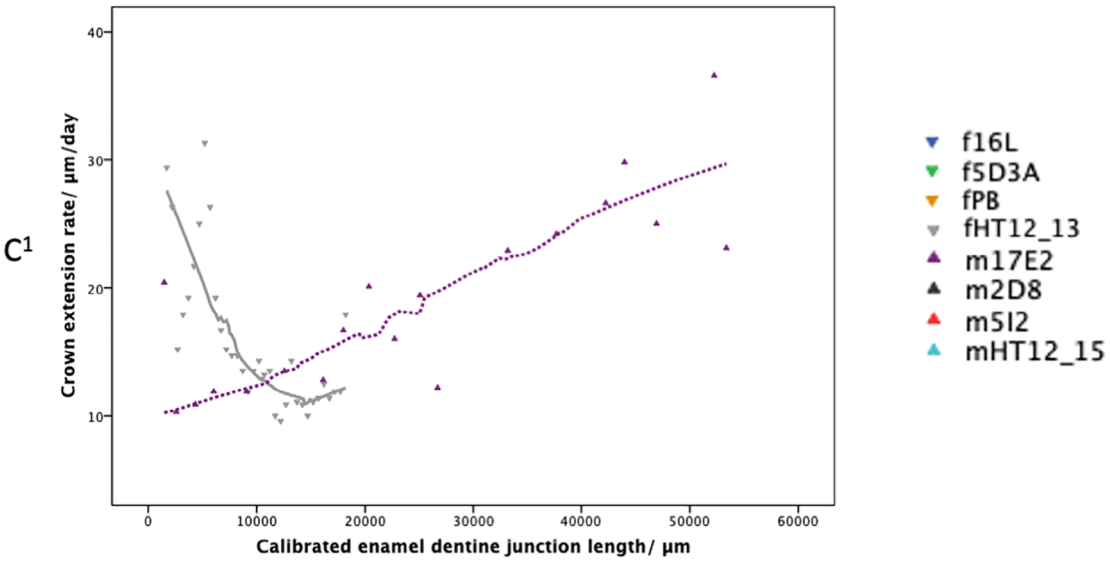



**FIGURE 4** LOESS extension rate curves for food processing successional teeth. Individual (left) and sex-specific (right) curves for I1, I2, P4, aligned by male and female maximum EDJ length at the cervix. Different colors indicate individuals, triangles pointing down and full lines are females; triangles pointing up and dashed lines are males. Differences in starting points along the calibrated EDJ length are due to differences in the degree of wear between teeth



