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Abstract

Recent studies of dental development have indicated that root growth rates are linked to the eruption of some permanent tooth types in modern humans and Pan troglodytes. Little is known about the potential links between these aspects of dental development in deciduous teeth of any primate species. This histology study calculates the rate at which roots extend in length for human deciduous maxillary teeth and a small sample of deciduous canines and premolars from Pan troglodytes and Pongo pygmaeus. Links are sought between root extension rates and previously published data for deciduous tooth emergence in each of these species. Results reported here provide the first evidence that the roots of human deciduous incisors, canines, and premolars extend in length at an accelerated rate as these teeth emerge. Accelerated extension rates in a deciduous canine from Pan coincided with the age that this tooth type emerged in captive chimpanzees. High extension rates in a canine from Pongo preceded emergence age. Preliminary observations indicate that deciduous canine and premolar roots of Pan and Pongo extend in length rapidly when compared to these tooth types from modern human children. This study provides a starting point from which to investigate new links between the incremental development of deciduous roots and tooth emergence in primates.

Keywords	Histology; dentine; extension rates; great apes; roots.
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Research Data Related to this Submission

There are no linked research data sets for this submission. The following reason is given:
Data for Pan troglodytes and Pongo pygmaeus are in the Tables. Data for modern humans can be made available upon request.

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19th December 2018

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Thank you very much for your continued consideration of my manuscript.

I accepted all of your edits and uploaded a clean version of the manuscript.

I made no other changes.

Sincerely yours

Patrick Mahoney

Root growth and dental eruption in modern human deciduous teeth with preliminary observations on great apes

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Recent studies of dental development have indicated that root growth rates are linked to the eruption of some permanent tooth types in modern humans and *Pan troglodytes*. Little is known about the potential links between these aspects of dental development in deciduous teeth of any primate species. This histology study calculates the rate at which roots extend in length for human deciduous maxillary teeth and a small sample of deciduous canines and premolars from *Pan troglodytes* and *Pongo pygmaeus*. Links are sought between root extension rates and previously published data for deciduous tooth emergence in each of these species. Results reported here provide the first evidence that the roots of human deciduous incisors, canines, and premolars extend in length at an accelerated rate as these teeth emerge. Accelerated extension rates in a deciduous canine from *Pan* coincided with the age that this tooth type emerged in captive chimpanzees. High extension rates in a canine from *Pongo* preceded emergence age. Preliminary observations indicate that deciduous canine and premolar roots of *Pan* and *Pongo* extend in length rapidly when compared to these tooth types from modern human children. This study provides a starting point from which to investigate new links between the incremental development of deciduous roots and tooth emergence in primates.

1. Introduction

Studies of dental development have started to investigate relationships between the rate at which roots extend in length (root extension rates: RERs) and eruption[1] in modern human and great ape permanent teeth. There is now mounting evidence that roots of both modern human permanent teeth and great apes have a growth trajectory that includes a period in which RERs are accelerated (Dean, 2007, 2010; Smith et al., 2007; Dean and Vesey, 2008; Dean and Cole, 2013). This peak in RERs coincides with the period during which permanent teeth erupt into function in *Pan troglodytes* (Dean and Vesey, 2008; Dean and Cole, 2013). This differs to modern humans where RERs peak prior to gingival emergence of permanent canines and molars, but accelerate as incisors move into function (Dean and Vesey, 2008; Dean, 2010; Dean and Cole, 2013). This is interesting because the eruption of permanent teeth, especially for molars, has provided an important source of information from which to infer the schedule of life history in fossil species (e.g., Smith, 1989).

In comparison with permanent teeth, much less is known about RERs for human deciduous teeth. Many studies have related fractional stages of deciduous root growth to chronological age in human children (e.g., Schour and Massler, 1940; Massler et al., 1941; Fanning, 1961; Moorrees et al., 1963; Deutsch et al., 1985; Liversidge et al., 1993; Liversidge and Molleson, 2004; AlQahtani et al., 2010). However, only a few studies have been undertaken with the aim of assessing the rate roots extend in length (Stack, 1967; Deutsch et al., 1985). Stack (1967) reported root length measurements for deciduous maxillary central incisors (dI^1) and observed that dI^1 roots attained a length of 6 mm by the twelfth month after birth. As the dI^1 enamel crown is complete 1.5 months after birth (AlQahtani et al., 2010), the roots extended at an average rate of 19.0 μm/day (6 mm/10.5

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[1] Eruption involves resorption of the alveolar bone above the crown leading to a developmental pathway for the tooth to move through the bone (intraosseous stage of eruption). The supraosseous stage of eruption commences as the tooth emerges through alveolar bone. The eruption process continues as the crown appears above the gum line (gingival emergence) and eventually moves into function with the opposing tooth (e.g., Haavikko, 1970; Cahill, 1974; Cahill and Marks, 1980).

months, or 6000 μm / 315 days). Deutsch et al. (1985) calculated average RERs from measurements of tooth length and reported an extension rate of 20 μm/day for dI^1 and 17.7 μm/day for lateral maxillary incisors (dI^2). It is unknown if human deciduous maxillary roots extend in length with a uniform velocity or if rates change over the duration of root growth. Neither is it know if RERs are linked to the eruption of some deciduous tooth types but not others, in the way that has been described for permanent teeth (Dean and Cole, 2013). Moreover, with so little data for deciduous RERs it has been difficult to determine if extension rates relate to other aspects of eruption. The rate that permanent teeth erupt differs between incisors and canines, which mirrors variation in RERs towards the end of root growth in these tooth types (Dean and Vesey, 2008). Whether eruption rates are linked to variation in RERs along the deciduous tooth row has not been explored previously.

Root growth rates are poorly understood for great ape deciduous teeth. As part of their pioneering study on dental development in juvenile great apes, Dean and Wood (1981) inferred a rapid rate of root growth for a deciduous maxillary canine (dC^1) of *Pongo pygmaeus*. Subsequently, only a few studies have considered great ape deciduous teeth but none provided data on aspects of the chronology of root growth (Aiello and Dean, 1990; Siebert and Swindler, 1991; Winkler et al. 1991).

Many factors could potentially influence the way RERs will relate to the eruption of modern human and great ape deciduous teeth, or to variation in these rates when compared among these species. Three of these factors are the ontogeny of facial development, eruption schedules, and root length. First, there is much greater growth and anterior displacement of the lower facial region in *Pan* and *Pongo* compared to human children (e.g., Schultz, 1940, 1941; Moore and Lavelle, 1974). This difference in facial ontogeny might determine the space that is available for root growth and thus the rate at which roots can develop at any point in time. Second, human deciduous teeth typically erupt over a period of 1.4 to 1.6 years (Hillson, 2014: Table 4). In comparison, deciduous teeth of captive chimpanzees and orangutans erupt in less than one year—median duration of eruption is 0.8 to 0.97 years in *Pan* (Nissen and Reisen, 1945; Conroy and Mahoney, 1991; Kuykendal et al., 1992) and 0.68 years in *Pongo* (Fooden and Izor, 1983). These different eruption schedules may determine the time available for root formation and thus the rate at which roots extend in length. Third, root length influences extension rates in modern human and great ape permanent teeth (Dean and Vesey, 2008, Dean and Cole, 2013), which could also relate to the time available for root growth. As root length varies between deciduous teeth of humans, *Pan* and *Pongo* (see Methods subsection) it would seem likely that this may contribute at least some variation to extension rates. These three factors (facial development, eruption schedules, and root length) may all comingle to generate variation in RERs.

