Patterns of permanent incisor, canine and molar development in modern humans, great apes and early fossil hominins.

M. Christopher Dean[1,2*], Sing-Ying Lim[3], Helen M. Liversidge[3]

1. Centre for Human Evolution Research, Natural History Museum, Cromwell Road, London, SW7 5BD, UK

2. Department of Cell and Developmental Biology, University College London, Gower Street, London, WC1E 6BT, UK.

3. Institute of Dentistry, Barts and The London School of Medicine and Dentistry, Queen Mary University of London, Turner Street, London, E1 2AD, UK

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*Author for correspondence:
Christopher Dean
Email: ucgacrd@ucl.ac.uk
Orcid.org/0000-0003-3783-7296

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Abbreviations:

M1, first permanent molar; M2, second permanent molar; M3, third permanent molar; UE, unerupted; AE, alveolar eruption; PE, partially erupted; FE, fully erupted; Cr, crypt; Crs, small crypt; Crm, medium sized crypt; Crl, large crypt; C, crown; Ci, crown initiation; CC, crown complete; CCa, anatomical crown complete; CCr, radiographic crown complete; R, root; Ri, root initiation; A, root apex; AC, root apex complete.

Abstract

Objective: The objectives of this study were to quantify the variation in coincident stages of incisor, canine and molar eruption and tooth formation in modern humans and great apes and then to ask if any early fossil hominins showed a dental development pattern beyond the human range and/or clearly typical of great apes.
Design: Four stages of eruption and 18 stages of tooth development were defined and then scored for each developing tooth on radiographs of 159 once-free-living subadult great apes and on orthopantomographs of 4,091 dental patients aged 1-23 years. From original observations, and from published images of eleven early fossil hominins, we then scored formation stages of permanent incisors when M1 was at root formation stage R¼ -R½ and R¾-RC.
Results: Incisor and canine eruption/development was delayed in great apes relative to molar development when compared with humans but there was overlap in almost all anterior tooth stages observed. Molar crown initiation was generally advanced in great apes and delayed in humans but again, we observed overlap in all stages in both samples. Only two fossil hominin specimens (L.H.-3 from Laetoli, Tanzania and KNM-KP 34725 from Kanapoi, Kenya) showed delayed incisor development relative to M1 beyond any individuals observed in the human sample.
Conclusions: For certain tooth types, the distribution of formation stages in our samples showed evidence of generally advanced or delayed development between taxa. However, it would rarely if ever be possible to allocate an individual to one taxon or another on this basis.

1. Introduction

Developing teeth pass through successive stages of formation. Patterns of dental development result when in several developing dentitions two or more teeth at different stages of formation consistently coincide with each other. There is also a pattern to the sequence of gingival emergence, or eruption, where teeth of different tooth types consistently erupt close in time to each other. Differences in the sequence or pattern of dental formation stages and of eruption have been described between modern humans and great apes and have been used to distinguish various early fossil hominin taxa as being like either living great apes or modern humans. In this study we revisited this issue using imaging and radiographic data derived from a larger number of individuals than has previously been available.

Studies of skeletal and dental growth in great apes have a long history and have sought to provide a comparative framework for both modern human growth and for studies of human evolution (Bingham, 1929; Brandes, 1928; Fooden & Izor, 1983; Gavan 1953; Gavan & Swindler, 1966; Kraemer et al., 1982; Krogman, 1930; Schultz, 1933; Tanner, 1978; Willoughby, 1978; Zihlman et al., 2007; Zuckerman, 1928). Studies of the timing of gingival emergence and of the sequence of permanent tooth emergence in great apes also have a long history. These studies have identified differences in the sequence, or pattern, of tooth eruption between great apes and modern humans and in many cases have provided chronological data for gingival emergence (Clements & Zuckerman, 1955; Conroy & Mahoney, 1991; Kuykendall et al., 1992; Machanda, et al., 2015; Nissen & Riesen, 1945; Nissen & Riesen, 1964; Simpson et al., 1990; Simpson et al., 1992; Smith, 1986;

Smith, 1994a; Smith, 1994b; Smith et al., 1994c; Smith, et al., 2010; Smith & Boesch, 2011; Smith, et al., 2013; Zihlman et al., 2004).

From these studies there is consensus about two things. First, compared with modern humans, the permanent incisor teeth of great apes emerge relatively later in the growth period, closer to second permanent molars than to first permanent molars as in modern humans. By way of example, the sequence of incisor emergence occurring before first permanent molar emergence, that occurs commonly in modern humans (Sato & Parsons, 1990) is unknown in great apes (Kuykendall et al., 1992). Second, the permanent canines in great apes also emerge relatively late in development compared with modern humans, closer to the third permanent molars than to the second permanent molars as they do in modern humans. Other so-called sequence polymorphisms, including those that involve the premolars and second permanent molars, have also been documented both within and between hominoid taxa but these seem to be less consistent and far more variable (Clements & Zuckerman, 1955; Cofran & Walker, 2017; Conroy & Kuykendall, 1995; Garn & Lewis, 1963; Kuykendall & Conroy, 1996; Simpson et al., 1990, 1992).

Radiographic studies of tooth development in great apes have provided further information about the sequence of crown and root formation stages both prior to and after gingival emergence (Anemone, Watts & Swindler, 1991; Boughner, Dean & Wilgenbusch, 2012; Boughner et al., 2015; Dean & Wood, 1981; Winkler et al., 1991) and when the chronological age of individuals has been known it has been possible to put a time scale to radiographically defined stages of tooth development in great apes (Anemone et al., 1996; Kralick, et al., 2017; Kuykendall, 1996). Besides these radiographic studies, histological studies have provided yet more evidence for the chronology of crown and root formation stages in developing great ape dentitions (Beynon et al., 1991; Dean, 2010; Kelley & Schwartz, 2010; Reid et al., 1998; Schwartz & Dean, 2001; Schwartz et al., 2006; Smith et al., 2007; Smith, 2016).

An unresolved issue arising from radiographic and histological comparisons of modern human and great ape dentitions is to what degree there is overlap in the development of M1 and M2 crown formation and of M2 and M3 crown formation and whether this relates simply to differential tooth size, space in the jaws and/or jaw growth (Boughner & Dean, 2004; Simpson et al., 1992; Tompkins, 1996a; Tompkins 1996b). Prolongation of dental development in modern humans compared with that in great apes has been attributed in part to a delay in the timing of molar initiation, however, variation in molar overlap has never been quantified adequately in modern humans and great apes in a comparable way.

Studies that have attempted to compare the sequence or pattern of dental development and eruption in fossil hominins with those observed in modern humans and great apes have overall been problematic. Clearly, gingival emergence can never be observed in fossils or in museum specimens and mixing observations about radiographic stages of development with assumptions about gingival emergence has generally been regarded as less than satisfactory. Observations about the stages of dental development or tooth eruption status made using the same definitions and on large enough samples of modern humans and great apes have not always been readily available for comparison (Beynon & Dean, 1991;

Broom & Robinson, 1951; Conroy, 1988; Dean, 1985; Dean, 1987; Dean et al., 1993; Dean & Liversidge, 2015; Garn et al., 1957; Garn & Lewis, 1963; Grine, 1987; Kelley & Schwartz, 2012; Kuykendall & Conroy, 1996; Mann et al., 1990; Moggi-Cecchi et al., 1998; Smith, 1986; Smith, 1994a, Smith, 1994b; Wallace, 1977).

