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Dental development of the Taï Forest chimpanzees revisited

T.M. Smith [a,b,*], B.H. Smith [c], D.J. Reid [d], H. Siedel [e], L. Vigilant [e], J.J. Hublin [b], C. Boesch [e]

[a] *Department of Human Evolutionary Biology, Harvard University, 11 Divinity Avenue, Cambridge, MA 02138, USA*
[b] *Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, D-04103 Leipzig, Germany*
[c] *Museum of Anthropology, The University of Michigan, Ann Arbor, MI 48109-1107, USA*
[d] *Department of Oral Biology, School of Dental Sciences, Newcastle University, Framlington Place, Newcastle upon Tyne NE2 4BW, UK*
[e] *Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, D-04103 Leipzig, Germany*

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ABSTRACT

Developmental studies consistently suggest that teeth are more buffered from the environment than other skeletal elements. The surprising finding of late tooth eruption in wild chimpanzees (Zihlman et al., 2004) warrants reassessment in a broader study of crown and root formation. Here we re-examine the skeletal collection of Taï Forest juvenile chimpanzees using radiography and physical examination. Several new individuals are included, along with genetic and histological assessments of questionable identities. Only half of the Taï juveniles employed by Zihlman et al. (2004) have age of death known with accuracy sufficient for precise comparisons with captive chimpanzees. One key individual in the former study, misidentified during field recovery as Xindra (age 8.3), is re-identified as Goshu (age 6.4). For crown formation we find that onset and duration greatly overlap captive chimpanzees, whereas root development may be more susceptible to acceleration in captive individuals. Kuykendall's (1996) equation relating captive tooth formation stage to age gives reasonable estimates of young wild subjects' true ages. Direct comparisons of tooth eruption ages are limited. A key 3.76 year-old individual likely possessed an emerging mandibular M1 at death (previously estimated from the maxillary molar as occurring at 4.1 years). Wild individuals appear to fall near the middle or latter half of captive eruption ranges. While minor developmental differences are apparent in some comparisons, our reanalysis does not show an "unambiguous pattern" of slower tooth formation in this wild environment. These data do not undermine recent developmental studies of the comparative life histories of fossil hominins.

Introduction

Nearly all knowledge of primate growth and development derives from the study of captive animals (e.g., Schultz, 1969; Ankel-Simons, 2007). When wild populations can be compared, studies suggest that captive primates grow their skeletons faster than their wild counter-parts (Matsuzawa et al., 1990; Kimura and Hamada, 1996; Zihlman et al., 2007), reach sexual maturity earlier (Pusey, 1978; Altmann et al., 1981; Hamada et al., 1996), and have a lower mortality rate (Hill et al., 2001). Enhanced growth and survival have been attributed to higher-quality diets, medical care, and less energy spent on thermoregulation, as well as an absence of natural predators, in captive environments (see also O'Regan and Kitchener, 2005).

A few reports find that captive primates erupt their teeth earlier than wild primates (Phillips-Conroy and Jolly, 1988; Zihlman et al., 2004, 2007). Phillips-Conroy and Jolly (1988), comparing eruption schedules in wild and captive yellow baboons, found median differences of 2 to 19 months. Differences increased from earlier-forming teeth (i.e., M1, I1) to later-forming teeth (C, M3) in both sexes. Recently, Zihlman et al. (2004) compared maxillary eruption schedules of six permanent teeth in captive and wild Taï Forest and Gombe chimpanzees, reporting that wild chimpanzees may differ by as much as 2 to 2.5 years, particularly for later-forming teeth (C, M3). The broader implications of this study are that dental development may not be an effective tool for discriminating among hominin taxa or for reconstructing life history in juvenile fossil hominins. Specifically, Zihlman et al. (2004) concluded that *Homo erectus* shows a developmental pattern similar to that of wild chimpanzees, in contrast to recent reconstructions of an intermediate condition between that of chimpanzees and living humans. Monge et al. (2007) subsequently argued that these later eruption ages for wild chimpanzees reduce the distinctiveness of the prolonged modern human developmental condition.

A dominant paradigm in studies of dental development is that dental tissues are under greater genetic control than is the skeleton,

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[*] Corresponding author.
E-mail address: tsmith@fas.harvard.edu (T.M. Smith).

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responding less to nutritional extremes or hormonal fluctuations during growth (e.g., Garn et al., 1959; Lewis and Garn, 1960; Garn et al., 1965a,b; Tonge and McCance, 1965, 1973; Demirjian et al., 1985; Smith, 1991; Cantu et al., 1997; Cameriere et al., 2007; Cardoso, 2007). In one of the first large-scale human radiographic studies, Garn et al. (1959) and Lewis and Garn (1960) note that tooth formation is less variable than ages of menarche and skeletal development. Tooth size, shape, and development are known to be highly heritable (e.g., Garn et al., 1965a; Alvesalo and Tigerstedt, 1974; Pelsmaekers et al., 1997; Merwin and Harris, 1998; Hlusko and Mahaney, 2003, 2007; Rizk et al., 2008). Within dental development, the *formation* of teeth appears to be more resistant to environmental effects than the *eruption* of teeth (Lewis and Garn, 1960). This finding has been clearly demonstrated in severe experimental malnutrition studies, in which teeth continue to grow in jaws too stunted to support them (Tonge and McCance, 1965, 1973; Luke et al., 1979, 1981). Given decades of findings on the stability of dental development relative to skeletal growth, this study sought to re-examine the individuals of the Zihlman et al. (2004) eruption study, and to collect novel data on crown and root formation to determine the source of reported differences between captive and wild eruption ages.

Methods

Seventy Taï forest chimpanzee skeletons were examined in the current study. All individuals with dental material were photographed (64 total), and of these, 31 were determined to be juveniles (ranging from infants to subadults with incomplete canine root formation). The 31 juveniles included 30 maxillary dentitions and 26 mandibular dentitions, which were variably preserved (some retained all deciduous and permanent teeth, while others were missing various deciduous teeth, anterior permanent teeth, or rarely M1 or M2). These remains were collected between 1995 and 2007 and are currently housed at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany. Chimpanzees in the primary field study group were systematically identified by 1982. Behavioral data have been collected continuously on this community since 1989, and the identity and genetic relationships of many individuals are known (Boesch and Boesch-Achermann, 2000; Vigilant et al., 2001; Boesch et al., 2006). Ages of birth and death (or disappearance) have been recorded when possible, in addition to estimates of birth year for several of the original group members (Boesch and Boesch-Achermann, 2000: Table 1). Field workers routinely recover and identify cadavers, although in many cases the individuals are not discovered immediately after death, leading to some uncertainty in identification. Cadavers are buried in marked graves to facilitate decay, and skeletal material is then transported from the Côte d'Ivoire to Europe (formerly Zürich, Switzerland; currently Leipzig, Germany) after CITES approval.