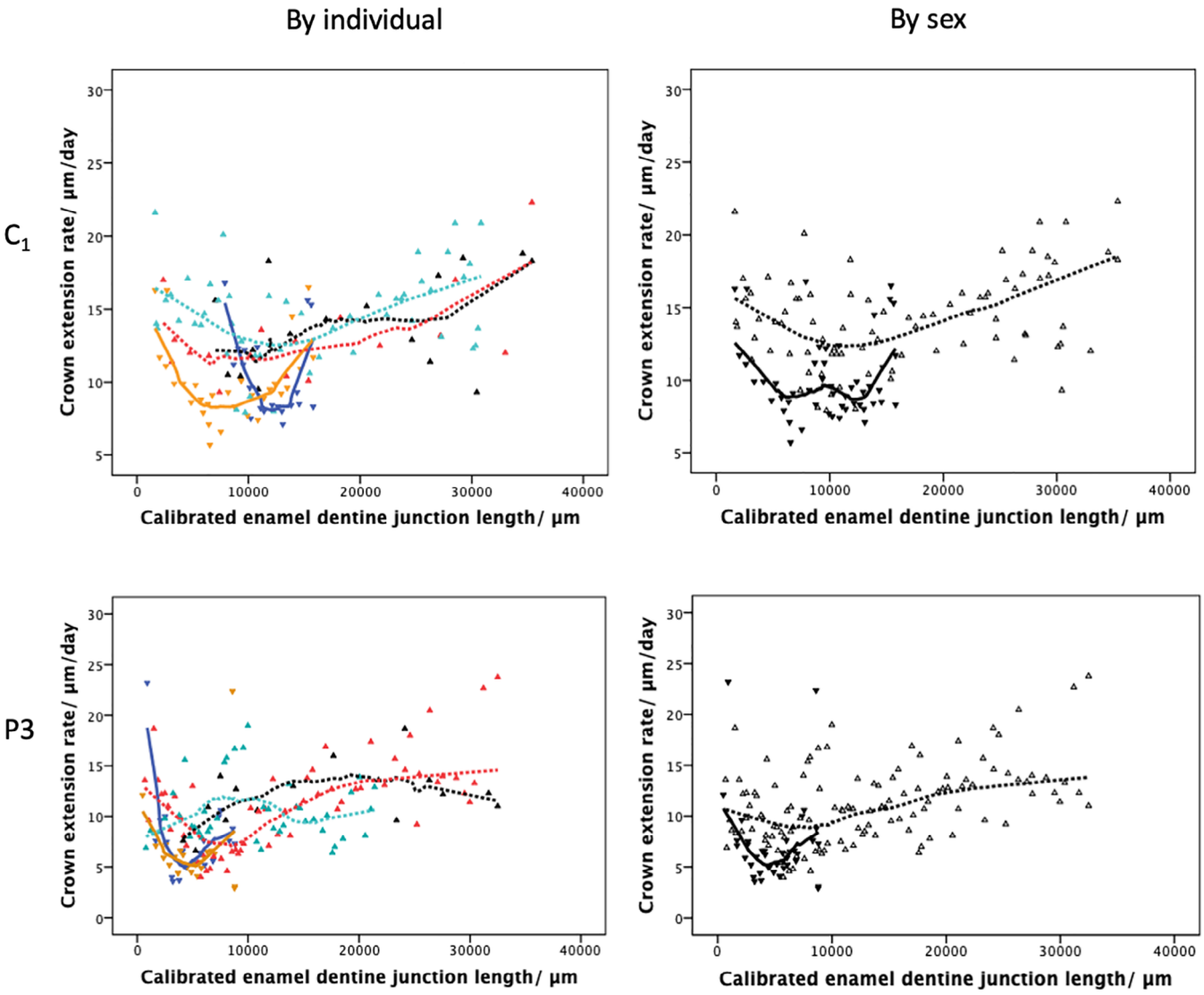




**FIGURE 5** LOESS extension rate curves for dental weaponry. A single plot for $C^1$ with individual (left) and sex specific (right) curves for $C_1$ and $P_3$. Different colors indicate individuals, triangles pointing down and full lines are females; triangles pointing up and dashed lines are males. Differences in starting points along the calibrated EDJ length are due to differences in the degree of wear between teeth. $C^1$ is aligned from the dentine horn while $C_1$ and $P_3$ are aligned from male and female maximum EDJ length at the cervix