Aims of the study

The aim of this study was to combine radiographic data for a large sample of modern humans with comparable data collected from existing radiographs of once free-living great ape specimens of *Pan, Gorilla* and *Pongo*. We aimed to resolve several issues that have compromised previous studies. First, we aimed to define stages of tooth eruption that can be scored on the same radiographs as tooth formation stages. Second, we defined stages of tooth development that are comparable across the morphologically distinct teeth of all three great ape taxa and modern humans. Third, by employing radiographs of great ape dentitions taken in three planes at right angles to each other we aimed to minimise error in defining stages of tooth formation that cannot always be clearly imaged in one plane alone. With this comparable database we then aimed to investigate ways to best quantify the variation in incisor and canine delay and of molar overlap in great apes compared with modern humans. Finally, we asked if any early fossil hominins, that are already well-described in the literature, fell beyond the range of variation observed in our modern human sample.

2. Materials and Methods

Radiographs taken in three planes, lateral, frontal and superior/occlusal, of 159 once free-living infant, juvenile and sub-adult great apes and that are now held in museum collections (Dean, 2022; Dean & Wood, 1981; Dean & Wood, 2003: Gordon et al., 2013) were available to us and were included in this study. Fig. 1 shows an age series of lateral radiographs of *Pan troglodytes* illustrating both molar and anterior tooth development. The composition of the great ape and human samples, including the numbers of individuals of known sex, is presented in Table 1. The great apes used in this study were previously each given a relative radiographic dental age (Dean, 1981; Dean & Wood, 2003) which was used here to illustrate the range of ages represented. The age distribution of the great ape and human sample is shown in Fig. 2. A further 41 high-quality sets of mandibular periapical radiographs of once free-living known sex and age at death infant, juvenile and sub-adult specimens of Virunga mountain gorillas (*Gorilla beringei beringei*) published by Kralick et al., (2017) were also scored for tooth eruption stage and tooth formation stage and included in this study where possible. The radiographs published by Kralick et al. (2017) are of mandibular posterior teeth only. These individuals are also included in Fig. 2 to show the overall distribution of ages represented in this study. Clinical orthopantomographs of 4,091 dental patients aged 1-23 years were available to us and made up the modern human reference sample used in this study. This archive of anonymised retrospective clinical radiographs is made up of panoramic radiographs previously taken with informed consent for diagnosis and treatment of healthy individuals at the Institute of Dentistry, Bart's and The London School of Medicine and Dentistry (AlQahtani, et al., 2010). Many have previously been scored for eruption stages and developmental stages (Liversidge, et al., 2006; 2008; 2016).

The distribution of ages of this sample are shown in Fig. 2. The archive includes radiographs of 1,981 males and 2,110 females.

Eleven early fossil hominins were identified that have been imaged with either computed tomography, traditional X-ray radiography or by high resolution synchrotron imaging and were included in this study for comparison (Fig. 3). Five fossils included here have been attributed to the genus *Australopithecus.* KNM-KP 34725 from Kanapoi, Kenya, has been described and the tooth formation stages illustrated by Smith, et al., (2015) and Le Cabec, et al., (2015). L.H.-2 and L.H.-3 from Laetoli, Tanzania are both described and illustrated by White, (1977); the Taung infant skull from South Africa by Skinner & Sperber, (1982) and Conroy & Vannier, (1987; 1991a); and Sts 24 from Sterkfontein, South Africa by Skinner & Sperber, (1982), Conroy & Vannier, (1991a), Smith et al., (2015) and Le Cabec, et al., (2015). One specimen (StW 151 from Sterkfontein, South Africa) remains equivocal in its attribution to either early *Homo* (Moggi-Cecchi et al., 1998; Spoor, 1993). StW 151 has been described in detail and the tooth formation stages illustrated by Moggi-Cecchi et al., (1998), Smith, et al., (2015) and Le Cabec, et al., (2015). Four specimens included in this study have been attributed to the genus *Paranthropus*. Three of these, SK61, SK62, SK63 from Swartkrans, South Africa, have been imaged and described by Skinner & Sperber, (1982), Grine, (1987), Conroy & Vannier, (1991a, 1991b) and Dean et al., (1993) and one of them, DNH 107 from Drimolan, South Africa, has been described and illustrated by Moggi-Cecchi, et al., (2010), Smith, et al., (2015) and Le Cabec, et al., (2015). KNM-ER 820 from Koobi Fora, Kenya, is attributed to early *Homo* and has been previously described and illustrated by Dean, (1987, 2000), Wood, (1994) and Le Cabec, et al., (2015).

2.1 Definition of eruption and tooth formation stages

We defined 4 stages of tooth eruption that can be scored from lateral radiographs and that are essentially similar to those that have previously been adopted in radiographic studies of modern humans and great apes (AlQahtani et al., 2010; Dean, 2007; Macho & Lee-Thorp, 2014; Liversidge, 2016). These were: Unerupted (UE) within the alveolar bone: Alveolar eruption (AE) where cusps were just above the level of the alveolar bone crest: Partially erupted (PE) where cusps were at least level with the mid-height of the fully erupted tooth mesial to it: Fully erupted (FE) with a tooth at the occlusal plane and in functional occlusion (Fig. 4).

Previous studies have either simply adopted tooth formation stages similar to those defined for modern humans (Anemone et al., 1996; Dean & Wood, 1981; Kralick, et al., 2017; Kuykendall, 1996; Simpson et al., 1990, 1992) or have defined stages specifically for *Pan, Gorilla* or *Pongo* (Boughner et al., 2012; Macho & Lee-Thorp, 2014; Winkler et al., 1991) or have devised definitions of tooth formation stages more suitable for virtual buccolingual sections of synchrotron and micro-CT images of fossil hominin teeth (Gunz, et al., 2020). Here we defined 18 stages of tooth development that can be applied to all three living great ape taxa in what we feel is an objective and comparable way (Figs. 5 and 6). However, the practicalities of allocating a tooth to a given developmental stage can often be problematic, especially when radiographs are less than ideal.

To test the suitability of these stage definitions of tooth formation, we first questioned whether they were sufficiently evenly spread across molar formation times by plotting the stages scored for M1, M2 and M3 against age (Fig. 7) in 40 gorilla individuals of known age at death (Kralick et al., 2017). To test the reliability and repeatability of tooth stage allocation two authors (CD and HL) scored all the developing great ape teeth used in this study and then scored 10% of the great ape radiographs a second time more than 6 months later. Kappa values showed good agreement for both tooth stages and eruption status calculated from duplicate scoring of 100 teeth (weighted kappa 0.956 and 0.952 respectively).

In the process of defining, and then refining, these tooth formation stages we considered the following points. Not all previous studies have recorded the presence of an empty crypt in great ape jaws, nor have they distinguished between small and large crypts. However, the earliest mineralising stages of cusp tips are easily lost from their crypts along with the soft tissues when specimens are macerated, and a large empty crypt may in fact often be the earliest indicator of tooth initiation. Occlusal crown morphology also differs between taxa and tall cusps may remain separate for longer than flatter cusps that coalesce earlier. Mandibular molars in great apes begin to develop with their occlusal surface orientated lingually and with their pulpal aspect facing buccally so that it is hard to define fractions of crown development from lateral radiographs alone.