As part of an on-going investigation into the familial relationships of the Taï forest chimpanzees (Vigilant et al., 2001; Boesch et al., 2006), samples of tooth roots from ten individuals were collected to confirm the identity of ambiguous skeletal remains that were not recovered immediately after death (or disappearance). An attempt was made to genotype all extracts at 19 microsatellite loci currently used for this population. Current loci, genotyping, and tooth extraction methods are detailed in Arandjelovic et al. (2009) and Rohland et al. (in press). These were then compared to previously obtained genotypes of all known individuals from the habituated communities, as well as unknown individuals from surrounding communities.

Zihlman et al. (2004) used only the unique referents “TF#” or “TM#” for the 13 Taï female and male individuals in their study (Zihlman et al., 2004: Table 1), a practice that has made it difficult to replicate using the original skeletal material. Here we use specimen accession numbers, adding individual names when relevant. For three individuals featured in the former study, a detailed histological study of tooth formation was conducted. Three M1s and two M2s were removed from 11788 (TF1), 11791 (TF3), and 13433 (likely TM4[1]) in order to assess molar formation times and to confirm identities and ages at death. The first two cases are the individuals illustrated in Zihlman et al. (2004: Fig. 1).

Following micro-CT scanning, photography, and molding, histological sections of the five teeth were prepared according to methods detailed in Smith et al. (2007a). Transmitted light microscopy (Olympus BX 51) revealed long- and short-period incremental features that were counted and measured with an Olympus DP 70 camera and analySIS software (Soft Imaging Systems, Inc). Cuspal enamel thickness, daily secretion rates, and long-period line number and periodicity were determined to estimate crown and root formation time following established methods (reviewed in Smith, 2008). Cusp-specific crown formation times were compared to data on additional wild-born and captive chimpanzees from Smith et al. (2007a). For the two key individuals in Zihlman et al. (2004), 11788 and 11791, age at death was determined by identification of the neonatal line, calculation of the postnatal crown formation, and calculation of the subsequent root formation prior to death. For individual 11791, developmental stress was matched from M1 to M2 in order to capture the entire period of development from birth to death (e.g., Boyde, 1963, 1990; Schwartz et al., 2006).

Thirty juvenile Taï dentitions were radiographed with a BIR micro-CT scanner (130 kV, 100 μA, brass filter, 50 μm resolution) in order to score the developmental status of each tooth using two predominant radiographic classification systems (Moorrees et al., 1963; Demirjian et al., 1973). Calcification stages of the crowns and roots of the permanent maxillary and mandibular dentition were scored from these radiographs (and directly from loose germs of one additional infant) on a scale of 1 to 14 as detailed in Moorrees et al. (1963) and Smith (1991). The development of the mandibular dentition of ten known-aged juveniles was also scored on Demirjian's scale of 1 to 8 (as detailed in Kuykendall, 1996), for comparison to Kuykendall's radiographic data on captive chimpanzees. Results are reported from both methods, but it should be noted that radiographic assessments of crown completion (stage 6 in the Moorrees system, stage 4 in the Demirjian system) are not always equivalent. Moorrees' system includes several more finely-distinguished categories, while the latter system's broader stages do not delineate developmental stages just prior to or after crown completion, resulting in wider age ranges for a given stage.

Assessment of wild chimpanzee tooth formation is hindered by limited knowledge of captives; published radiographic data are only available for the mandible of captive chimpanzees scored with the Demirjian scale (Anemone et al., 1991, 1996; Kuykendall, 1996). Anemone et al. (1991, 1996) studied 33 captive juvenile chimpanzees longitudinally (up to age 14) but only presented tabular radiographic data on molar development. Given that Anemone's older subjects were radiographed only annually from age six to 14, developmental standards for M2 and M3 are potentially imprecise. Our primary radiographic comparison is with the mandibular calcification data in Kuykendall (1996). Although Kuykendall (1996) included numerous young subjects in his cross-sectional sample ($n = 118$), subject number tapers off rapidly after age nine, and the oldest male in his sample was approximately eleven years of age. The best comparisons with his study, therefore, will be for

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[1] The first and second authors of the 2004 study have not clarified the identity of their TM4 (Table 1).

Table 1
Individuals in the Taï craniodental collection that are relevant to the current study[a]

Cat no.	Name	Sex	Birth date	Death date	Est birth/death	Age days	Age years	Zihlman et al
11775	Agathe	F	1977[b]	11.XX.92	07.01.77 & day 15	5616	15.39	TF7 (16.5)
11776	Ariane	F	1982[b]	11.XX.94	07.01.82 & day 15	4520	12.38	TF5 (12.8)
11777	Bambou	M	02.06.89	03.25.91		777	2.13	TM2 (2.1)
11779	Clyde	M	1971[b]	01.21.84	07.01.71	4587	12.57	TM5 (13.8)
11782	?	M	?	?			?	? TM4 (8.5)
11783	Manon	F	09.10.87	11.15.92		1893	5.19	TF2 (5.2)
11787	Ovide	M	11.03.92	11.19.92		16	0.04	
11788	Piment	F	02.12.91	11.15.94		1372	3.76	TF1 (3.8)
11790	Tina	F	1979[b]	02.06.89	07.01.79	3508	9.61	TF4 (10.8)
11791	Goshu	F	03.10.86	08.19.92		2354	6.45	TF3 (8.3)
11792	Zerlina	F	1982[b]	10.XX.94	07.01.82 & day 15	4489	12.30	TF6 (12.5)
11903	Fitz	M	1975[b]	12.XX.94	07.01.75 & day 15	7107	19.47	TM6 (14.2)
12175	Hector	M	12.10.90	08.16.96		2076	5.69	TM3 (5.7)
13432	Leonardo	M	08.31.97	06.08.99		646	1.77	TM1 (1.8)
13433	Lefkas	M	10.07.91	05.14.99		2776	7.61	? TM4 (8.5)
13437	Kana	F	06.05.87	10.21.98		4156	11.39	
14991	Endora	F	03.25.96	03.10.04		2907	7.96	
14993	Ophelia	F	06.XX.03	03.10.04	day 15	269	0.74	
14995	Oreste	M	12.14.98	03.10.04		1913	5.24	
15005	Max	M	1995[b]	12.08.01	07.01.95	2352	6.44	
15007	Janine	F	07.16.98	12.XX.04	day 15	2344	6.42	
15008	Nerone	M	?	03.01.05			?	
15011	Noah	M	1995[b]	02.13.02	07.01.95	2419	6.63	
15015	Isha's baby	?	12.06.05	02.10.06		66	0.18	
15020	Dorry	F	11.24.91	11.15.01		3644	9.98	
15021	Gargantua	M	09.21.91	11.15.01		3708	10.16	

[a] Dates are in the form: month.day.year when known.