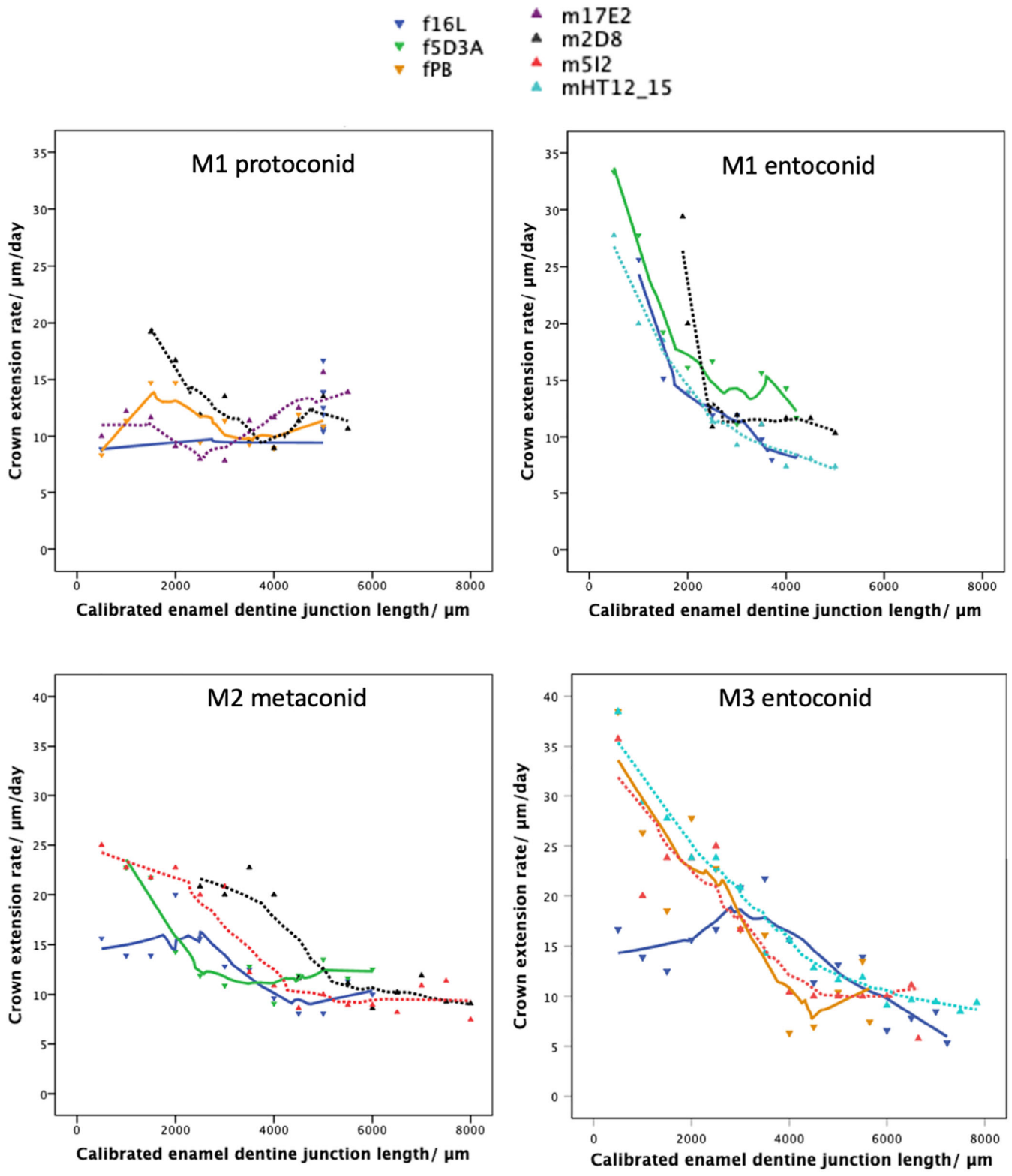



**FIGURE 6** LOESS extension rate curves for individual molar cusps. Different colors indicate individuals, triangles pointing down and full lines are females; triangles pointing up and dashed lines are males. Differences in starting points along the calibrated EDJ length are due to differences in the degree of wear between teeth. The $M_3$ entoconid is aligned from the dentine horn

localized variation in the recruitment of ameloblasts during crown formation. LOESS curves for each individual for each tooth do not overlap consistently, although the shape of the curve is frequently the same between individuals (Figure 4). Despite the localized variation in extension rates, there is a general trend for the extension rate to start high, then drop, and then rise again. When male and