Defining the stage of crown completion and the end of enamel formation from radiographs taken in the buccolingual plane is difficult as enamel forms last on the buccal surface of the crown which is often indistinct on lateral radiographs (Beynon, et al., 1998). Crown completion is almost always defined on the mesial and distal aspects of a tooth in radiographic studies. Gleiser & Hunt (1955) defined minimal cleft formation (their stage VIII A) in modern humans as occurring immediately after radiographic crown completion mesially and distally (their stage VII). However, anatomical crown completion differs from this and may occur some months later than radiographic crown completion. Examination of the specimens used in this study, and explored here further (Fig. 8), suggest there is considerable variation in buccal enamel cervix morphology. In the gorilla and chimpanzee molars observed in this study it is the distobuccal enamel that extends furthest cervically, while in orangutan molars it is the mid-buccal enamel that extends furthest cervically, even into the root furcation area as a chevron-like spur of enamel (Fig. 8). This not only complicates definitions of what constitutes crown completion (the end of enamel formation) but has contributed to apparent differences in histologically derived data for molar enamel formation times compared with radiographically derived data (Beynon, et al., 1998). The root furcation in great ape molars is positioned higher than in modern human molars and we observed that furcation initiation with the first evidence of inter-radicular process development appears to coincide with anatomical crown completion. Beynon et al., (1991) previously noted that root furcation and root initiation can in fact precede enamel completion in some great ape tooth types. Both Boughner et al., (2012) for *Pan paniscus* and Swindler & Gavin, (1962) and Swindler et al., (1982) for macaques have previously noted that an inter-radicular cleft forms prior to root initiation when the furcation is higher than in modern human molars.

Compared with modern humans, tall great ape anterior teeth show a more marked difference in the height of the enamel cervix mesially and distally compared with that on the buccal or lingual and enamel completion on the buccal aspect. Viewed buccolingually on radiographs this appears only as a faint shadow after enamel is completed whereas it is more clearly imaged on lateral radiographs beneath the contour of the cingulum and buccal enamel cervix. Fig. 8 illustrates some of these issues. To clarify our definitions of certain radiographic tooth formation stages we applied radio-opaque paste around the cervix of selected isolated great ape teeth and on this basis two stages of crown completion (CC) were defined, radiographic crown completion mesially and distally (CCr) and anatomical crown completion buccally (CCa). Radiographic stages of crown or root formation are often defined as fractions of height or length (Fig. 9). Familiarity with large samples of radiographs of modern humans make it easier to anticipate what the final crown height or root length will be and so to judge what fraction has formed. Root length estimates of a quarter (R¼), a half (R½), three quarters (R¾) and root length at or greater than 90% completed (RC) were defined here as well as two subsequent stages of root apex formation, apex half formed (A ½) and apex complete (AC). However, estimating what fraction of crown height or root length has formed in great apes (and more so in fossil hominins), where variation both within and between taxa is less well documented, make these proportional judgements less reliable.

With these observations in mind 18 stages of tooth formation were defined and given a numerical value (Table 2). Some scores for great apes were not made in the same way or did not have an equivalent score in the human sample and/or were added later when issues of resolution arose and so appear here with an intermediate (0.5) numerical score. Once scored for all tooth types on all radiographs there was then an option to combine more than one great ape stage once the sample sizes for each analysis were known and to best match the equivalent scores for human and great ape samples in each analysis.

2.2 Analysis of the data

Having scored all teeth, we first investigated differences between pairs of upper and lower teeth of the same tooth type in the same individuals at representative stages of development throughout the whole dental developmental period. We chose tooth types where it was important for the subsequent analyses to establish whether differences between upper and lower teeth were consistently scored as either advanced or delayed with respect to each other. Only when no differences between upper and lower tooth scores were found to exist was a stage of formation used as the basis of a subsequent analyses that combined both uppers and lowers. In the analyses that included fossil hominins, and where incisor scores differed in other analyses, both maxillary and mandibular teeth were always represented separately. Where sample sizes of individuals of known sex allowed, we looked for differences at each developmental stage. Despite the large sample of great ape specimens overall there were relatively few in each of the analyses. In two analyses where the total number of individuals was sufficient and distributed over 6 or more formation stages we presented the data for *Pan, Pongo* and *Gorilla* separately.

We then explored the dataset and chose eight stages of tooth formation and/or eruption, where samples sizes were sufficient, with which to compare the formation stages and/or eruption stages in other teeth forming at the same time. We sought the best ways to express i) the development/eruption of anterior teeth relative to molars,

ii) to document the degree of sequential molar overlap, and finally, iii) to document the variation in incisor development relative to first permanent molar (M1) root stage R½-R¾ and at M1 root stage RC-A½ in great apes and humans with a view to including eleven early fossil hominin dentitions for comparison. The Mann Whitney test is a non-parametric test and is therefore appropriate here as it does not assume any particular distribution for the variables of either group when comparing whether the distribution of two groups is the same or not. Mann Whitney tests were performed for each of the comparisons between the great apes and human distributions at defined stages of dental development shown in Figs. 9-14. The difference in distributions was significant ($P< .05$) for them all (Table 3).

3. Results

3.1. Differences between upper and lower stages of active canine eruption

At active eruption of the canines (eruption stages 2 & 3) there were 16 specimens with actively erupting canines of which 14 had both maxillary and mandibular canines. Only in one case was a lower canine scored at a delayed stage of eruption relative to an upper (UC stage 2 versus LC stage1) and in only one case was a lower canine scored at an advanced stage of eruption relative to an upper (LC stage 2 versus UC stage 1). Of these 14 individuals the sex of only 5 was known (4 females and 1 male) but the sex of the two individuals with different scores for upper and lower canines was unknown.

3.2. Differences between upper and lower stages of molar crown initiation

At M1 initiation (stages 2 & 3, Crl & Ci) there were only 4 specimens, (1 *Pan*, 3 *Gorilla*) with both UM1 and LM1 present at initiation stages 2 & 3. In 1 specimen stages were scored equal, however in 3 specimens LM1 was ahead of UM1 by one stage. At M2 initiation (stages 2 & 3) there were 12 specimens, (4 *Pan*, 5 *Gorilla* and 3 *Pongo*) with both UM2 and LM2 present at initiation stages 2 & 3. In 2 specimens, stages were scored equal, in 9 specimens, LM2 was ahead of UM2 by one stage but in only 1 specimen was UM2 ahead of LM2. At M3 initiation (stages 2 & 3) there were 18 specimens, (9 *Pan*, 7 *Gorilla* and 2 *Pongo*) with both UM3 and LM3 present at initiation stages 2 & 3. In 2 specimens, stages were scored equal, in 13 specimens, LM3 was advanced with respect to UM3, and in 3 specimens UM3 was advanced with respect to LM3. Out of the sample of 18 individuals at M3 initiation there were only 6 known males and 1 known female. In general, there were insufficient numbers of individuals of known sex at M1, M2 and M3 initiation to compare. Overall, lower molar initiation was found to be advanced by approximately 1 stage with respect to upper molar initiation (UM1 mean score = 2.2, LM1 mean score = 3.0; n=4; UM2 mean score = 2.2, LM2 score = 2.8, n=12; UM3 mean score = 2.1, LM3 mean score = 2.9, n=18).