This study reconstructs RERs for modern human dI^1, dI^2, dC^1, maxillary third premolars (dP^3), and fourth premolars (dP^4). Root extension rates are also reconstructed for deciduous maxillary and mandibular canines (dC1) and a dP^3 of *Pan troglodytes*, and a dC^1 and dP^4 of *Pongo pygmaeus.* The main aims are (i) to describe the trajectory of RERs for each tooth type, and (ii) to determine if RERs correspond with the emergence of deciduous teeth. Correspondence between deciduous RERs and emergence will be sought in two ways. Human RERs will be assessed in the portion of the root that forms as deciduous teeth emerge through alveolar bone (Liversidge and Molleson, 2017). The portion of the root that forms as deciduous teeth emerge in *Pan* and *Pongo* is unknown. Therefore extension rates will be related to previously published ages at which gingival emergence occurs in captive chimpanzees and orangutans (Nissen and Riesen, 1945; Fooden and Izor, 1983; Kuykendall et al., 1992). Two additional aims of this study are to (iii) compare variation in human RERs along the tooth row to the rate that deciduous teeth erupt, and (iv) to conduct a preliminary comparison of RERs between human, chimpanzee and orangutan deciduous teeth. All samples studied here were selected because long period or accentuated growth markings were present and visible in thin sections of the roots, and because the roots had not resorbed. The principle goal of this study is to provide a starting point, to gain clues about the potential of deciduous RERs for comparative studies of dental development, and to determine if deciduous RERs relate to tooth emergence.

2. Materials and methods

2.1. Samples

<u>Humans</u> The twenty-eight thin sections of deciduous maxillary teeth were from the Skeletal Biology Research Centre, University of Kent, UK and were prepared previously for studies of enamel growth and thickness (Mahoney, 2010, 2011, 2012, 2015). The skeletons from which the teeth were obtained were from one cemetery in Canterbury, England, that dates to the early 16th century AD (Hicks and Hicks, 2001).

<u>Great apes</u> Five thin sections of great ape deciduous teeth were selected. Three sections were from the Elliot Smith Collection, University College London. These sections are of dC^1 from *Pan troglodytes* (reference number CA20A.2.36-c), and a dC^1 and dP^4 from *Pongo pygmaeus* (CA28 J57-c; CA28 J57-E respectively). These individuals were wild shot specimens from the 1920s. Thin sections from these specimens were first prepared for a paper on tooth wear by Aiello et al. (1991). Root extension rates have not been reported previously for these sections.

A thin section of dC_1 (reference number 906-11-73) from *Pan troglodytes* was selected from a collection held at The Ohio State University. Another unsectioned dP^3 (reference number SF001) of *Pan troglodytes* was chosen from a collection held at Simon Frasier University. These were captive animals. The dP^3 from Simon Frasier University was sectioned for this study using standard methods (Mahoney, 2015).

2.2. Methods

Each section was examined with a high resolution microscope (Olympus BX53) at magnifications of 4× to 60× using transmitted light. Images were captured with a microscope digital camera (Olympus DP74) and analyzed using Olympus cellSens software.

<u>Dentine daily secretion rates</u> Dentine daily secretion rates (DSRs) in µm per day are needed to calculate root extension rates, but daily incremental lines are inconsistently preserved in thin sections of roots from human and ape deciduous teeth. One way of overcoming the absence of these lines is to calculate crown dentine DSRs and then transfer this estimated rate to the root of the same thin section. Doing so likely underestimates the dentine DSR. Prenatal crown dentine DSRs were calculated by measuring the length of a dentine tubule from the dentine-enamel junction (DEJ) to the neonatal line, and dividing it by the corresponding enamel prism formation time (see Fig. 1). This method is adapted from Dean and Scandrett (1995) and Le Cabec et al. (2017). The selected enamel prism formed over 30 to 40 days. These prenatal prisms lengths were selected because they were present within all tooth types, they avoided the zone of enamel decussation near the horn, and the 30 to 40 day period over which they formed standardized the measurement between tooth types. Cross striations were counted along this length of the enamel prism (e.g., Reid et al., 1998), to calculate the amount of time taken by ameloblasts to deposit enamel between locations 1 and 2 in Figure 1. Since it takes the same amount of time to form the equivalent portion of the corresponding dentine tubule, this amount of time was divided into the length in µm of the corresponding dentine tubule, which is shown as the dotted line leading to location 3 (Fig. 1). The accentuated line at location 3 is the reflection of the neonatal line in dentine (Fig. 1). This calculation gives an average rate in µm/day that prenatal dentine matrix is secreted in the crown.

<u>Root extension rates</u> Postnatal RERs were calculated using two methods. The first method was adapted from Dean and Vesey (2008) and used to calculate rates for all of the human and great ape teeth studied here. Rates were calculated at fixed intervals of 200, 500, and 1000

μm, and every 1000 μm thereafter beginning at the cervix and extending apically down the CEJ for the first 5 mm of root length. Figure 2 illustrates the extension rate calculation using the orangutan dC^1 thin section. Roots are greatly 'splayed' in human dP^4 and the more apical portions were not captured when the thin sections were made. So it was only possible to calculate extension rates for the first millimeter beyond the human dP^4 enamel cervix.

Correspondence between human deciduous RERs and eruption was sought by assessing rates in the portion of the root that formed during alveolar emergence, relative to extension rates from times relating to before and after emergence. Alveolar emergence occurs for each human deciduous tooth type when roots are on average between 1.8–3.2 mm in length (Liversidge and Molleson, 2017), which is well within the 5 mm window of root growth studied here.

Correspondence between RERs and eruption of dC^1 in *Pan* and *Pongo* was sought by relating extension rates to the previously published age at which gingival emergence occurs in captive chimpanzees and orangutans (Nissen and Riesen, 1945; Fooden and Izor, 1983; Kuykendall et al., 1992). To do this, it was necessary to calculate an additional set of extension rates for the two dC^1, as the first 5 mm of root growth might not capture the eruption phase as these teeth might emerge when the root is longer. The two dC^1 were selected because accentuated and long period markings were well preserved in the entire root. This second methodology is based upon Dean and Cole (2013), wherein extension rates are calculated for successive segments of root, rather than at fixed locations (i.e., 200, 500, or 1000 μm) to try and capture the entire trajectory of root growth for the chimpanzee dC^1 (root length of 11.19 mm) and the orangutan dC^1 (9.28 mm; rates determined using the second methodology are reported in Table 1 footnotes). Following this, the formation age for each segment of root was calculated by combining postnatal dC^1 enamel formation time from the neonatal line, with root formation time calculated from extension rates (enamel formation times are calculated using standard methods for deciduous teeth; e.g., Mahoney, 2012). The formation age for each segment of root was then compared to the previously published age at which gingival emergence occurs for dC^1 in captive chimpanzees and orangutans. In doing so, it was possible to identify the portion of the root that forms as dC^1 emerges, so that extension rates at this location of the root could be assessed.