[b] Signifies estimated birth year. For individuals of unknown birth year, a birth date of July 1 was estimated to yield an age (indicated in est birth/death column). These individuals were not employed in the current study. XX signifies day of month unknown. For individuals of unknown birth or death day, the 15th day of the month was assigned to yield an age (noted as 'day 15' in est birth/death column). Note that 11775 (Agathe) was not classified as a juvenile in the current study; all teeth were erupted and the canine roots were observed to be closed via radiography, but this individual was included in Zihlman et al. (2004) as TF7. Similarly 11903 (Fitz) also died as an adult, but this individual was believed to be 14.2 year-old Sartre and was designated TM6 by Zihlman et al. (2004; Zihlman, pers. comm.).

subjects younger than age nine, perhaps stretching to age ten, because range statistics will become increasingly biased due to tailing out and truncation of the normative sample.

When wild and captive radiographic data are compared, it is critical that the same kinds of chronologies are employed. It is necessary to specify whether a comparison is "age for stage" or "stage for age" (see Smith, 1991; Kuykendall, 1996). Although commonly computed, both are subject to bias when age distributions are highly variable and/or truncated. One approach to gauging captive-wild differences that avoids some pitfalls of maturation data is to use captive standards to predict age of wild subjects. Kuykendall (1996) computed an age-prediction formula, based on a Demirjian-style maturity scale, for use on chimpanzees from birth to about nine years of age. Here, individuals are scored as the sum of maturity scores (1–8) for each forming mandibular I1-M2 (M3s are omitted because they contribute little to successful prediction in this age range). A polynomial regression equation describes the relation between age and summary tooth score (Dm) in captive data: $\text{Age} = 0.078\ (\text{Dm}) + 0.002\ (\text{Dm}^2)$. Because the equation requires complete I1-M2 data, only four of the known-age Taï individuals could be tested with this method.

Finally, maxillary eruption was re-examined in the 13 individuals from the Zihlman et al. (2004) study, with particular attention to the two key individuals illustrated (TF1 and TF3, 11788 and 11791) and several new juveniles. Because comparative captive data are scored for emergence through the gingiva, we reassessed the Taï individuals based on the height of the tooth at the alveolar margin and the presence of dental calculus (tartar), staining, or wear facets; all of which indicate that a tooth has emerged past the gingival margin into the oral cavity. We note that comparisons of mean or median values determined from cross-sectional and longitudinal data are problematic; this is less of a concern when individual wild chimpanzees are compared with ranges derived from captive studies of longitudinal design (e.g., Nissen and Riesen, 1964; Kraemer et al., 1982; Conroy and Mahoney, 1991; Kuykendall et al., 1992). An extensive statistical analysis of Taï and Gombe eruption data will appear elsewhere (Smith and Boesch, in prep). It is noted that one known-age individual (15020, Dorry, 9.98 years old) was omitted from developmental analysis (calcification and eruption observations) due to a marked pathological condition of right mandibular P4 and left mandibular M1 and M2. Oddly, her mandibular M3 development lags maxillary M3, suggesting that mandibular molar crown completion was pathologically delayed.

Results

Identification

Of the 31 juvenile skeletons currently in the Taï skeletal collection, 23 have been identified as specific individuals that were under behavioral observation (Table 1). Sixteen of these 23 individuals are considered to be of known age at death (known to within a month, in contrast to six others of estimated birth year, and one of unknown birth year). One age was determined by histology, and identification was subsequently confirmed from field notes (detailed below). All 16 individuals were represented by maxillary dentitions, and 12 of these also had mandibular dentitions.

Re-examination of the 13 Taï individuals included in the Zihlman et al. (2004) study revealed that one individual was misidentified during field recovery (TF3), and another individual was apparently misidentified after accession (TM6). Furthermore, five additional individuals are of uncertain age; each individual's year of birth was estimated to have occurred prior to consistent field observation (Table 1). The misidentification of TF3 (11791) was discovered by histology and subsequently confirmed with recovery records and skeletal inspection. Incremental dental features

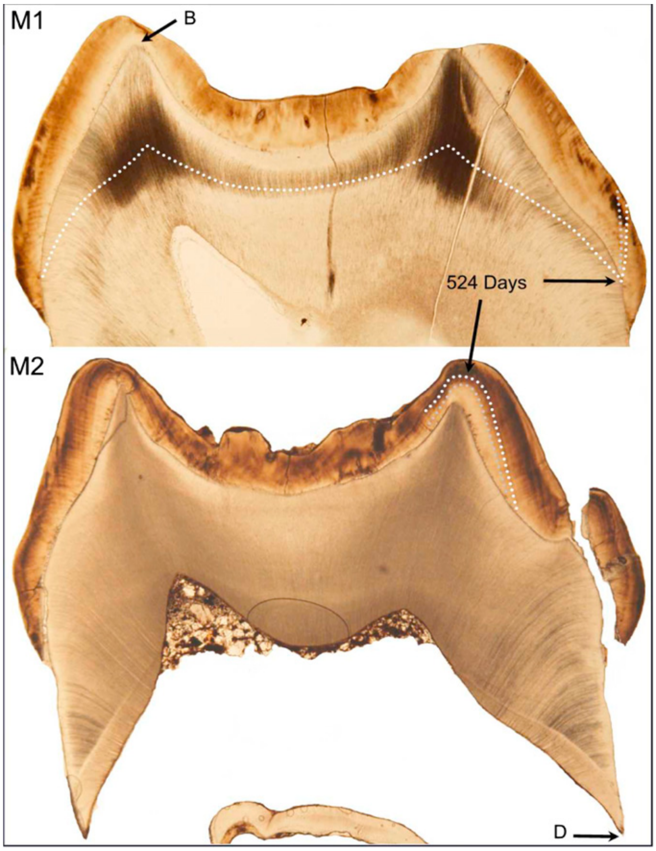

Fig. 1. Illustration of the maxillary M1 and M2 of chimpanzee 11791 showing age at death reconstruction. The neonatal (birth) line was first identified in the M1 mesiobuccal cusp (upper left arrow B), formation time was added until the major pair of stress lines were reached (gray and while dotted lines: 524 days of age for the latter one), and the count was continued at the synchronous lines in the M2 until death at 6.41 years of age (lower right arrow D). The age at death was calculated three separate times over the course of two years, yielding a range of estimates from 6.40–6.42 years. Subsequently, the individual was identified as Goshu, aged 6.42–6.45 years.