3.3. Differences between upper and lower stages of molar crown completion

At M1 crown completion (stages 6.5 and 7 combined, CCr & CCa) there were 13 specimens (5 *Pan*, 4 *Gorilla*, 4 *Pongo*) with both UM1 and LM1 present at (stages 6.5 & 7). In only 1 case (*Pan*) did the score for UM1 and LM1 differ (6.5 for UM1 versus 6 for LM1). At M2 CC there were 14 specimens (5 *Pan*, 5 *Gorilla*, 4 *Pongo*) with both UM2 and LM2 present at stages 6.5 & 7. In only 1 case of *Pan* did the score for UM1 and LM1 differ (7 for UM2 versus 6.5 for LM2). There were 5 specimens (3 *Pan*, 1 *Gorilla*, 1 *Pongo*) with both UM3 and LM3 present at stages 6.5 & 7. In only 1 case of *Pan* and 1 case of *Pongo* did the score for UM3 and LM3 differ (7 for UM3 versus 7.5 for LM3 in *Pan,* and 6.5 for UM3 and 6 for LM3 in *Pongo* - i.e., LM3 was ahead in one case and UM3 ahead in the other). There were insufficient numbers of individuals of known sex at M1, M2 and M3 crown completion to compare. Overall, there was no difference in the scores for upper and lower molars at crown completion (UM1 mean score = 6.8, LM1 mean score = 6.8; n=13; UM2 mean score = 6.8, LM2 score = 6.8, n=14; UM3 mean score = 6.9, LM3 mean score = 6.9, n=5).

3.4. Differences between upper and lower stages of root completion

At M1 root stages 11 & 11.5 (RC-A½) there were 32 specimens (19 *Pan*, 8 *Gorilla*, 5 *Pongo*) with both UM1 and LM1 present at stages 11 and 11.5. All stages were scored equal in UM1 and LM1 except in 2 *Pan* specimens where UM1 was at stage 12 versus 11.5 in LM1 in one and where in the other LM1 was at stage 12 and LM1 at stage 11.5. At M2 root stages 11 & 11.5 there are 8 specimens (2 *Pan*, 2 *Gorilla*, 4 *Pongo*) with both UM2 and LM2 present at root stages 11 and 11.5. In only 1 *Pan* specimen did stages differ with UM2 at 11.5 and LM2 at stage 11. At M3 root stages 11 & 11.5 there were only 4 specimens (3 *Gorilla*, 1 *Pongo*) with both UM3 and LM3 present at root stages 11 and 11.5. In 2 *Gorilla* specimens the stages scored differed with UM3 scored stage 10 versus 11.5 in LM3 in one and the reverse in the other with UM3 scored 11.5 and LM3 scored 11. There were insufficient numbers of individuals of known sex at M1, M2 and M3 root completion stages to compare. Overall, there was no difference in the scores for upper and lower molars at these root completion stages (UM1 mean score = 11.4, LM1 mean score = 11.4; n=32; UM2 mean score = 11.2, LM2 score = 11.2, n=8; UM3 mean score = 11.1, LM3 mean score = 11.4, n=5).

3.5. Relative incisor and canine development in humans and great apes

The stage of incisor eruption in humans and great apes was compared at two stages of second permanent molar (M2) formation, CC and R¾-RC. Two stages of active canine eruption (AE and PE) were also then compared to the corresponding stage of third permanent molar (M3) formation in humans and great apes. The results are presented as histograms aligned to the same formation or eruption stages in great apes and humans (Figs. 10, 11 and 12).

At stage M2 crown completion (CC) (Fig. 10) the corresponding stages of combined great ape upper and lower central incisor eruption were between UE and FE. All stages of incisor eruption were also observed in the human sample. However, whereas great ape incisors tended to be unerupted, human central incisors tended to be fully erupted at M2 stage CC. Human lateral incisors, however, (not illustrated) tended to be unerupted at M2 stage CC and so resembled the great ape pattern. There were insufficient numbers to compare upper and lower great ape incisor types individually, but all appeared to show the same great ape trend. The greatest number of great ape specimens had unerupted central incisors, split near-equally between *Gorilla* (4), *Pan* (5) and *Pongo* (3) and with no obvious pattern of distribution across the four eruption stages.

At stages M2 root three quarters formed to root complete (R¾-RC) (Fig. 11) the corresponding stages of both great ape and human permanent canine eruption spanned all stages (UE-FE). For both upper and lower canines in great apes most individuals had unerupted canines while among the modern human sample the majority were more advanced and had either actively erupting (AE-PE) or fully erupted (FE) canines. The greatest number of great ape specimens had unerupted canines, split near-equally between *Gorilla* (16) and *Pan* (15). There were only 6 *Pongo* specimens represented in this analysis with 2 each at stages 1, 2 and 3. Bearing in mind the smaller *Pongo* sample size, no obvious pattern of distribution between the great ape genera could be identified across the four stages of canine eruption.

At active eruption of the canine (AE-PE) the corresponding stages of M3 development were different in the human and great ape samples (Fig. 12). The range of M3 stages in great apes was from C½-R½. In the human sample the range of M3 stages was from Cr0-C¾. M3 formation was therefore shifted towards more advanced stages in the great ape sample but to relatively delayed stages of development in humans. The relative distribution of numbers of individuals at each of the M3 stages appeared similar in great apes and humans. The great ape specimens scored in active canine eruption are distributed over 6 formation stages (Fig. 12) and, more so in some other analyses, are split by near-equal numbers between *Gorilla*, *Pan* and *Pongo*. There is no discernable pattern to the distribution of *Gorilla*, *Pan* or *Pongo* that would distinguish any of them but it is 4 *Gorilla* specimens that were scored at the most advanced stage (C½) of M3 formation.

3.6. Molar overlap in humans and great apes

Three molar formation stages in the human and great ape samples were chosen that spanned the period of dental development: M1 stage CC, M2 stage CC and M1 stage RC-A½. The results are shown in Figs. 13, 14 and 15. Since the numbers of great apes at these stages was relatively small the three stages of crypt formation originally scored, Crs, Crm and Crl, were combined to a single ‘crypt present’ stage to match the human score ‘crypt’. We were able to score the stages of M2 formation in 29 great apes where M1 was at stage CC (Fig. 12) and to score stages of M3 formation in 32 great apes where M2 was at stage CC (Fig. 13) and compare the degree of variation in molar overlap with 125 individuals at M1 stage CC and 133 individuals at M2 stage CC from our human sample.

At stage M1 crown complete (CC) the corresponding stages of M2 formation in humans and great apes are shown in Fig. 13. There were no great apes where the M2 score was zero (no crypt visible, Cr0) but there were some humans at this stage. All other stages of M2 formation occurred in both humans and great apes but with a greater proportion of the great ape sample at more advanced stages and a greater proportion of the humans at earlier stages. A larger proportion of great apes were at relatively more advanced stages of M2 development, and a larger proportion of the human sample were relatively delayed at earlier stages of M2 development. A generally advanced pattern of M2 development in great apes and of delayed M2 development in humans relative to M1 at stage CC is apparent from these results but importantly, it would not be possible to assign an individual to one pattern or the other based only on the stage of M2 development. *Gorilla, Pan* and *Pongo* are represented at each of the M2 formation stages, and no obvious pattern of distribution was apparent with such small numbers of individuals at each stage.