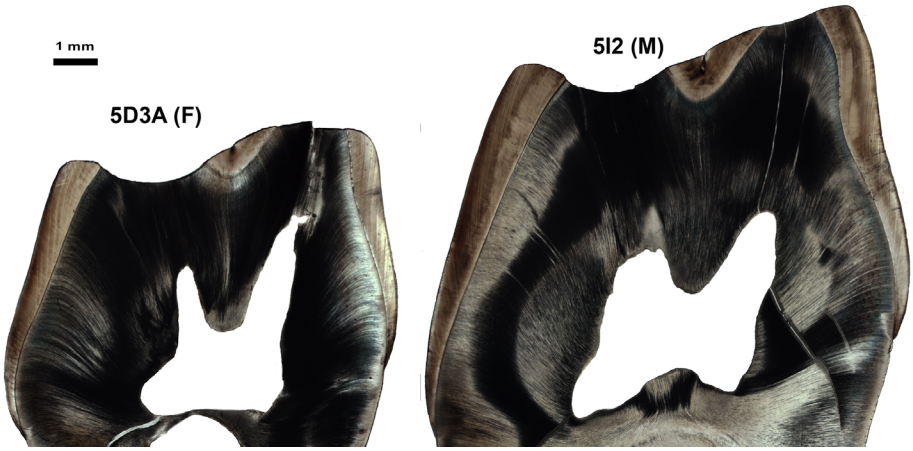



**FIGURE 7** $M_2$ mesial cusps of female 5D3A and male 5I2 at similar stages of wear, illustrating the sexual dimorphism between the teeth

female LOESS curves are plotted, however, CER is consistently higher in males than in females. This is particularly pronounced in the $I_2$, in which there is no convergence of the curves.

The teeth making up the male weaponry complex, the canines and the $P_3$, appear to become dimorphic through a combination of earlier initiation, higher CER and a longer CFT (Figure 5). The $C^1$ differs between the male and female in our sample in both rate and duration of growth. The male $C^1$ EDJ is much longer than the female's and the differences in the CER indicate that the teeth grow in very different ways. The female $C^1$ starts with a very rapid CER which then falls quickly to a rate below the male's. The male's $C^1$ starts slowly and then CER increases with some variation with a sharp rise and then fall at the end of formation. Generally, the male rate is higher than the female's. In the $P_3$ and the $C_1$, there are differences between individuals, but the shapes of the curves are similar in each sex. Both rate and duration are higher in males than females with no convergence of LOESS curves.

Molars differ from the successional teeth in the degree of difference between the sexes. The $M_1$ protoconid and entoconid differ from each other in both sexes and the LOESS curves overlap considerably between the sexes, indicating that rate differences are minimal (Figure 6). The cusps in the males both take longer to form than in the females, consistent with their earlier initiation. Sexual dimorphism in this tooth appears to due to bimaturism, but is small.

The $M_2$ metaconid presents a sharp contrast to the $M_1$ cusps. The teeth are visibly dimorphic in size (Figure 7) and the calibrated EDJ length is 2 mm shorter in females than in males (Table 3). Although the LOESS curves have the same shape in the two sexes, beginning at a high CER and then dropping toward the cervix, the males start at a higher rate than the females. The curve and the differences between the sexes are similar to that of the $P_4$, in which male and female curves are also similar. The male curve starts out faster and the curves converge toward the cervix.

The $M_3$ entoconid EDJ length is not calibrated to the cervix as all the teeth had intact dentine horns. In this instance, female PB has the shortest EDJ but female 16L's EDJ length is longer than male 5I2's. The LOESS curves are similar to the shape of those for the M1 entoconid. In both sexes, the CER starts high and then decreases. It is interesting that PB's cusp grows similarly to the two males' while 16L's has a somewhat different shape. The difference in the two females makes it appear that the males' cusp grows at a higher rate, but the differences may be more due to individual differences than sexual dimorphism.