Eruption rates The average rate at which each human deciduous tooth type erupts was estimated by dividing the average crown height (in mm: $dI^1 = 6.79$; $dI^2 = 6.37$; $dC^1 = 7.85$; $dP^3 = 6.20$; $dP^4 = 6.75$; Liversidge and Molleson, 2017) by the average duration over which these teeth erupt in males and females (in days: $dI^1 = 73$; $dI^2 = 100$; $dC^1 = 128$; $dP^3 = 237$; $dP^4 = 152$; Al-Batayneh and Shaweesh, 2018).

3. Results

3.1. Humans

Dentine daily secretion rates Average crown dentine DSR's (in µm per day) were 3.15 (±1 SD = 0.51) for dI^1, 3.10 (±1 SD = 0.43) for dI^2, 3.85 (±1 SD = 0.30) for dC^1, 2.70 (±1 SD = 0.40) for dP^3, and 3.18 (±1 SD = 0.51) for dP^4. When these average rates were transferred to the root of the corresponding tooth type it gave a dentine formation time—from the cementodentine junction inwards for 200 µm towards the pulp chamber (Fig. 2)—of 63 days in dI^1, 64 days in dI^2, 52 days in dC^1, 74 days in dP^3, and 63 days in dP^4. The range of crown dentine DSRs reported here for dI^1 and dP^4 lie within the range of rates previously reported for one individual (dI^1 = 3.08 to 4.42 µm/day; dP_4 = 3.60 to 4.30 µm/day; Schour and Poncher, 1937).

Root extension rates Each tooth type displayed a root extension trajectory that included a 'growth spurt' (Table 1). On average, roots extended in length at a faster rate in single-rooted anterior teeth (dI^1, dI^2, and dC^1) compared to premolars (Fig. 3a).

The overall average extension rate for dI^1 of 23.17 µm/day is greater than the average rate of 19.0 µm/day recalculated from data reported by Stack (1967), and it is slightly higher than the average rate of 20.0 μm/day calculated from tooth height measurements by Deutsch et al. (1985). The average extension rate of 22.65 μm/day for dI^2 is higher than the average rate of 17.7 μm/day reported by Deutsch et al. (1985) for this tooth type.

Eruption rates The estimated average rate of tooth eruption (in μm per day) differed between the single-rooted anterior teeth (dI^1 = 93.0; dI^2 = 63.7; dC^1 = 61.3) compared to premolars (dP^3 = 26.2; dP^4 = 44.4).

3.2. Great apes

Dentine daily secretion rates Average crown dentine DSRs of 3.32 μm per day for the chimpanzee dC^1 forms 200 μm of dentine in 60 days. This dentine DSR was used to calculate extension rates for the upper and lower canine of *Pan*. A dentine DSR of 2.40 μm per day for the chimpanzee dP^3 forms 200 μm of dentine in 83 days. A dentine DSR of 3.59 μm per day for the orangutan dP^4 forms 200 μm in 56 days. This crown dentine DSR for dP^4 was transferred to the orangutan dC^1 as it was not possible to accurately calculate this rate in the canine thin section. Doing so probably slight underestimates RERs for the dC^1 if *Pongo* is similar to *Pan* and shows a reduced crown dentine DSR in premolars compared to dC^1.

Root extension rates Average extension rates for the great ape deciduous teeth are reported in Table 1. The dC^1 of *Pan* displayed a trajectory of root growth that included a 'growth spurt' (Fig. 3b). The spurt occurred near the enamel crown with a high initial rate followed by steady decline until the root was 4 mm in length, after which rates accelerated. When extension rates were recalculated for the entire length of the dC^1 root, rates accelerated from 4 mm until the root had lengthened to 5 mm and then gradually decelerated until the root was complete (Table 1 footnotes; see Fig. 4a).

The trajectory of root growth in the dC^1 of *Pongo* over the first 5 mm of root growth was more gradual compared to that of dC^1 in *Pan* (Fig. 3b). Rates accelerate away from the dC^1 cervix of the *Pongo* crown increasing to maximum values as the root lengthened between 2 to

4 mm. Rates slowed down when the root was 5 mm in length. When rates were recalculated for the entire length of the root, extension rates continued to slow down until root growth was complete (Table 1 footnotes; Fig. 4b).

Only a few RERs were calculated for premolars of *Pan* and *Pongo* near the enamel crown. When these rates were compared to equivalent locations in the dC1 roots of these species, roots extended in length at a faster rate in canines compared to premolars (Table 1).

Crown formation times Total crown formation time was 458 days for the chimpanzee dC^1 with 140 days of prenatal enamel growth, giving a postnatal enamel formation time of 318 days. Total crown formation time for the orangutan dC^1 was 367 days with 114 days of prenatal enamel growth, giving a postnatal enamel formation time of 253 days.

4. Discussion

4.1. Human deciduous root extension rates

Figure 5a–d depicts plots of extension rate data combined with data from Liversidge and Molleson (2017) for varying root lengths of deciduous maxillary teeth. These plots illustrate that RERs accelerate as each tooth type emerges. The exception is dC^1 where root extension accelerates just after alveolar emergence (Fig. 5c). These findings indicate that the trajectory of root growth for this sample of human deciduous maxillary teeth was not linear, and that RERs accelerated as, or just after, alveolar emergence. This link between accelerated RERs and emergence of deciduous teeth differs compared to permanent teeth. Accelerated extension rates occur before permanent canines and molars erupt, while these teeth are still contained within alveolar bone (Dean and Cole, 2013).

Extension rates varied along the deciduous maxillary tooth row (Fig 3a). Roots of deciduous anterior teeth extended faster than premolars, either when equivalent locations were compared over the first 5 mm of root growth or when the overall average values were considered (Table 1). The variation in extension rates corresponds with average root length, as typically anterior deciduous teeth will have a much longer root than dP^3 and a slightly longer root than dP^4 (Liversidge and Molleson, 2017). Thus, longer roots of deciduous anterior teeth seem to extend at a faster rate, which parallels the situation reported for permanent teeth where roots of taller teeth extended faster (Dean and Cole, 2013).