yielded an age at death of 6.41 years (Fig. 1), 1.9 years younger than the individual it had been assumed to represent previously (8.3 year old Xindra). Genetic testing of 11791 was inconclusive, due to the poor organic quality of the sample. The cadaver was in an advanced state of decay when it was discovered in November 1992 in the core area of the North Group (which was not visited by other groups at the time). It is now identified as the female Goshu, a member of the North Group who was last seen alive in early August 1992 with severe wounds from a leopard attack. At the time of the attack Goshu was 6.42 years of age. She was estimated to have died less than two weeks later (as her mother left the focal group presumably with her and returned alone), yielding a maximum age at death of 6.45 years of age. Observed injuries to Goshu's head and neck are consistent with damage to the zygomatic arch, temporal bone, and mandibular ramus of individual 11791. For a second individual, however, histological sectioning of the maxillary M1 of TF1 (11788) confirmed assigned identity. The individual was identified in the field as Piment (actual age: 3.76 years); dental histology yielded an age of death of 3.82 years (illustrated in Smith and Tafforeau, 2008: Fig. 2), which is further evidence of the accuracy of this approach.

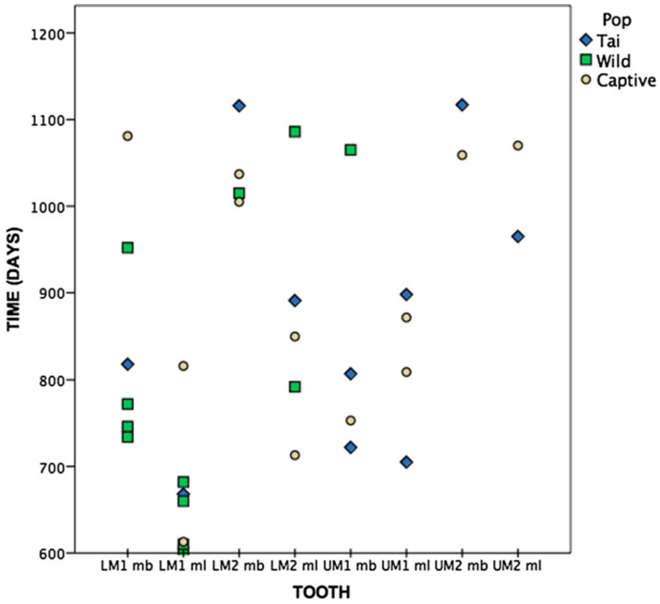

Fig. 2. Molar crown formation times (histologically-derived) in the mandibular (L–lower) and maxillary (U–upper) M1 and M2 of 17 chimpanzees, showing a substantial degree of overlap between wild and captive individuals. The Taï data represent ten mesial cusps (mb–mesiobuccal and/or ml–mesiolingual) from five molars of three individuals. Additional data on non-Taï wild and captive chimpanzees are from Smith et al. (2007a); captive data derive from 12 mesial cusps of ten molars of six individuals, and wild data derive from eleven cusps of seven molars from eight individuals.

Crown formation, maturity scores, and age prediction

Molar crown formation times of three Taï individuals determined histologically show a large degree of overlap with a small sample of captive chimpanzees (Fig. 2). The calculated times for certain tooth positions (maxillary M1 mesial cusps and M2 mesiolingual cusp) are lower than those of some captive individuals. The upper first molar of 11788 represents a particularly striking case; a long-period line periodicity of 5 days led to short crown formation times of 722 and 705 days for the mesiobuccal and mesiolingual cusps, respectively. In five of eight (tooth and cusp-specific) comparisons the highest value is from a wild individual (Taï or unknown provenience); in most cases this was due to differences of a few months of formation time.

Seven individuals from the Taï forest yielded radiographic data on ages of subjects with complete crowns—an “age for stage” result (Table 2). Ages are presented with three caveats: there are no published data available for comparison; this is likely to be a biased statistic with such small sample sizes; and radiographic ages are known to underestimate actual ages of crown completion (Lewis and Garn, 1960; Beynon et al., 1998). When comparisons could be made using Demirjian's mandibular stage 4 (the closest to a “crown complete” stage), Taï subjects' ages either overlap or are very close to the upper end of captive age ranges (Fig. 3; Kuykendall, 1996). The mandible of a single 5.24 year old individual (14995) is the source of I1 and I2 crown completion ages approximately two months greater than the maximum value of the captive sample.

Comparison of Taï subjects' mandibular “stage for age” to Kuykendall's (1996: Table 4) captive yearly cohorts revealed almost identical development for individuals younger than six years old (Table 3). One male (11777, Bambou) remained in canine stage 2 when captives in his age group had moved on to stage 3. When “stage for age” data are compared for the two individuals between six and nine years of age, there is evidence for a difference of one stage in approximately 20% of the dental comparisons, rising to 40% in the more problematic age group 10–12, where few captives make up the range data.

Table 2
Age of Täi forest subjects in the radiographic stage “crown complete” (Moorrees et al., 1963: stage 6) in years

Row	Tooth	Age[a]	*n*
Maxillary	I1	3.76	1
	I2	5.19	1
	C	6.45	1
	P3	5.83	2
	P4	–	
	M1	2.13	1
	M2	–	
	M3	7.96	1
Mandibular	I1	5.24	1
	I2	5.24	1
	C	5.84	2
	P3	–	
	P4	–	
	M1	1.77	1
	M2	5.24	1
	M3	–	

[a] The Moorrees scoring system yields a narrower range of ages than Demirjian's due to the discrimination of additional stages of crown and root formation. This accounts for differences when compared to captive values in Figure 3 (Demirjian method).