## 4 | DISCUSSION

Our results clearly show that all mandrill teeth are sexually dimorphic in size, as in other cercopithecoids (Swindler, 2002), as the EDJ is longer in males than in females in all teeth (Table 3), supporting our first hypothesis. While sexual selection may have worked on canine size and the honing complex to create male weaponry, the larger male teeth used in food processing may have evolved through selection for efficiency in energy turnover in the larger of the two sexes (reviewed in Ungar, 1998), or simply be an effect of selection on the timing of tooth formation to match that of jaw growth (Boughner & Hallgrimsson, 2008). The differences between the sexes in the size of the $M_2$ mesial cusps suggest that the former explanation is more likely. This tooth is critical in food preparation and its crown formation in both sexes occurs between 1 and 4 years of age, before the divergence in growth trajectories between the sexes (Setchell, Lee, Wickings, & Dixson, 2001).

Our results show that sexual dimorphism in the mandrill dentition is achieved via both bimaturism and rate differences, supporting hypothesis 5 (Table 1). Males have longer CFTs than females with the exception of the first incisor, in which female CFT is longer, the fourth premolar, in which CFT is equal in males and females, and the $M_3$. Males have higher CERs in all successional teeth. We also found sex differences in the age at initiation of the teeth making up the male weapon complex, the $P_3$, and canines, supporting hypothesis 9. The $C^1$ begins to form prenatally in a male. These findings show that mandrills differ from both extant great apes and *Cantius* in the way that they achieve canine sexual dimorphism, contra hypotheses 2 and 3. Unlike the results reported for *Papio* and *Cercocebus* (Guatelli-Steinberg et al., 2009), rate differences play a prominent role in creating sexually dimorphic canines in mandrills, contra hypothesis 4.

The differences between the successional teeth and the molars are also striking. Dental development and skeletal development must be closely coordinated to ensure that jaw growth accommodates teeth as they develop and erupt. As part of the primary dentition, molars develop directly from the dental lamina as it lengthens into the oral cavity. The first molar, which begins to form prenatally, appears to achieve dimorphism through duration alone, and this occurs through an earlier initiation in males than females. Dental sexual dimorphism is achieved in the successional teeth and the second molar via both bimaturism and differences in growth rate—the same mechanisms as body mass dimorphism, rather than CRL dimorphism, which is primarily attained via bimaturism. We suggest that sexual selection has operated on CRL, body mass, and the canine complex but that the mechanisms for achieving this dimorphism are specific to the system on which selection is working. Selection will also have operated on the teeth used for food processing and weaponry separately, yet in a coordinated fashion. Cell proliferation may be finely tuned at the local level via cellular clocks operating separately while selection for coordinating different biorhythms and developmental processes occurs on the master clock, the SCN (Boughner & Hallgrimsson, 2008; Bromage et al., 2009; Schibler, 2017). This suggests that there is no causal relationship between the development of dental dimorphism and body mass; rather they are achieved separately with superficially similar mechanisms.

### 4.1 | Interindividual variation in odontochronology

The results of our study highlight the degree of variation in the ages at initiation and completion of crown formation within a developmentally constrained sequence and chronology of dental development among individuals and between the sexes in even a small sample of a single species. Interindividual variation in dental development is ubiquitous among the primates studied to date (Guthrie & Frost, 2011; Henderson, 2007; Jogahara & Natori, 2012; Machanda et al., 2015; Setchell & Wickings, 2004; Smith et al., 1994; Wang, Turnquist, & Kessler, 2016). Variation in the ages at tooth mineralization stages among primates has been documented extensively in radiographic studies (Anemone, Watts, & Swindler, 1991; Boughner, Der, & Kuykendall, 2015; Kuykendall, 1996; Reed, 1973; Sirianni & Swindler, 1985; Swindler & Meekins, 1991; Winkler, Schwartz, & Swindler, 1996). The labor intensive nature of dental histology means that smaller sample sizes are available, but all published studies show interindividual variation in ages at initiation and completion of teeth, CFT, and intracusp patterns of DSR (Dirks, 2003; Dirks et al., 2002; Mahoney, 2008; Reid, Schwartz, et al., 1998; Smith, 2016; Smith, Reid, Dean, Olejniczak, & Martin, 2007; Swindler & Beynon, 1993). Our mandrills are no exception and vary in most of these aspects of dental development.