Deciduous anterior teeth erupt faster than premolars. When the estimated eruption rates are compared to the average extension rates in Table 1 it is apparent that anterior teeth emerge rapidly with roots that form quickly, when compared to premolars. Of the anterior teeth, dI^1 had the fastest rate of eruption and achieved the highest RER when its root had extended to a length of 2 mm. This is interesting because it suggests a mechanism by which tooth eruption rates may relate to RERs. Rapid tooth emergence could create space beneath the root apex in the crypt into which the root could lengthen quickly (Marks and Schroeder, 1996). This makes sense as the surface area of a root provides an attachment point for periodontal fibres that stabilize the tooth against chewing forces (reviewed by Spencer, 2003). Under this scenario, the rapid RERs of anterior teeth might provide more root surface in a shorter period of time from which to stabilize their crowns as they moved rapidly into function relative to premolars.

4.2. Great ape deciduous root extension rates

Figure 4a illustrated that the higher extension rates for the dC^1 of *Pan* lay within the range of ages that this tooth type emerged in captive chimpanzees (Nissen and Riesen, 1945; Kuykendall et al., 1992), which also encompasses the age of dC_1 emergence reported for a sample of wild East African chimpanzees (Machanda et al., 2015). Faster extension rates occurred during the first 5 mm of root growth as this tooth type emerged. Slower extension rates occurred as the root lengthened between 7 to 11 mm, which is after the age dC^1 has emerged.

Figure 4b illustrated that the highest extension rate for the dC[1] of *Pongo* occured before the age that this tooth type emerged in captive orangutans (Fooden and Izor; 1983). Furthermore, if great ape deciduous teeth emerge with the same amount of root that is present in human deciduous teeth, which is about half the length of the crown (Liversidge and Molleson, 2017), then this orangutan dC[1] (with a crown height of 8.66 mm) would have emerged when the roots were slightly longer than 4 mm in length (Fig. 4b). This would have occurred as extension rates were decelerating. By comparison, and using the same calculation, the chimpanzee dC[1] with a crown height of 8.02 mm would have emerged when the root was 4 mm, which would have coincided with accelerating extension rates.

Extension rates were faster in the dC[1] of *Pan* and *Pongo* compared to data for permanent canines of these species (Dean and Vesey, 2008). When equivalent locations were compared along the first 5 mm of root, the chimpanzee dC[1] root extended in length four to five times faster (range = 24.57–30.33 µm/day; Table 1) compared to permanent canines of *Pan* (range = 5.10–12.90 µm/day; Dean and Vesey, 2008). Rates of extension between 9.0 to 10.9 µm/day for the first 5 mm of root growth in a combined sample of permanent lower canines from orangutans and gorillas (Dean and Vesey, 2008) are less than the values reported here for dC[1] of *Pongo* that lie between 23.07–30.86 µm/day (Table 1).

4.3. Humans compared to great apes

The overall average rate at which roots extended to a length of 5 mm is greater in dC1, dP[3], and dP[4] of *Pan* and *Pongo* compared to the same tooth types of human children (Table 1). When equivalent locations along the root are compared between these species, RERs are generally still higher in the great ape teeth compared to humans (Table 1). Rates for the dC[1] of *Pan* begin to overlap with those of human dC[1] roots when they have lengthened to 3 mm, but rates from the dC[1] of *Pongo* remained faster than human dC[1] until the root has lengthened to 5 mm (Fig. 3b). Only a few rates were calculated for great ape premolars, but these were also accelerated compared to human premolars, especially in *Pan*. It seems unlikely that a higher rate of root extension in the great ape teeth can be attributed to just variation in root length. The dC^1 root of *Pongo* was 9.28 mm in length, which was close to the average length of 9.11 mm for the human dC^1. The dC^1 root of *Pan* was 11.19 mm and extended faster than the shorter human dC^1 roots, but there were still portions of the root where extension rates overlapped between these species. Clearly, the extent of the overlap in extension rates between these species has yet to be determined and the data analyzed here are only a 'first step'. With this in mind, future studies might explore potential links between RERs and the slowed schedule of eruption for human deciduous teeth compared to *Pan* and *Pongo*.

Conclusions

Root extension rates were calculated from 28 thin sections of modern human deciduous maxillary teeth, and for five sections of deciduous canines and premolars from *Pan* and *Pongo*. Rates were used to reconstruct the trajectory of deciduous root growth, and to determine if root extension rates corresponded with tooth emergence. All teeth examined here had a growth trajectory that included a peak in the rate that roots extended in length. Rates peaked at different stages of root growth in different tooth types. The peak in root extension rates occurred in the portion of the root that formed as human deciduous incisors and premolars emerged through alveolar bone, and just after alveolar emergence for the canine. Accelerated extension rates in a deciduous canine from *Pan* coincided with the age that this tooth type emerged in captive chimpanzees. High extension rates in a canine from *Pongo* preceded emergence age. For *Pan* it was possible to combine root formation time up until the root growth spurt with the crown postnatal enamel formation time to reconstruct the known age of dC^1 emergence. Preliminary observations indicate that extension rates in deciduous canines and premolars from *Pan* and *Pongo* are higher than these rates in the same tooth types of modern human children. This study provides a starting point from which to explore root extension rates and eruption in primate deciduous teeth.

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FIGURE CAPTIONS

Figure 1. Thin section of a dC^1 crown of *Pan troglodytes* (catalogue number CA20A.2.36). A) Thin section image produced at a magnification of 4× using polarized microscopy. Light blue circle denotes dentine; light green circle denotes enamel. White arrows point to the neonatal line, which is an accentuated marking in enamel and dentine. B) Section image produced at a magnification of 20×. The dashed white line traces an enamel rod between the enamel-dentine junction (1) and the neonatal line (white line) to the right (2). A dashed white line traces a dentine tubule to the neonatal line in dentine (3). The length of the dentine tubule is shorter compared to the length of the enamel rod