Table 3
Formation of Täi mandibular teeth assessed with Demijian's 1–8 maturity scale[a]

Skeletal ID	Name	Age yr	I1	I2	C	P3	P4	M1	M2	M3
14993	Ophelia	0.74	2	–	1	–	–	2	–	–
13432	Leonardo	1.77	3	3	2	2	2	4	1	–
11777	Bambou	2.13	3	3	***2***	2	2	4	2	–
11788	Piment	3.76	3	4	3	3	3	–	3	–
14995	Oreste	5.24	4	4	3	–	–	–	4	2
11791	Goshu	6.45	***5***	***5***	4	5	5	7	5	3
13433	Lefkas	7.60	6	6	4	***5***	6	–	–	3
15021	Gargantua	10.16	–	–	***5***	–	***6***	8	7	***5***
13437	Kana	11.39	8	7	6	***6***	7	8	7	6

[a] Numbers in bold italics indicate lesser (“delayed”) wild score compared to Kuykendall's (1996) captive chimpanzee ranges. Stages for individual teeth run from 1–8 (see Kuykendall (1996) for definitions and comparative captive sample sizes by age). Note that teeth in stage 8 (root completion) cannot be compared because this is the final stage.

Table 4 presents the application of Kuykendall's polynomial function to predict the age of young Taï subjects. In Kuykendall's (1996) study, 95% of captive ages fell within one year (+/−) of age predicted by his equation. Here, three of four Taï individuals fell within one year, with one outside it slightly, which is similar to Kuykendall's (1996) captive accuracy. However, there is a tendency for the captive maturity scores to underestimate wild ages (3/4 cases), as expected if tooth formation is accelerated in captive subjects. There is also a trend towards underestimation of age with increasing subject age, suggesting more divergence between captive and wild individuals as formation progresses.

Tooth eruption

A reanalysis of the remaining known-age wild individuals reveals that only one Taï individual died at the approximate “point” of maxillary incisor, canine, or molar gingival eruption (11791, TF3 featured in Zihlman et al. 2004: Fig. 1). This individual, now identified as 6.4 year-old Goshu rather than 8.3 year-old Xindra, does not show markedly later eruption ages than captive individuals; I1, I2, and M2 ages are within captive ranges from longitudinal studies (Table 5). Unfortunately, there are no other known-age Taï individuals that died while in the early stages of gingival eruption. Two individuals of estimated birth years (TF4 [11790] and TF6 [11792]) yield canine and third molar eruption ages that also fall within the ranges of comparative captive studies, assuming that the year of birth is correct (Table 1).

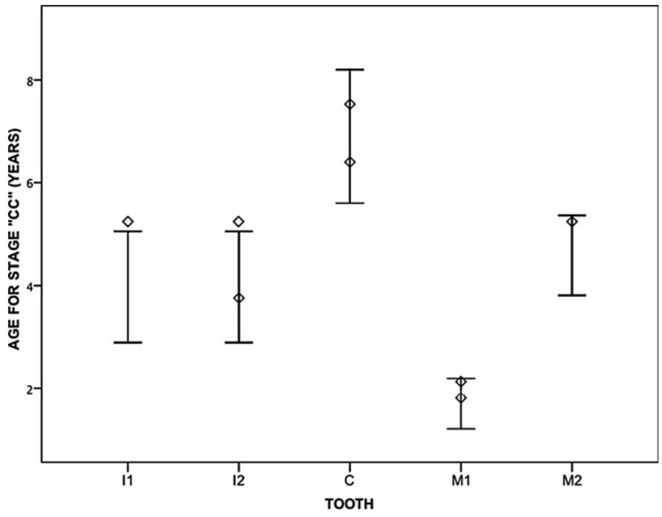

Fig. 3. “Age for stage” comparison of the ages of wild and captive chimpanzees when a mandibular tooth is in the radiographic stage “crown complete to CEJ” (Demirjian stage 4). Captive data (vertical bar) from Kuykendall (1996) are compared to ages observed in six Taï forest chimpanzees (open diamonds). Kuykendall (1996) reports the following number of observations (at stage 4): I1:15; I2:15; C:10; M1:9; M2:7. Wild subjects fall within captive ranges in six of eight comparisons, and are close to captive ranges in the remaining two.

Discussion

It has been argued that a trait's heritability does not predict the effect of genetic or environmental change (Bailey, 1997). However, natural and controlled experiments have demonstrated that changes in environment (nutrition) result in greater changes in skeletal rather than dental growth (Garn et al., 1965a,b; Tonge and McCance, 1965, 1973; Luke et al., 1979; Marzke et al., 1996; O'Regan and Kitchener, 2005). Furthermore, the degree of dental development is regarded as a more accurate indicator of a juvenile's chronological age than is skeletal development (reviewed in Liversidge, 2008; Schmidt, 2008), presumably due to greater resistance to environmental influences. Zihlman et al. (2004) reported that I2 and M2 eruption of wild chimpanzees occurred outside of captive ranges, and that C and M3 differed by approximately 2–2.5 years. A conservative reanalysis of the Taï forest juveniles in this study suggests that the developmental environment does not have as profound an effect on tooth growth as reported by Zihlman et al. (2004, 2007). The data presented here show substantial overlap with captive standards, although there is evidence for some developmental differences, particularly in older subject comparisons. We note that this may be a result of limited comparative data on older captive individuals; larger samples should be employed to further assess these differences. (Significant differences may exist even when ranges are highly overlapping, although this requires larger samples to detect.) In the subsequent discussion, evidence for variation in aspects of crown and root formation, as well as eruption ages, is considered for wild and captive primates. These new results are then considered in the context of hominin dental development and life history studies.

Crown and root calcification

Novel radiographic data on age at crown completion, in addition to additional histologically-derived molar formation times, indicate

Table 4
Predicting age of wild chimpanzees from captive data using the maturity scale from Kuykendall (1996)[a]

ID	Name	True age	Demirjian maturity scores (1–8)								Predictions		
			I1	I2	C	P3	P4	M1	M2	Sum (Dm)	Predicted age (yr)	Error (yr)	Error %
13432	Leonardo	1.77	3	3	2	2	2	4	1	17	1.83	−0.06	3
11777	Bambou	2.13	3	3	2	2	2	4	2	18	1.98	0.15	8
11788	Piment	3.76	3	4	3	3	3	6[b]	3	25	3.13	0.63	20
11791	Goshu	6.45	5	5	4	5	5	7	5	36	5.33	1.12	21

[a] Predicted age $= 0.078(\mathrm{Dm}) + 0.002(\mathrm{Dm}^2)$ -0.073, where Dm = sum of maturity scores I1-M2.
[b] Stage estimated from root alveoli in the mandible.

that wild chimpanzees do not consistently grow their tooth crowns slower than captive individuals. Although comparisons of radiographic calcification stages are limited to mandibular data, a similar trend is expected for maxillary teeth, as the timing of mandibular and maxillary teeth is highly synchronized (e.g., Nissen and Riesen, 1964; Kuykendall et al., 1992; Reid et al., 1998). Furthermore, histological data on molar formation times have suggested a substantial degree of developmental variation within both captive and wild primates (Schwartz et al., 2006; Smith et al., 2007a), which was confirmed in the present study. Accurate histological data for anterior teeth are limited. Reid et al. (1998) reported an individual maxillary canine crown formation time of 6.23 years for a presumably captive individual (43/87), which falls within the range of times reported for wild chimpanzees (5.91–7.58 years) by Schwartz and Dean (2001). The results of the current study suggest that any differences in eruption ages between captive and wild individuals are due to other aspects of dental development. Importantly, data on crown formation in captive apes (e.g., Beynon et al., 1991; Dirks, 1998; Schwartz et al., 2006; Smith et al., 2007a) remain suitable for comparison with living wild apes and fossil apes and humans.