At stage M2 crown complete (CC) the corresponding stages of M3 formation in humans and great apes are shown in Fig. 14. All stages of tooth formation from no crypt present (Cr0) to coalescence of the occlusal surface (Cco) were present in humans and great apes but only the more advanced stage of M3 crown a quarter formed (C¼) was present in the great ape sample. While the spread across formation stages was relatively even in great apes, the human sample tended towards the earlier stages (no crypt visible to crypt present) with very few individuals at stages Ci and Cco. While this supports a tendency for delayed M3 development in humans relative to M2 at CC, any observations made on a single individual from our human sample would not reveal this. There was no obvious distribution pattern of *Gorilla, Pan* and *Pongo* specimens across the M3 formation stages.

At stages M1 root complete (RC) to apex half closed (A½) the corresponding stages of M3 formation in humans and great apes are shown in Fig. 15. At M1 stage RC-A½ the sample size of great apes (n=72) and humans (n=389) with M3 developing is much larger than at M2 stage CC. All stages from Cr0-C¾ were present in both humans and great apes. Again, humans showed a greater proportion of individuals with no M3 crypt visible (Cr0) or at early stages of crown formation and great apes showed a greater proportion of individuals at more advanced stages of M3 crown formation. Even though the later stages of M3 crown formation in humans were proportionately fewer in number when M1 was at stage RC-A½, yet again, observations on individuals would not distinguish a great ape from a human at this stage of M1 root development as both are equally variable across their coincident stages of M3 formation. As there was a larger number of great apes (n=72) distributed across 7 M3 formation stages, the data for *Gorilla, Pan* and *Pongo* were split in Fig. 15 to show individual distributions. *Pongo* numbers were small but there was one specimen with no crypt formed and one at stage C¾. Ten specimens were distributed across stages Cco and C¼. *Pan* was represented across all M3 formation stages but *Gorilla* only in the middle 5 M3 formation stages. There was then no obvious distribution pattern to distinguish *Gorilla, Pan* and *Pongo* specimens across these M3 formation stages.

3.7. Incisor formation in great apes, humans and fossil hominins

Since there are several early fossil hominins at well-defined stages of M1 formation, two M1 root formation stages were chosen to compare with corresponding stages of incisor formation across humans, great apes and 11 early fossil hominins. The results are shown in Figs. 16 and 17. In all cases mandibular and maxillary incisor tooth types were scored separately for human, great ape and fossil hominin samples. When present, the formation stage score for mandibular and maxillary molars was always identical. Great ape incisor samples were small and so were not split by genera.

At M1 stages root a half formed (R½) and/or root three quarters formed (R¾), (Fig. 16) great ape incisors spanned the stages C¼-CC while the human incisors spanned a larger number of more advanced stages from C¾-A½. In the case of both upper and lower incisors of all tooth types, great ape incisor development was relatively delayed compared with humans, while human incisors were all relatively advanced in their stage of development compared with great apes at these same stages of M1 root formation. Five fossil hominins were at stages of incisor development observed in both humans and great apes. However, with respect to lower central incisor development relative to the M1 root stages R½-R¾, five fossil hominin specimens were at a relatively advanced stage of development, beyond the stages observed in the great ape LI1 sample (Fig. 16) although larger great ape incisor sample sizes might well contain individuals with a greater distribution of formation stages.

At M1 stages root three quarters formed (R¾) and/or root complete (RC), (Fig. 17) great ape incisors spanned stages C¾-R¼. It is, however, highly likely this range of distribution of incisor formation stages would be greater given a larger sample size. Human incisors on the other hand were more advanced and the much larger sample size spanned stages Ri-AC, although just one individual out of 442 was observed at UI1 stage C¾. At these later stages of M1 root formation, all great ape incisor types scored in this study were relatively delayed in their development with respect to humans and all human incisor types were relatively advanced in their incisor formation with respect to great apes.

Two fossil hominin specimens were at more advanced stages of incisor development than any in the great ape sample. StW 151 was at stage RC and KNM-ER 820 at A½. One early hominin specimen (L.H.-3) was at the earliest, most delayed, stage observed for UI1 in the human sample. However, another fossil hominin specimen (KNM-KP 34725) fell outside the range of stages observed for humans and was more delayed in incisor development with respect to M1 at this late stage of root formation. With these two exceptions, no other fossil hominin specimens were observed to be both within the great ape range and/or beyond the most delayed individuals in the human sample.

4. Discussion

The living great apes, *Pan, Pongo* and *Gorilla,* each have a long and independent evolutionary history are easily distinguished by many morphological craniodental characters. They are also distinguished by differences in the timing of enamel formation as determined by histology (Smith, 2016, Table 10) and by their rates of molar root formation (Dean, 2006). Here, we defined stages of dental formation that recognise the morphological differences between tooth types in the three living great ape genera and in humans. We have also taken care to try and establish developmental equivalence across the definitions of their tooth formation stages. While some differences between humans and great apes that have been described previously seem clear, we were not able to resolve any more subtle differences in formation pattern that distinguish between *Gorilla, Pan* and *Pongo*. Previously, Schultz (1935) suggested these might exist in premolar and second permanent molar eruption sequences which were not explored in this present study. Future studies of eruption and formation patterns with larger samples sizes of individuals at specific ages are likely to be more successful.

The total time taken to form a tooth, as well as the rate of its formation, varies both within and between individuals, although what data there are for great apes suggests that total tooth formation times are broadly similar to those in modern humans (Dean & Cole, 2013; Kralick et al., 2017; Kuykendall, 1996). However, histological studies have shown that the time taken to complete each defined stage of tooth formation differs within and between tooth types as well as between taxa (Dean & Cole, 2013; Dean, et al., 2020). The time taken between defined radiographic stages of tooth formation, for example, between initiation of the crown and coalescence of the enamel occlusal surface, may only be a matter of weeks. On the other hand, the first quarter of total root length may take a year or more to form (Liversidge et al., 2006; Moorrees et al., 1963). It follows from these observations that the stage of formation or eruption of one tooth type in a dentition may or may not be consistently coincident with those of another tooth type.

Combining observations about the pattern of dental development with other observations on the relative timing or pattern of gingival eruption has been problematic since tooth development and tooth eruption are to some extent independent processes. Here, by defining the stage of eruption and the stage of development for each tooth individually, we have been able to compare the sequence or pattern of both together.

Despite the comparatively large sample of great apes available for study here, the number of individuals at the specific stages of development we analysed was small compared with the human sample. Nevertheless, the large number of individuals in the human sample allowed us to describe the range of variation in co-incident stages of tooth formation with greater confidence than before. Much of the variation in coinciding radiographic formation stages seen in this study at defined reference stages of e.g., molar formation, is likely to be the result of three things. First, the cross-sectional nature of the study, second, because certain radiographic stages capture long periods of time (e.g., active eruption of the canine), and third, because, in the case of the great ape sample, combining relatively small but unequal numbers of great apes from three very distinct taxa to represent a single sample may mask patterns of variation within individual taxa that larger numbers of individuals would reveal. Larger samples of great apes could only ever increase the variation we have observed in this study but would also likely reveal differences between *Pan, Pongo* and *Gorilla.* Previous studies have adopted sophisticated methods to identify differences in pattern across the whole developing dentition that consider the scores of all teeth in the mouth developing at the same time (Bayle et al., 2009; Modesto-Mata et al., 2022). Here we chose to compare just two scores or stages at a time in a way that would allow future studies to easily visualise and compare the results of a single individual modern human, great ape or early fossil hominin against our own data set.