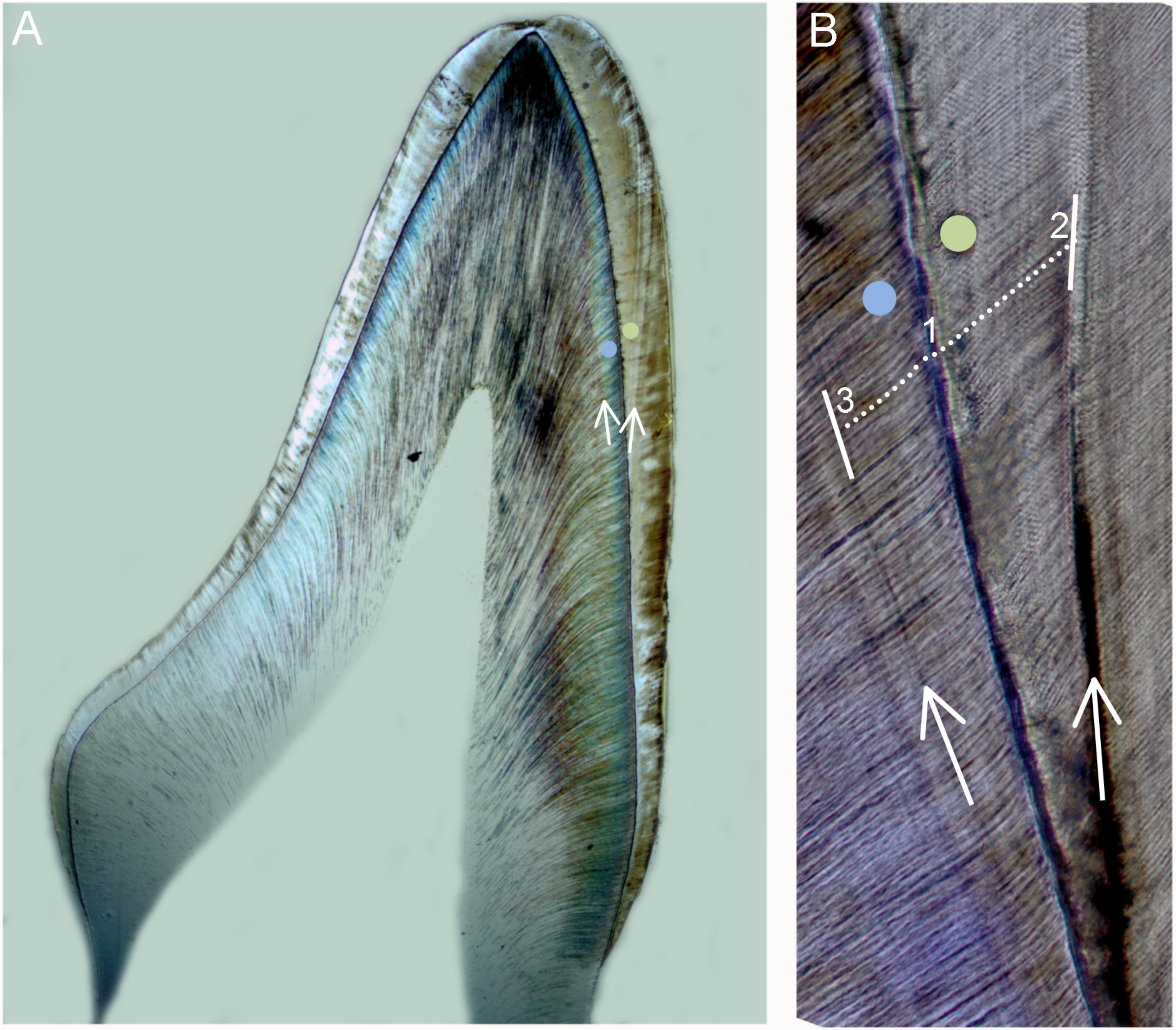
because odontoblasts secrete new matrix at a slower rate compared to the rate that ameloblasts secrete new matrix. See text for calculating an estimate of crown dentine DSRs.

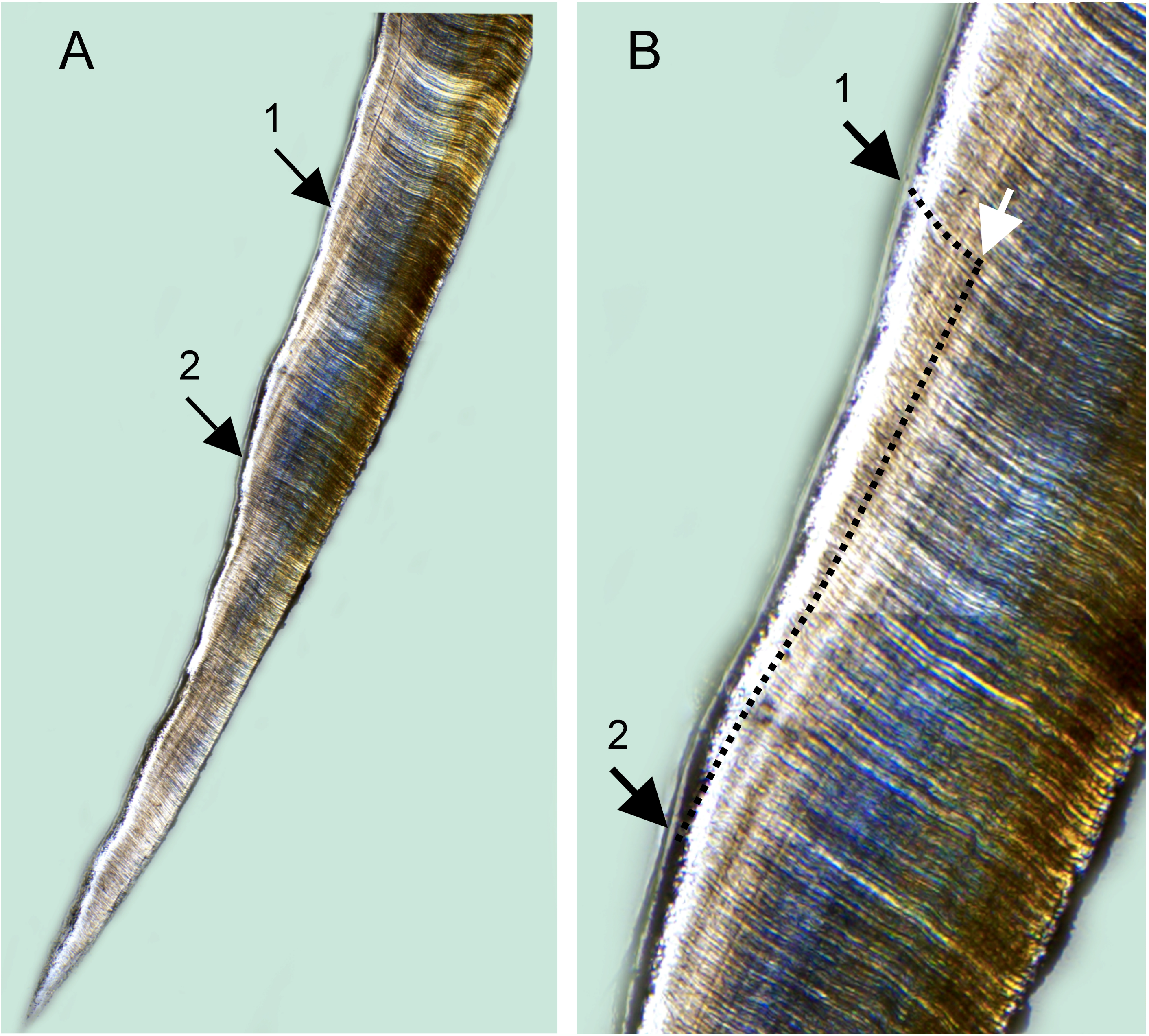
Figure 2. Thin section of a dC^1 root of *Pongo pygmaeus* (catalogue number CA28.J57c). A) Thin section image produced at a magnification of 4× using polarized microscopy. B) Section image produced at a magnification of 20×. Black arrow 1 points to a black dashed line that traces a dentine tubule from the cement-dentin junction inwards for a distance of 200 μm to the white arrow. This distance of 200 μm between these two arrows formed in 56 days. The dashed line between the white arrow and black arrow 2 traces an accentuated growth line. The length of the root in μm between black arrow 1 and black arrow 2 divided by 56 days gives an estimate of the rate in μm/day that the root extends in length between the two black arrows.