Smith et al. (2007a) suggested that variation between wild and captive primate molar eruption ages is most likely due to variation in the timing of tooth initiation and/or rates of root development (as opposed to crown formation time). Relatively few data are available on the timing of tooth initiation in nonhuman primates, due to the difficulty of detecting early stages of tooth germs radiographically (Winkler, 1995; Beynon et al., 1998; Boughner and Dean, 2004), as well as the time-consuming nature of histology. Initiation ages for Taï forest M1 and M2 cusps determined during the course of this study are similar to values from other wild and captive individuals (Smith et al., 2007a). Prenatal initiation of maxillary and mandibular mesial M1 cusps ranged from 31–38 days, and the initiation of the maxillary M2 mesiobuccal cusp (11791) was estimated as 1.0 year of age, which is slightly younger than a small sample of wild-born chimpanzees (Smith et al., 2007a) and a single captive chimpanzee (Smith and Reid, unpublished data). It has also been shown that limited space availability in the mandible does not influence the initiation of primate tooth crowns (Boughner and Dean, 2004).

For the mandible, only 3% (1/32) of comparisons of crown calcification stages (1–4) showed differences in wild individuals (Table 3). However, differences are more common in root development, as 30% (3/10) of comparisons of radiographic root formation stages (5–7) differed for individuals less than ten years of age. This suggests that differences in eruption ages, when present, are likely due to slower rates of root formation in wild primates. A case in point is illustrated by the comparison of 11791 (Goshu) to a captive individual approximately 6 months younger, who shows slightly advanced M2 root formation (Fig. 4). Unfortunately there are very limited histological data for further comparisons. The majority of root extension rate data in Smith et al. (2007a: Fig. 5) do not permit comparisons of equivalent regions of captive and wild primate roots (for particular molar types). Dean and Vesey (2008) note that rates of root extension appear to be more variable than other aspects of tooth formation (e.g., daily secretion rates, crown formation times), although the causes of variation within teeth are poorly understood. One possibility is that "delayed" tooth roots may be responding to limited space availability (Luke et al., 1981), which is explored further below.

Following the pioneering work of Garn and colleagues (e.g., Garn et al., 1959; Lewis and Garn, 1960; Garn et al., 1965b), recent attention has been paid to the potential role of hormones during dental development (e.g., Schwartz and Dean, 2005; Guatelli-Steinberg et al., 2008). As noted above for studies of environmental influences on hard tissue development, the general consensus of numerous endocrinological studies is that abnormal hormonal levels do not affect dental development as dramatically as skeletal development (e.g., Schour et al., 1934; Cohen and Wagner, 1948; van Wagenen and Hurme, 1950; Seipel et al., 1954; Garn et al. 1965b; Edler, 1977; Hansson et al., 1978; Roberts et al., 1985; Pirinen, 1995; Berkovitz et al., 1998; but see Keller et al., 1970). Growth hormone, insulin, thyroid hormones, and sex hormones are known to affect numerous physiological processes, including stimulating bone growth and metabolic functions, increasing calcium deposition in bone (lowering blood levels), and mediating reproductive growth and development. Growth hormone is considered the most important endocrine regulator of postnatal growth. It is secreted in a circadian fashion, stimulating the production of insulin-like growth factor I (IGF-I). In bone,

Table 5
Chimpanzee emergence age (in years) of four maxillary tooth positions reported in various studies compared to the two most informative Taï chimpanzees: 11788 (Piment or TF1) and 11791 (Goshu or TF3)

Maxillary tooth	Captive[a]				Wild Piment and Goshu[b]	
	Nissen & Riesen, 1964	Kraemer et al., 1982	Kuykendall et al., 1992	Total range	Zihlman et al., 2004	Present study
M1	2.75–3.75	3.33–4.00	2.26–4.38	2.26–4.38	4.1	> 3.8
I1	4.50–6.75	5.08–5.42	4.47–6.43	4.47–6.75	≤ 8.0	< 6.4
I2	5.83–8.25	5.83–6.42	4.67–6.83	4.67–8.25	8.6	6.4
M2	5.67–7.83	5.83–6.42	5.23–7.37	5.23–7.83	8.2	6.4
Study n	15	17	58		2	2

[a] Note that captive values are determined by different methods in each study depending on observances and exam intervals.
[b] These two cases are illustrated in Zihlman et al. (2004: Fig. 1).