The degree of overlap between the second and third molars in mandrills appears to be highly variable due largely to variation in the age at third molar initiation. A study of molar development in a small sample of hylobatids also shows variation in the initiation of third molars (Dirks, 2003) and it is the most variable tooth developmentally among human populations (Liversidge, 2008). Two female and two male mandrills show overlap between the completion of the $M_2$ and the initiation of the $M_3$, while in one female and one male there is none. Initiation of the $M_3$ occurs when the mandible is fully developed but still growing and the dental lamina extends distally into the lengthening jaw. The proposed coordination between the central and peripheral clocks declines with age (Boughner & Hallgrimsson, 2008) and this might explain the variability in the last tooth to initiate. Alternatively, the timing of the mineralization of the third molar may respond to delays in skeletal development if space is not yet available for crown formation to progress, as suggested by a study of third molar impaction and mineralization in humans (Marchiori, Packota, & Boughner, 2016). In this case, biomechanical stimuli may alter signaling in the extracellular matrix around the developing tooth germ. A third possibility is based on the inhibitory cascade model, in which development of sequential molars is inhibited through cell signaling until the dental lamina moves beyond the inhibitory zone (Kavanagh, Evans, & Jernvall, 2007; Marchiori et al., 2016). In mandrills, either of these two latter mechanisms would mean that differences among individuals in jaw growth create variability in the initiation of the third molar crown. In our sample, the third molar crown initiates between 3 and 4 years of age in females and between 2 and 6 years of age in our males. In females, this corresponds to a decrease in the rate of CRL growth, which ceases at around 6 years of age. In males, there is a similar decrease in rate but CRL continues to increase until 11 years of age (Setchell, Lee, Jean Wickings, & Dixson, 2001). This longer period of skeletal growth may contribute to the higher degree of variation in initiation of $M_3$ in our male sample than in our females.

### 4.2 | Intersex variation in odontochronology

Based on hypothesis 7 (Table 1), we predicted that the first molar and the incisors would initiate earlier in females than in males because these teeth erupt earlier in females than in males. We could not test this prediction for incisors in our sample due to wear. However, in the first molar, the position of the neonatal line indicates a longer period of prenatal crown formation in males than in females, contra our prediction. The difference between the midpoint of the range for age eruption of this tooth in male and female mandrills is small (Setchell & Wickings, 2004). The simple explanation for longer CFT in males is that the tooth is larger than in females, so needs longer to form despite forming at similar rates as in females. Even in our sample of worn teeth, both the $M_1$ protoconid and entoconid both have longer EDJ lengths than the females.

Across primates, there is a statistically significant relationship between the age at weaning and the age at eruption of the first molar (Smith, 1989; Smith et al., 1994), although this relationship is not necessarily true for individual primate species (Dirks & Bowman, 2007; Leigh & Bernstein, 2006; Smith et al., 2013). In both male and female mandrills, the median age at weaning, determined using median

interbirth interval minus the median gestation length, is 7.7 months (Setchell, Lee, & Wickings, 2002). $M_1$ eruption in males (18.2–-36.8 months) and females (18.2–32.9 months) overlaps but occurs long after weaning in both sexes (Setchell & Wickings, 2004). Although weaning may be somewhat accelerated by provisioning in the CIRMF colony, these results suggest that the proposed relationship between weaning and first molar eruption does not apply in this species, as is the case in *Papio* (Dirks & Bowman, 2007) and *Pan* (Smith et al., 2013).

The $M_3$ erupts later in females than in males (Setchell & Wickings, 2004) but the high degree of interindividual variability in its development makes it difficult to test our predictions that this tooth initiates earlier or has a shorter CFT in males than in females. Female PB stands out from the rest of the sample. Her teeth were larger than the other females yet her $M_3$ was smaller. As this tooth is part of the primary dentition and forms as the dental lamina extends into the growing jaw, perhaps cessation of jaw growth combined with larger permanent teeth created less room for the $M_3$ to form.