Figure 3. A) Scatter plot illustrating extension rates for the first 5 mm of root growth in human deciduous teeth. B) Extension rates for the first 5 mm of root growth in dC^1 of modern humans, *Pan troglodytes*, and *Pongo pygmaeus*.

Figure 4. Root extension rates related to the age at which dC^1 emerges for *Pan* and *Pongo*. A) Crown completion occurs at 318 days after birth (see Table 1 footnotes). Root extension rates are taken from the footnotes of Table 1 and have been calculated for consecutive segments of root length. Median dC^1 crown emergence times for captive male and female chimpanzees lie between 335 to 372 days (1.02 yr: Kuykendall et al., 1992; 0.97 yr for males and 0.92 yr for females, average of left and right maxilla: Nissen and Riesen, 1945). The 5th to 95th percentile of 0.64 yr to 1.35 yr is taken from Kuykendall et al. (1992). B) Crown completion occurs 253 days after birth in this *Pongo pygmaeus* dC^1 (see Table 1 footnotes). Root extension rates are taken from the footnotes in Table 1 for consecutive segments of root length. Tooth emergence times are taken from Fooden and Izor (1983) and are for captive modern orangutans nursed by their mothers. Mean emergence times for males = 412 days (342 to 487 days). Mean emergence time for females = 434 days (427 to 448 days); the greater range of values for males is illustrated.

Figure 5. Mean root extension rates for human deciduous maxillary teeth related to the portion of root that forms as each tooth type emerges through alveolar bone. A) Alveolar emergence occurs when dI^1 root is a mean length of 1.81 mm ±1 SD of 1.14 (range of 0.67 to 2.95 mm; recalculated from data in Liversidge and Molleson, 2017: their Tables 5 and 6). B) Alveolar emergence occurs when dI^2 root length is a mean of 2.64 mm (±1 SD of 1.48 to 3.80 mm). C) Alveolar emergence occurs when dC^1 root length is a mean of 1.76 mm (±1 SD of 1.03 to 2.49 mm). D) Alveolar emergence occurs when dP^3 root length is a mean of 2.56 mm (±1 SD of 2.41 to 2.71 mm).