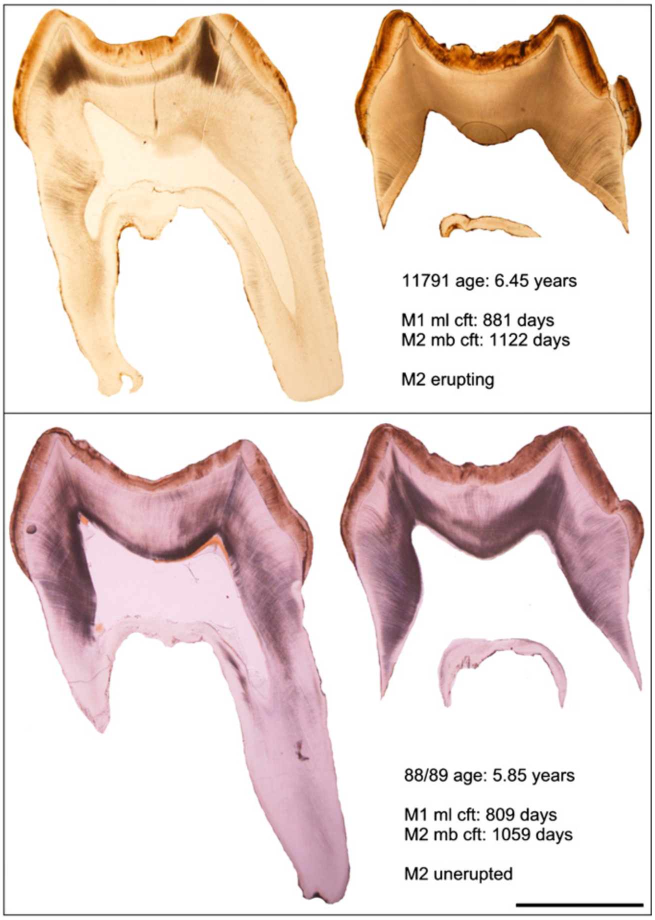

Fig. 4. Comparison of first and second maxillary molars (left and right images, respectively) of wild and captive individuals (above and below, respectively). Both M1s are root complete but roots are sectioned slightly obliquely. Note the slightly advanced degree of root formation in the developing second molar of the captive individual. The scale bar in the lower right image is equal to 5 mm (all sections are equally scaled).

growth hormone stimulates the differentiation of cartilage-forming cells (chondroblasts), while IGF-I stimulates chondoblast cell division (Widmaier et al., 2006).

Smid et al. (2007) recently reviewed studies that have demonstrated that growth hormone also promotes cell differentiation in the early stages of tooth development, which appears to be mediated by IGF-I and bone morphogenic proteins (also reviewed in Li et al., 1998). Studies of knockout and transgenic mice have demonstrated specific positive effects of growth hormone on coronal dentine apposition and the induction and proliferation of odontoblasts in Hertwig's epithelial root sheath (Smid et al., 2007). Proffit and Frazier-Bowers (2009) report a relationship between the time of day that growth hormone levels peak and the time that tooth eruption peaks in human children. Numerous studies have also demonstrated a link between growth hormone deficiency and delayed dental development, including eruption delay, impaction, and jaw overcrowding, due to a lack of deciduous root re-absorption, delayed root development, and stunted jaw growth (e.g., Schour, 1934a,b,c; Schour et al., 1934; Cohen and Wagner, 1948; Garn et al., 1965b; Krekmanova et al., 1999; Kjellberg et al., 2000; Campbell et al., 2009). Crown size and development were generally found to be normal in these studies.

It is hypothesized that if the same pattern holds true for nonhuman primates, differences in root development and dental eruption between captive and wild primates may be influenced by differences in growth hormone levels, which are regulated by other hormones and influenced by general health and nutrition. While it is unlikely that either wild or captive chimpanzees routinely exhibit pathological hormonal levels (as in the human clinical studies referenced above), the finding of differences in root development (and potentially dental eruption) in a subset of older individuals is consistent with differences in growth hormone or IGF-I levels. Some support for this explanation comes from an examination of leptin (a hormone related to hunger and energy expenditure) in vervet monkeys. Whitten and Turner (2008) found that leptin levels in captivity were abnormally low relative to wild monkeys, concluding that there is a complex interplay between environmental variation, energy balance, reproductive state, and overall hormone levels. Future work is needed to address this issue as there are no comparative data available on growth hormone in wild and captive primates (Bernstein pers. comm.; Thompson, pers. comm.), save for an anecdotal report on a wild-caught baboon that was transported to the US and sampled after treatment for a parasitic infection (Nobrega-Lee et al., 2007). Growth hormone is very difficult to assess in wild primates due to its pulsatile secretion pattern and low concentrations in urine (but see Saugy et al., 1996).

Tooth eruption

The current study demonstrates greater overlap between captive and wild chimpanzee dental eruption ages than was reported by Zihlman et al. (2004:10541), who assert “an unambiguous pattern of a slower growth rate in wild vs. captive chimpanzee populations.” Unfortunately only one known-age Taï juvenile died at the “point” of maxillary gingival emergence of I2 and M2 (11791). Few data are available from later-forming teeth. Precise maxillary eruption ages for C and M3 are uncertain as the Taï individuals nearest to eruption, 11790 (Tina) and 11792 (Zerlina), were estimated to have been born in 1979 and 1982, respectively. If these birth year estimates are correct, these two teeth erupted in the latter half of captive ranges reported in Nissen and Riesen (1964), Kraemer et al. (1982), and Kuykendall et al. (1992). Furthermore, Gombe data reveal a high degree of overlap between wild and captive chimpanzees; a broader statistical analysis of this sample is underway (Smith and Boesch, in prep).

Tooth eruption is a dynamic process, as illustrated by a comparison of two individuals at varying stages of M2 eruption who are separated by approximately 1.2 years of age (Fig. 5; also see a similar M1 condition in Smith et al., 2007a: Fig. 6). Part of the variation in eruption ages in this comparison is likely due to the partially impacted M2 in the older individual. Eruption may be delayed by malocclusion, impaction, and dental crowding (e.g., Holt et al., 2000), which are apparent in several individuals from the Taï collection. These developmental anomalies appear to be more common in later-forming wild chimpanzee teeth (e.g., P3, P4, M2, M3), which may be influenced by more (post-weaning) environmental variability (e.g., Luke et al., 1979).

Zihlman et al. (2004) estimated the age that a tooth emerged in wild subjects by adding or subtracting a few months, depending on eruption status. It appears that three types of corrections were made: one and a half months were subtracted to correct for partially emerged teeth (citing a Ph.D. Dissertation on langurs), three months were subtracted to correct for recent fully-emerged teeth at death, and either three or four months were added to correct for the delay between alveolar and gingival emergence (citing a study on captive baboons by Kelley and Smith [2003]). However, catarrhine primates do not all show equivalent periods between alveolar and gingival emergence events, and eruption rates do not appear to be constant across the dentition. Kelley and Smith (2003) reviewed the only published data on the delay between mandibular M1 alveolar and gingival emergence in