The teeth that form part of the male weaponry complex, the $P_3$ and $C_1$, initiate earlier and have longer CFTs in males than in females, as in other papionins (Reed, 1973; Sirianni & Swindler, 1985; Swindler & Beynon, 1993), supporting hypothesis 9.

### 4.3 | Interindividual and intersexual variation in the rate of crown formation and the development of sexually dimorphic teeth

Our results make it clear that the rate of ameloblast differentiation varies between individuals and that selection for both the age at tooth initiation and the CER has occurred independently in males and females to ensure that the teeth develop at appropriate times relative to the growth of the sexually dimorphic jaws. The sexually dimorphic canine-P3 honing complex is created through a combination of bimaturism, a higher CER, and earlier initiation in males than in females. The teeth that are part of the food processing complex (the incisors, fourth premolar and molars) are also dimorphic. This dimorphism is also achieved via rate differences (a higher CER in males than in females) with the exception of the $M_1$ and potentially the $M_3$.

Our data show that canine dimorphism in mandrills is achieved through both differences in CER and CFT, unlike in either extant great apes or *Cantius* (Schwartz et al., 2001; Schwartz, Miller, & Gunnell, 2005). Numerous questions arise immediately. Do other cercopithecoids achieve sexual dimorphism in the same way as *Mandrillus*? There is some evidence that rate differences as well as duration contribute to canine dimorphism in *Papio* and *Cercocebus* (Guatelli-Steinberg et al., 2009). How did alternative ways of creating a dimorphic canine arise? Do hominids retain the primitive condition of bimaturism and did changes in extension rate occur during cercopithecoid evolution or are the relatively short hominid canines and the growth mechanisms that underlie them derived relative to ancestral catarrhines? We know, for example, that the Miocene cercopithecoid *Victoriapithecus* exhibited canine dimorphism (Benefit, 1993) but not precisely how it was achieved. Dean and Leakey (2004) used perikymata counts to examine the duration of canine crown formation time in *Victoriapithecus macinnesi* and found that it was longer in males than in females, but we do not know if there were also differences in rate. Histological studies of fossil catarrhine species have not focused on canine extension rates, even in those species with canine dimorphism such as *Ekembo* (Beynon et al., 1998) and *Anapithecus* (Le Cabec et al., 2017; Nargolwalla et al., 2005). How did early anthropoids with dimorphic canines, such as *Aegyptopithecus* (Fleagle, Kay, & Simons, 1980), *Catopithecus*, and *Proteopithecus* (Simons, Plavcan, & Fleagle, 1999) achieve sexual dimorphism? Conclusions about mechanisms for achieving dental dimorphism during primate evolution should be reserved until a wider range of species is sampled.

All teeth are sexually dimorphic in mandrills but dimorphism has evolved in some teeth as a result of sexual selection on male weaponry (canine-$P_3$ honing complex), while in those teeth that are part of the food processing complex, sexual dimorphism is probably a result of selection for larger body size, which creates a longer face in males than in females. The underlying differences in development, such as earlier initiation and higher extension rates in some of these teeth are undoubtedly a result of selection to erupt these larger teeth at the appropriate time for their functions in food ingestion and mastication. Because tooth and jaw growth appear to be controlled separately by cellular clocks, a complex interplay of selective forces will have operated to coordinate these timing mechanisms.

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#### AUTHOR CONTRIBUTIONS

**Wendy Dirks:** Conceptualization; formal analysis; funding acquisition; investigation; methodology; supervision; visualization; writing-original draft; writing-review and editing. **Simone AM Lemmers:** Data curation; formal analysis; investigation; visualization; writing-original draft; writing-review and editing. **Barthélémy Ngoubangoye:** Resources; writing-review and editing. **Anaïs Herbert:** Resources; writing-review and editing. **Joanna M Setchell:** Conceptualization; formal analysis; investigation; resources; supervision; visualization; writing-original draft; writing-review and editing.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available at doi:10.15128/r1ns0646015.

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