A
B
2
1
3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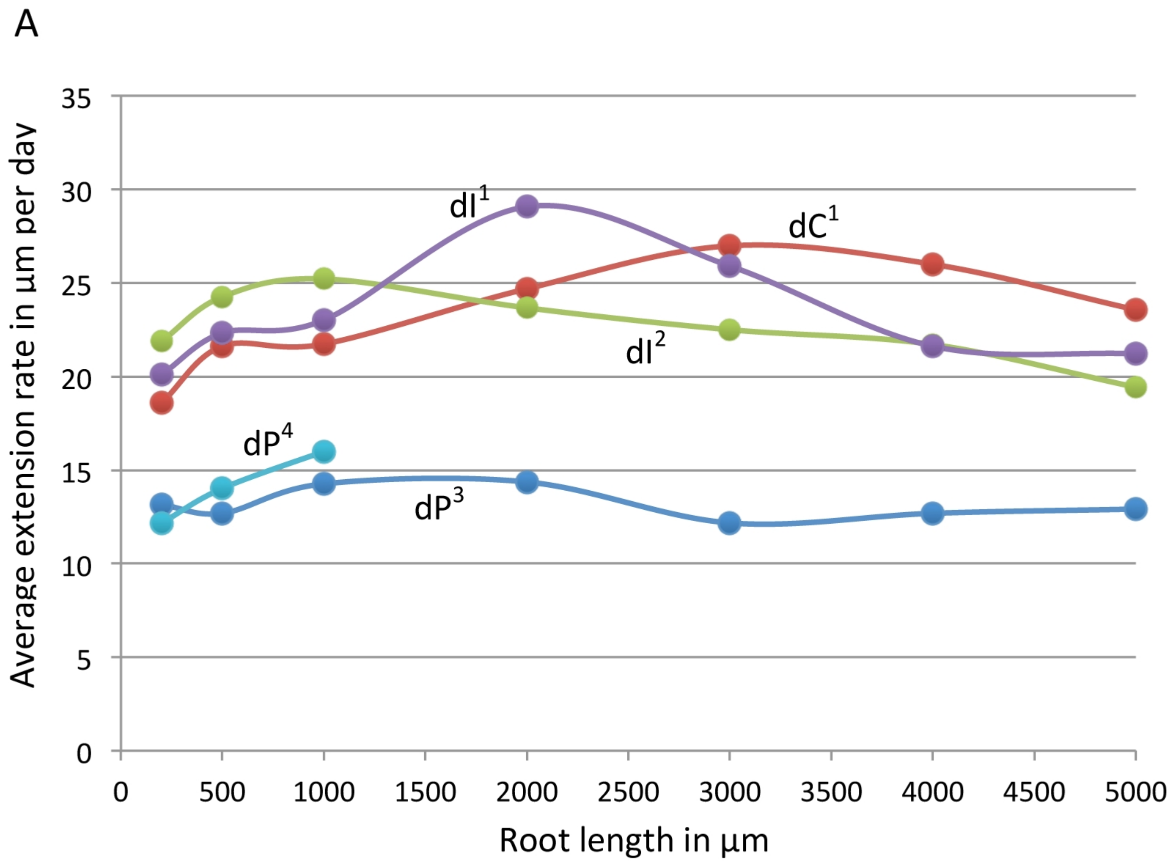
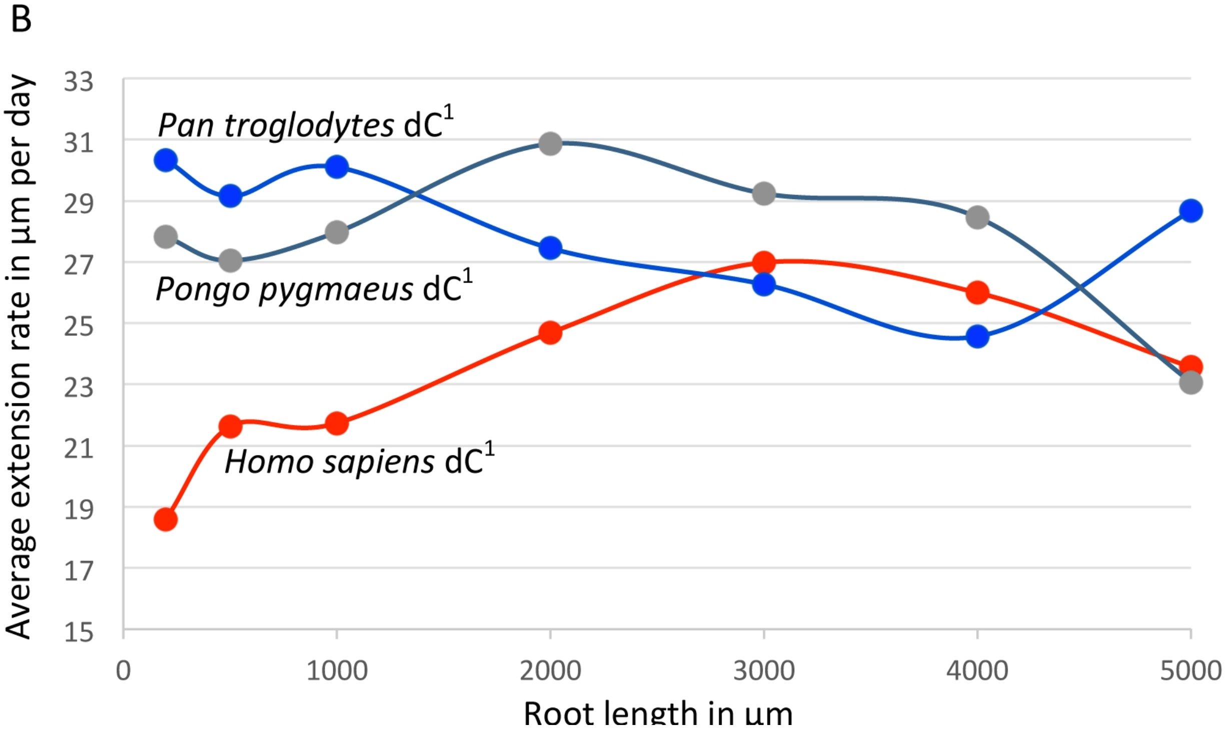
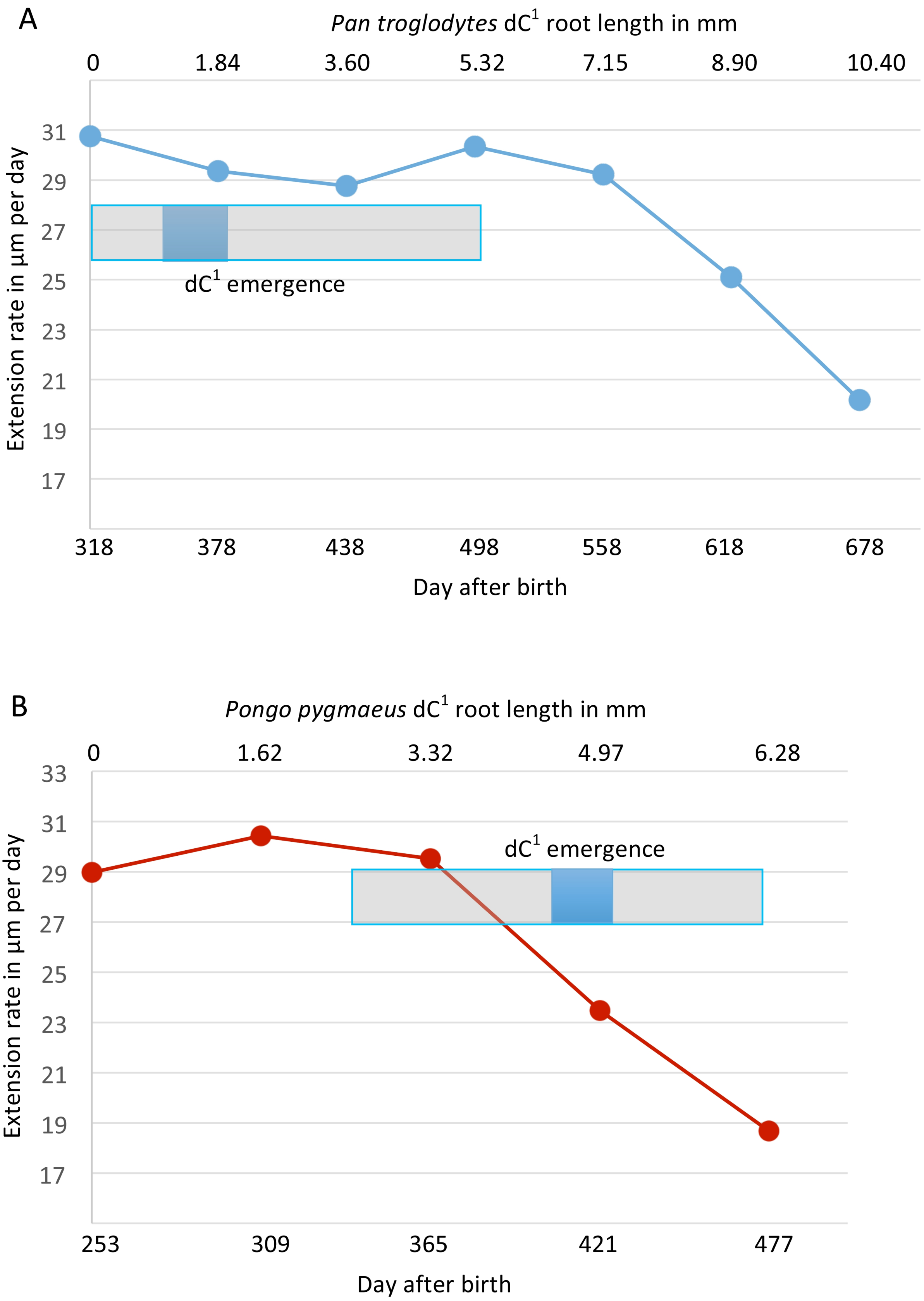

A
Average extension rate in µm per day
35
30
25
20
15
10
5
0
0
500
1000
1500
2000
2500
3000
3500
4000
4500
5000
Root length in µm
dI1
dC1
dI2
dP4
dP3


B
Average extension rate in µm per day
33
31
29
27
25
23
21
19
17
15
0
1000
2000
3000
4000
5000
Root length in µm
Pan troglodytes dC1
Pongo pygmaeus dC1
Homo sapiens dC1


A
Pan troglodytes dC¹ root length in mm
0
1.84
3.60
5.32
7.15
8.90
10.40
Extension rate in µm per day
31
29
27
25
23
21
19
17
dC¹ emergence
318
378
438
498
558
618
678
Day after birth
B
Pongo pygmaeus dC¹ root length in mm
0
1.62
3.32
4.97
6.28
Extension rate in µm per day
33
31
29
27
25
23
21
19
17
dC¹ emergence
253
309
365
421
477
Day after birth