4.1 Differences in maxillary and mandibular tooth scores

It is established in the literature that there is a sex difference in tooth development where females are slightly ahead of males. Demrijian & Levesque (1980) quantified this for modern humans as between one to six months generally but with canines, the most dimorphic tooth type, advanced by as much as 11 months by the later stages of development. They also noted that for molar initiation and the subsequent early stages of molar crown formation (prior to their stage D) no sex differences could be seen. Kuykendall (1996) has documented the same pattern in developing chimpanzee teeth, again with no discernible difference in the early stages of tooth formation and with the greatest differences appearing in the later stages of canine development. Conroy & Mahoney (1991) and Kuykendall, et al., (1992) have also documented significantly earlier gingival emergence times in female chimpanzees than in males. While insufficient numbers of known sex individuals in each of the analyses we carried out made it impossible to detect any sex differences in this study, it is highly likely they exist.

What is surprising in the light of previous studies of sex differences in tooth development is the findings of this study for differences between mandibular and maxillary teeth in the same individual. While once again, the numbers in each analysis are small, the findings of this study appear to follow the opposite pattern. Anderson et al., (1975) and Haavikko (1970) have previously shown there are no difference between maxillary and mandibular molar formation stage scores in either early or late stages of formation in large numbers of children. With respect to great ape canines in this study, the most sexually dimorphic tooth, we found no evidence of a difference in stage of root development between upper and lower great ape teeth during active eruption (stages 2 & 3) even though this event takes place late in dental development in great apes. For M1, M2 and M3 we identified a difference in the earliest stages of development (Cl & Ci combined) of approximately one stage advanced in all mandibular molars relative to maxillary molars but not in the subsequent later stages of molar development (CC and RC-A½) where the scores for upper and lower teeth were essentially the same. This finding justifies combining scores for the later stages of molar teeth (at or beyond stage CC) and for canine eruption stages but not for incisor eruption stages or incisor formation stages. For fossil hominin specimens where both maxillary and mandibular molar teeth are preserved, we also noted identical scores for each molar pair. However, in all cases upper and lower incisor stages were represented separately as they clearly often differed in formation stage.

4.2. Relative incisor and canine eruption in humans and great apes

Previous studies have observed that gingival eruption of permanent incisors is earlier and closer to M1s than to M2s in *Hylobates, Symphalangus, Homo* and certain early fossil hominins, including *Paranthrous,* than in all other hominids studied (Schultz, 1935; Smith. 1986; Smith et al. 1994a; 1994c;). In this study we asked how in modern humans and living great apes the eruption stage of incisors varies relative to M2 at stage CC and then again later in development at M2 at stages R¾-RC. These stages of M2 development are sufficiently separated in time to provide two snapshots of the incisor eruption process. Because the sample of great ape incisors at M2 stage CC was small, all incisor types were combined in this analysis. Nonetheless, all stages of incisor eruption from unerupted to fully erupted were represented in both the great ape and human samples. A greater proportion of great ape incisors were unerupted at M2 stage CC than human central incisors, although the pattern for human lateral incisors was reversed and resembled that in great apes. This makes clear the importance of considering incisor tooth type when describing similarities and differences in incisor eruption status between taxa at this stage of M2 development.

The sample of great ape incisors available when M2 was at stages R¾-RC was larger. At this later stage of M2 development a difference in pattern was clear. Great ape incisor eruption (both upper and lower) was generally delayed relative to M2 while human incisor eruption was advanced. However, since all stages of eruption are represented in both great apes and humans at this stage of M2 development, it would never be possible to assign any one individual to a human or great ape pattern.

Late canine eruption, close to M3 eruption, appears to be the general anthropoid condition and only in hominins does it occur prior to or close to M2 eruption (Schultz, 1935; Smith et al. 1994c). Active eruption of the canines in great apes (stages AE and PE) occurs over a long period of time and may occur earlier in females and continue for longer in males (Kuykendall et al., 1992). Large erupting permanent male gorilla canines have been reported to take 2 to 3 years to reach full eruption (Osman Hill, 1947-1954), much longer than in humans where active eruption may still take 8 to 18 months (Berkovitz & Bass, 1976; Sato & Parsons, 1990). Relative to active canine eruption, great ape M3 development is advanced and human M3 development is delayed. However, despite the presumed longer period of time over which great ape canines erupt, 5 stages of M3 formation, from Ci-C¾, occur over this time in great apes and 7 in humans where M3 stages are more variable at active canine eruption. Despite the much earlier chronological eruption times of human canines there is still some overlap of coincident M3 formation stages at C½ and C¾. It follows that M3 formation stages do not completely distinguish great apes from humans during the active phase of canine eruption but there is greater distinction between them than in any other analysis made in this study.

4.2. Molar overlap in humans and great apes

When the initiation of molar mineralisation occurs before the end of crown completion of the preceding molar, there is overlap of their crown formation stages. Great ape dentitions have been characterised as having molar overlap and it has been suggested this reflects the fact that the time taken to complete dental development is reduced in great apes compared with modern humans. Molar initiation in modern humans, on the other hand, has been characterised as delayed beyond the end of crown completion in the preceding molar such that this then reflects the prolonged period of dental development. On this basis, delayed M3 initiation relative to M2 crown development has in the past been interpreted as evidence for a prolonged period of growth in early fossil hominins (Mann, 1975). However, molar overlap may also result from a long crown formation time in the preceding molar with no change to the initiation time of the succeeding molar. Similarly, a short molar crown formation time in the preceding molar with no change to the initiation time of the succeeding molar may give the appearance of delayed initiation. This is likely the case in monkeys and baboons where there is no molar overlap but a much shorter period of dental development than in great apes (Boughner & Dean, 2004; Swindler & Gavin, 1962; Swindler et al., 1982; Swindler & Meekins, 1991).

When the range of variation of coincident stages of molar development in modern humans and great apes have been scored together in the same way, these supposed differences in molar overlap have not always been evident (Simpson et al., 1990). Other studies have suggested that even though there is considerable variation in the relative timing of molar development within modern humans worldwide, some populations appear to be more advanced than others (Liversidge, 2008; Tompkins, 1996a). While this seems likely to be the case the range of variability encompassed by the large number of children included in this study may in fact exceed that reported in some previous studies. For example, when in Tompkins (1996a, Fig. 13) M1 stage 10 (broadly equivalent to RC-A½ in this study), is used as a reference stage, then the coincident M3 stages span zero crypt visible to stage 2 (broadly equivalent to C½), whereas in the present study, with larger numbers of children included the range of M3 stages span zero crypt visible to C¾. Relatively advanced M3 initiation in Early, Middle and Upper Pleistocene hominins compared to modern humans has also been reported (Bermudez de Castro et al., 2001; Modesto-Mata et al., 2022; Tompkins, 1996b) but was dependent on the modern human reference population used for comparison.

What stands out in this study is the much greater degree of variation in stages of M2 development at M1 CC and of M3 development at M2 CC in both the modern human and great ape samples than has been reported previously. The implication of this is that individuals of any taxon, known or unknown, could not be assigned to the great ape or modern human distribution of M2 and M3 stages unless these stages fell beyond the ranges of overlap. Even though patterns of dental development do not provide information about timing, the results presented here raise the possibility that earlier molar initiation times in great apes may make less of a contribution to the overall shorter period of dental development in great apes than has sometimes been assumed.

4.4. Incisor formation in great apes, modern humans and fossil hominins

Seven early fossil hominins were identified that have previously been described with M1 at root stage R¼-R½ (Fig. 2). In most cases the M1 was also actively erupting. When M1 was at root stage R¼-R½ in great apes and humans the overall distribution of incisor formation stages was relatively advanced in humans compared to great apes (Fig. 15). This was true for all incisor types, both upper and lower. For lower central incisors, there were 5 early fossil hominins that fell beyond the range of stages observed in this small sample of great apes. When all incisor tooth types were considered, no fossil hominin specimens at M1 root stage R¼-R½ were observed that did not either overlap with both great apes and humans in their stage of incisor development or fell only within the observed range of stages in the human sample. While there is clear evidence of relatively advanced incisor development in the human sample relative to the small great ape sample at M1 root stage R¼-R½, only two of the fossil hominins (Taung and L.H.-2, both attributed to the genus *Australopithecus*) fell consistently at the delayed end of the human distribution but were not beyond the range observed in humans.

Four fossil hominins were relatively more advanced in their M1 development (Fig. 2). At M1 root stage R¾-RC, the distribution of central incisor formation stages showed clear evidence of relatively delayed great ape and advanced human incisor development relative to M1 at root stage R¾-RC (Fig. 16). This difference was clear in both upper and lower central incisors. However, there were insufficient numbers of great ape lateral incisors to explore this observation further. Two early fossil hominins fell entirely within the human incisor distribution and well beyond the observations made in the great ape sample. Both KNM-ER 820 and StW 151 have been attributed to early *Homo* (Moggi-Cecchi et al., 1998; Spoor, 1993; Wood, 1994) despite the latter retaining a mosaic of dental characters (Zanolli, et al., 2022) including a dental development sequence that has been suggested might more likely have resembled Taung and Sts 24 (attributed to *Australopithecus*) had the specimen been slightly younger than ~5 years of age (Moggi-Cecchi et al., 1998).

Of all the fossil hominins compared here with great apes and humans, only one (KNM-KP 34725 attributed to *Australopithecus anamensis*, from Kanapoi, Kenya) showed a stage of lower central incisor development relative to M1 root development not observed in the human sample but rather one commonly observed in the great ape sample. Another fossil specimen (L.H.-3, attributed to *Australopithecus afarensis* from Laetoli, Tanzania) showed a stage of upper central incisor development only observed in an extremely small proportion of humans at M1 stage R¾-RC but one common in the great ape sample. This observation, however, does depend on the root preservation in this fossil specimen being undamaged and the score of UI1 root initiation (Ri) being reliable. All other fossils either fell within the human range of incisor stages observed or within both the great ape and human ranges where their stages of incisor development overlap. Even so, the generalisation that relative to M1 development at stages R¼-R½, (i.e., during active M1 eruption), early hominin specimens attributed to *Australopithecus* distribute among the more delayed individuals for incisor formation stages and those attributed to *Paranthropus* and early *Homo* among the more advanced individuals for incisor development appears to hold true (Beynon & Dean, 1991; Simpson et al., 1990).

4.5. Patterns of tooth formation may change through time

The most likely underlying reason for differences in dental development pattern between great apes, modern humans and fossil hominins is that different stages of tooth formation, as defined in this study, may each take different times to form. When, as in humans, the later stages of molar and incisor tooth formation form relatively slowly, but take similar times to form, the pattern of dental development is different to that in great apes where the relatively slower later stages of incisor crown formation coincide with the relatively faster forming early stages of molar root formation. Stages that are coincident in humans and great apes at one time in tooth development may become staggered later in development as subsequent stages of crown and root formation develop either faster or slower. They may, however, 'catch up' again and it is therefore important to realise that later in tooth development, differences in pattern may shift back to become more similar as the later stages of tooth development align again in great apes and humans (Moggi-Cecchi et al. 1998). In this way similarities and differences in the pattern or sequence of tooth formation stages may change over time.

5. Conclusions

At defined stages of molar development, both incisor and canine formation and eruption, are relatively advanced in humans and relatively delayed in great apes. When large samples of modern humans and great apes are compared, the distribution of eruption and formation stages differ significantly. However, the degree of overlap in formation stages is so great that when individuals are considered only those matching stages at the extremes of each distribution could be assigned to one pattern or the other. Only two out of 11 early fossil hominins (L.H.-3 from Laetoli, Tanzania and KNM-KP 34725 from Kanapoi, Kenya) showed a pattern of incisor/M1 delay that was equivalent to or beyond the most delayed individuals in the human sample.

Conflict of Interest

The authors declare no conflicts of interest.

Ethics Statement

All work carried out was exempt from any requirements set out in The Code of Ethics of the World Medical Association (Declaration of Helsinki).

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Author statement

MCD: Conception, methodology, definitions and design of the study. Acquisition of data. Analysis and interpretation of data. Drafting the article and critical revision of intellectual content. Approved the final version submitted. SYL: Methodology, definitions and design of the study. Analysis and interpretation of data. Drafting the article and critical revision of intellectual content. Approved the final version submitted. HML: Conception, methodology, definitions and design of the study. Acquisition of data. Analysis and interpretation of data. Drafting the article and critical revision of intellectual content. Approved the final version submitted.

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Table 1

Great ape and human sample composition

	Total number	Maxillae only	Mandibles only	Collection	Known sex
Pan	59	3	none	NHM n=28	
				PCM n=29	15 male
					14 female
Gorilla	59	none	none	NHM n=30	
				PCM n=29	11 male
					17 female
Gorilla	41	none	41	Kra n=41	25 male
					16 female
Pongo	41	5	none	NHM n=32	
				UCL n=10	
Human sample	4,091			BLSMD	1,981 male 2,110 female

NHM (Natural History Museum, London); PCM (Powell-Cotton Museum, Kent, UK); UCL (Elliot Smith Collection, UCL, UK); Kra (radiographs of Virunga mountain gorilla mandibular teeth published by Kralick et al. 2017). All great ape specimens used in this study were originally wild free-living individuals. BLSMD (Bart's and The London School of Medicine and Dentistry).