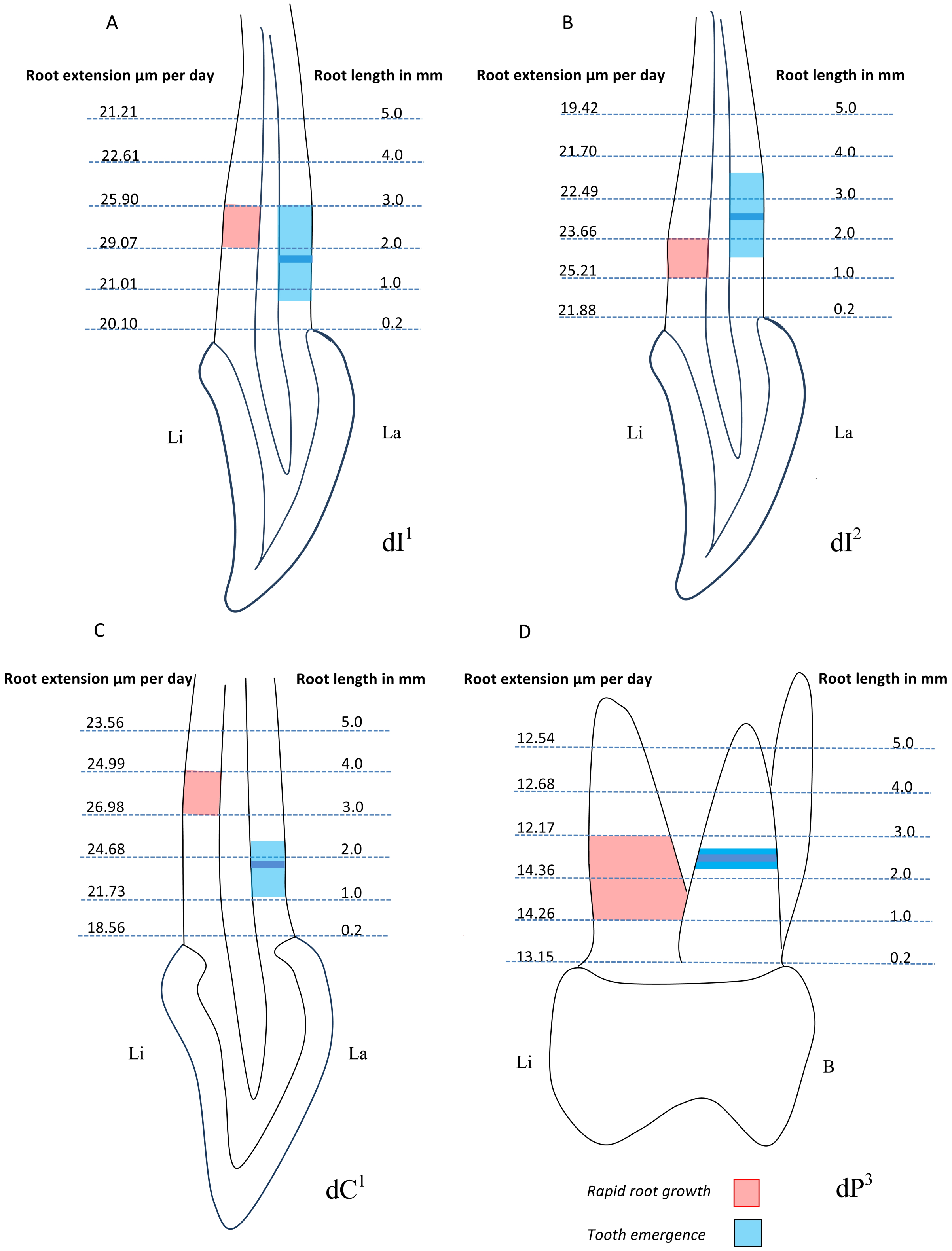

A
Root extension µm per day
Root length in mm
21.21
5.0
22.61
4.0
25.90
3.0
29.07
2.0
21.01
1.0
20.10
0.2
Li
La
dI^1
B
Root extension µm per day
Root length in mm
19.42
5.0
21.70
4.0
22.49
3.0
23.66
2.0
25.21
1.0
21.88
0.2
Li
La
dI^2
C
Root extension µm per day
Root length in mm
23.56
5.0
24.99
4.0
26.98
3.0
24.68
2.0
21.73
1.0
18.56
0.2
Li
La
dC^1
D
Root extension µm per day
Root length in mm
12.54
5.0
12.68
4.0
12.17
3.0
14.36
2.0
14.26
1.0
13.15
0.2
Li
B
dP^3
Rapid root growth
Tooth emergence

Table 1

Extension rates in µm/per day (SD) in deciduous teeth at intervals between 200 µm and 5000 µm of root length.

Species	*n*	Tooth	200	500	1000	2000	3000	4000	5000	Average
H. sapiens	5	dI^1	20.10	22.32	21.01	29.07	25.90	22.61	21.21	23.17
			(2.03)	(1.65)	(1.79)	(1.50)	(1.05)	(1.53)	(1.53)	(1.58)
	5	dI^2	21.88	24.25	25.21	23.66	22.49	21.70	19.42	22.65
			(3.08)	(3.04)	(1.69)	(1.46)	(0.99)	(0.96)	(1.03)	(1.75)
	6	dC^1	18.56	21.62	21.73	24.68	26.98	24.99	23.56	23.16
			(3.69)	(2.82)	(0.93)	(1.66)	(1.75)	(0.92)	(1.44)	(1.88)
	6	dP^3	13.15	12.68	14.26	14.36	12.17	12.68	12.54	13.12
			(3.48)	(1.79)	(2.02)	(1.42)	(1.63)	(0.99)	(1.06)	(1.77)
	6	dP^4	12.17	14.0	15.99	—	—	—	—	14.05
			(2.43)	(2.20)	(2.10)	—	—	—	—	(2.24)
P. troglodytes[a]	1	dC^1	30.33	29.15	30.10	27.45	26.27	24.57	28.67	28.08
	1	dC_1	31.67	32.03	28.20	25.45	—	—	—	29.33
	1	dP^3	20.47	22.71	—	—	—	—	—	21.59
Po. Pygmaeus[b]	1	dC^1	27.83	27.05	27.97	30.86	29.24	28.46	23.07	27.78
	1	dP^4	17.71	17.25	16.45	—	—	—	—	17.13

[a] Using the methodology of Dean and Cole (2013) to reconstruct rates for consecutive segments of dC^1 root length in *Pan* commencing at the enamel cervix and continuing down along the root towards the root apex: 30.76 µm/day (cervix to 1.84 mm); 29.35 µm (1.84 to 3.60 mm); 28.77 µm (3.60 to 5.32 mm); 30.55µm (5.32 to 7.15mm); 29.33 µm (7.15 to 8.90 mm); 25.10 µm (8.90 to 10.40 mm); 20.16 µm (10.40 to near apex).

[b] Reconstructing rates for consecutive segments of dC^1 root length in *Pongo* commencing at the enamel cervix and continuing down along the root towards the root apex: 28.98 µm/day (cervix to 1.62 mm of root length); 30.44 µm/day (1.62 to 3.32 mm); 29.53 (3.32 to 4.97 mm); 23.48 (4.97 to 6.28 mm); 18.67 (6.28 to 7.32 mm).