Table 2

Definition of tooth formation stages

Stage	Abbrev	Descriptions

0	Cr0	no crypt visible.
1	Crs	small size crypt too small to contain any mineralising cusp tips.
1.5	Crm	medium sized crypt too small to contain any mineralising cusp tips.
2	Crl	large empty crypt – large enough to contain invisible cusp tips or that may once have previously contained cusp tips now lost.
3	Ci	crown initiation, one or more thin cusp tip/tips visible either spaced or clumped - or (orangutan molars and incisors) a continuous thin mineralising edge.
3.5	Cco	coalescence of cusps - partial fusion of one or more cusps – or (orangutan molars and incisors) a thicker mineralising band of occlusal enamel/dentine.
4	C¼	crown ¼ – not more than ¼ final crown height formed from tallest cusp tip in molars and canines (or mineralising edge in incisors) to the lowest part on the developing tooth margins.
5	C½	crown ½ – not more than ½ final crown height formed from tallest cusp tip in molars and canines (or mineralising edge in incisors) to the lowest part on the developing tooth margins. Full mesiodistal dimension of tooth formed.
6	C¾	crown ¾ – not more than ¾ final crown height formed from tallest cusp tip in molars and canines (or mineralising edge in incisors) to the lowest part on the developing tooth margins.
6.5	CCr	crown complete (radiographic) – enamel complete mesially and distally.
7	CCa	crown complete (anatomical) – evidence of a mineralising line of the developing molar inter-radicular process at the level of last formed buccal enamel. Evidence in incisors and canines of completed enamel formed below the lingual cervical cingulum.
7.5	Ri	root initiation – small crescent-shaped molar furcation present – thin root spur formed mesially and distally with clearly defined EDJ at the cervix. Evidence in incisors and canines of a thin root dentine spur formed below the buccal and lingual cervix/cingulum with a clearly defined EDJ.
8	R¼	root ¼ formed – ‘U-shaped’ molar furcation – perpendicular root length (in molars on the longest root) from a line between the mesial or distal (buccal or lingual in anterior teeth) cervix not greater than ¼ final root length.
9	R½	root ½ formed (in molars, on the longest root) – perpendicular root length from cervix approximately equal to crown height but not greater than ½ final root length – wide root canals with thin diverging dentine walls
10	R¾	root ¾ formed (in molars, on the longest root) - perpendicular root length from cervix greater than crown height but not greater than ¾ final root length – wide root canals with thin diverging dentine walls.
11	RC	root complete (in molars, on the longest root) – root length almost complete (greater than 90%) with near-parallel dentine walls.
11.5	A½	apex ½ closed (in molars, on the longest and last root to complete) – root length complete – relatively thicker dentine walls – greater root cone angle than at root complete stage with apical radiolucency.

12	AC	apex complete (in molars, on the longest and last root to complete) – apex closed with no more than a thin parallel walled root canal and uniform periodontal ligament width.

Table 3

Mann Whitney tests for great ape and human stage distributions

	U	Z	Probability	N great apes	N humans
Incisor er when M2 CC, Fig. 9	1496.5	-7.085	P<0.0005	23	449
Canine er when M2 RC, Fig. 10	2021.0	-11.091	P<0.0005	42	682
Canine at AE-PE, Fig. 11	1174.5	-8.136	P<0.0005	46	211
M2 when M1 CC, Fig. 12	755.5	-5.153	P<0.0005	29	125
M3 when M2 CC, Fig. 13	540.0	-7.000	P<0.0005	32	133
M3 when M1 RC-A½, Fig. 14	3789.5	-10.084	P<0.0005	72	389

At the defined stages of dental development shown in Figs. 9-14, the difference in distributions was significant for each of the comparisons between great apes and humans (Incisor er = incisor eruption stage, canine er = canine eruption stage).

Figure legends

Fig. 1. Lateral radiographs of a series of developing *Pan troglodytes* dentitions. Note the changing orientation of the molars during crown development, the appearance of the completed enamel cervix below the lingual cingulum in anterior teeth and the different stages of crown and root formation in each tooth type.

Fig. 2. The age distribution of individuals in the great ape sample and the human sample used in this study.

Fig. 3. A. Photographs of seven early fossil hominin specimens together with published CT scans and/or radiographs of developing teeth. Each of these specimens has M1 at stage R¼ or R½ judged as root length equal to or less than anatomical crown height or greater than this but less than R¾. CT scans of Taung, SK 61, SK 62; modified from Fig. 4, 8, & 11 in Conroy and Vannier (1991b), CT scans of DNH 107; modified from Fig. M, SI file of Smith et al. (2015). Radiographs of SK 63 and SK 61; modified from Dean (1993) and from Fig. 2 in Grine (1987).

B. Photographs, CT scans and/or radiographs of four early fossil hominin specimens where M1 is at stage R¾-RC. CT scans of KNM-KP 34725 modified from Fig. D, SI file of Smith et al. (2015) and radiographs of KNM-ER 820 modified from Fig. 6 in Dean (2000) and Wood (1994). The photograph of the reconstruction of StW 151 is of a cast.

Fig. 4. Periapical radiographs of developing molars and incisors in *Pan troglodytes* illustrating the different stages of eruption defined in this study. UE, unerupted; AE, alveolar eruption; PE, partially erupted; FE, fully erupted.

Fig. 5. Stage of molar development defined in this study in *Pan, Gorilla* and *Pongo*.

Fig. 6. Stages of anterior tooth development defined in this study in *Pan, Gorilla* and *Pongo*.

Fig. 7. The distribution of formation stages as defined in this study and scored for lower molars and then plotted against known age for LM1, LM2 and LM3 in the series of Virunga mountain gorillas from Rwanda published by Kralick et al., (2017).

Fig. 8. Photograph (top left) of a lower central incisor (*Pan troglodytes*) alongside a periapical radiograph of the same tooth. The same tooth (top middle) is then shown with radio-opaque paste applied to the cervix with a radiograph of this showing the difference in position of the mesial and distal enamel cervix (white arrows) and the buccal enamel cervix. Top right are three molars of *Pan,* (top) *Pongo* (middle) and *Gorilla* (bottom) with matching periapical radiographs of each showing the faint shadow of the buccal enamel cervix extending to the level of the root bifurcation. In *Pan* and *Gorilla,* the lowest point on the enamel cervix is distobuccal while in *Pongo* (middle tooth) it is mid-crown buccal between the roots. Bottom left are eight further isolated great ape molars showing the outline of the buccal enamel cervix. The first and third tooth of the top row are *Pan* molars, all the others are *Pongo* (note the mid-crown cervical extension in *Pongo*). Bottom right are matching periapical radiographs taken after radio-opaque paste had been applied around the cervix. In all cases, the lowest point on the enamel cervix extends to the level of the root bifurcation.

Fig. 9. A series of great ape molars at different stages of root formation aligned at the lowest point on the buccal enamel cervical margin (anatomical crown completion). The last tooth in the series at root stage Apex ½ closed is a modern human molar where the bifurcation is at a lower level.

Fig. 10. Combined upper and lower central incisor eruption status in great apes and modern humans when M2 is at stage crown completion (CC).

Fig. 11. Combined upper and lower canine eruption status in great apes and modern humans when M2 root formation is between stages R¾-RC.

Fig. 12. M3 formation stages in great apes and modern humans when canines are actively erupting (stages AE and PE).

Fig. 13. M2 formation stages in great apes and modern humans when M1 is at stage crown complete (CC).

Fig. 14. M3 formation stages in great apes and modern humans when M2 is at stage crown complete (CC).

Fig. 15. M3 formation stages in great apes and modern humans when M1 is at root stage RC-A½.

Fig. 16. Stages of incisor formation when M1 is at stage R¼-R½. Each incisor tooth type is shown for great apes and modern humans. Early fossil hominin specimens shown in Fig. 2a, are all at the same stage of M1 formation and are superimposed onto these plots indicating the stage of formation for each preserved incisor tooth type.

Fig. 17. Stages of upper central and lower central incisor formation in great apes and modern humans when M1 root formation stage is R¾-RC. Early fossil hominin specimens shown in Fig. 2b are all at the same stage of M1 root formation and are superimposed onto these plots indicating the stage of formation for each preserved incisor tooth type.