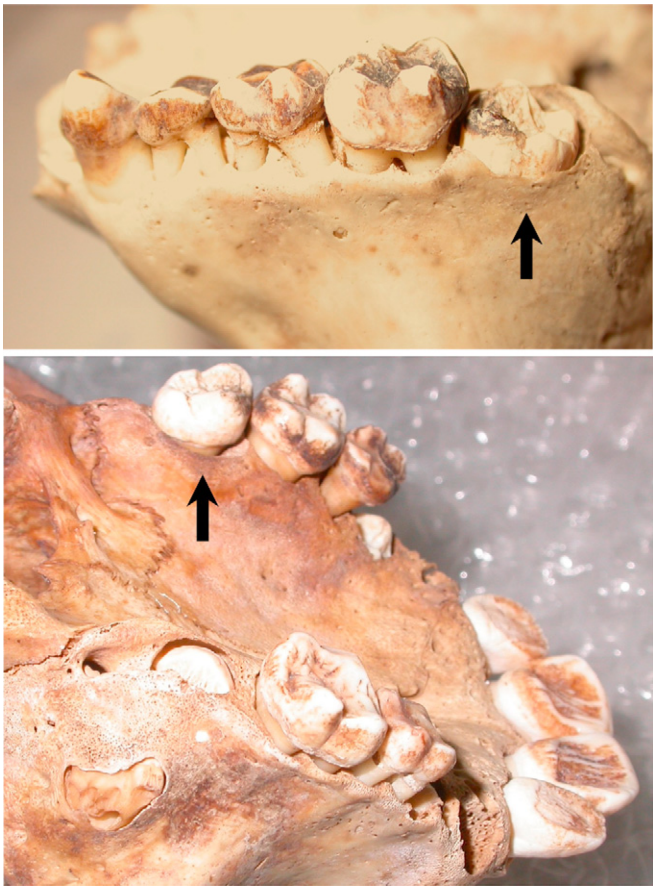

Fig. 5. Comparison of M^2 eruption (black arrows) in 6.4 year old (11791–above) and 7.6 year old individuals (13433–below). Note that although the degree of staining is similar between the two teeth, the M^2 in 13433 is more elevated relative to the alveolar margin. It is also possibly slightly impacted, which is consistent with the state of the impacted left M^2. The left side of 13433 has an anomalous M^4 (note developing roots sticking out in the lower left of the image). Radiographs reveal that the right side does not have an M^4.

chimpanzees (Zuckerman, 1928), which was estimated from a single individual to be four to five months. Dean (2007) recently reported that the transition from alveolar to full gingival emergence in human mandibular M1s takes approximately 12 months. Liversidge (2003) reviewed Haavikko's (1970) study of the time between alveolar and gingival emergence in humans, noting this ranges from four months to more than two years depending on tooth type and sex. Given these findings, as well as limited data suggesting substantial variation in root length and extension rate near eruption (Kelley et al., 2009), individuals that had yet to erupt their teeth were not corrected (e.g., 11788, TF1), nor were those who had already erupted their teeth prior to death.

Of the 70 individuals collected from the Taï forest community, Piment (11788) is the only individual near M1 eruption at death. First molar eruption is of particular significance as it is correlated with the age of weaning across primates, as well as with brain size (Smith, 1989; Smith et al., 1994). It is apparent from the lack of staining on the maxillary M1s of 11788 that they had not emerged prior to death at 3.76 years (see Zihlman et al. 2004: Fig. 1). However, studies of captive chimpanzees demonstrate that the mandibular M1 may erupt a few months earlier than the maxillary M1 (Nissen and Riesen, 1964; Kraemer et al., 1982; Conroy and Mahoney, 1991). Piment's mandibular M1s were lost prior to collection, but her mandible is preserved in pristine condition, suggesting that the teeth were unobstructed by alveolar bone. Her alveolar crypts are completely open with resorbing margins and well-defined root impressions and cleft formation (Fig. 6a), conditions that suggest that mandibular M1 gingival emergence had occurred or was imminent. Comparison with a wild-shot Liberian individual at a late stage of mandibular M1 eruption show a similar amount of root development (Fig. 6c-d), further demonstrating that Piment's mandibular M1 may have reached gingival emergence at death.

The distinction between maxillary and mandibular molar emergence is not always acknowledged, but it is important to consider when comparing ages. Correlations and regressions relating age of M1 emergence to brain size in primates, and comparisons with fossil hominins, are based on mandibular data (e.g., Smith, 1989; Kelley and Smith, 2003; but see comparisons in Zihlman et al., 2004). If this single individual (11788) is employed for the first molar emergence age of wild chimpanzees in general, it is likely that this mandibular tooth was emerging at age 3.76 years. The increasingly cited "paradigm" (e.g., Zihlman et al., 2007; Gibbons, 2008; Ponce de Leon et al., 2008) that chimpanzees erupt their M1s at 4.1 (or ∼4) years of age is problematic for two reasons. It is based on an extrapolation about Piment's maxillary molar, which leads to a potentially inflated mandibular molar value. Furthermore, it also ignores the natural range of eruption ages, which is over two years in captive chimpanzees (Table 5 and references therein). Even in the more uniform captive environment, the standard deviation for maxillary and mandibular M1 emergence age is approximately 0.4–0.5 years (Kuykendall et al., 1992).[2] It is also worth noting that wild groups can differ from each other, as shown by studies of eruption in *Macaca fuscata* (Iwamoto et al., 1987). Thus, it is highly likely that expanded samples of wild chimpanzees will show a range of eruption ages even as they overlap greatly with captive standards.

Hominin life history

Reduced eruption ages for the Taï forest chimpanzees have implications for studies of hominin life history. In the original study, Zihlman et al. (2004) suggest that the developmental patterns of *Homo erectus* (broadly defined) appeared to be similar to wild chimpanzees. Dean et al. (2001) estimate that mandibular M1 and M2 erupted in *H. erectus* at approximately 4.4 and 7.6 years of age, respectively, based on Sangiran S7-37 (see also Dean and Smith, 2009). If chimpanzees in the wild are typically older than four years of age when M1 emerges, there is little distinction between early *Homo* and *Pan* dental trajectories. Our reassessment of the lone wild chimpanzee, however, places mandibular M1 eruption near 3.76 years. If the mean age of M1 emergence in *H. erectus* was 4.4 years, this taxon lies more than 1.4 standard deviations above the wild chimpanzee value (4.4–3.76/0.44 s.d.). While additional data on wild chimpanzee dental development are clearly needed, other life history-related variables, such as body mass and cranial capacity (e.g., Skinner and Wood, 2006), also distinguish fossil *Homo* from earlier hominins and chimpanzees.

Mandibular M1 emergence in australopiths has been estimated to occur between 3 and 4 years of age (Bromage and Dean, 1985; Dean, 1987), which is younger than estimates for members of the genus *Homo* but is similar to the single wild chimpanzee value and captive chimpanzee ranges. This reevaluation of the Taï material also has implications for the relative dental development and life

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[2] A general rule is that age of emergence of any permanent tooth in primates, including humans, tends to have a coefficient of variation of about 10 (i.e., the standard deviation is about 1/10 the mean), as is evident in tabulations in Smith et al. (1994).

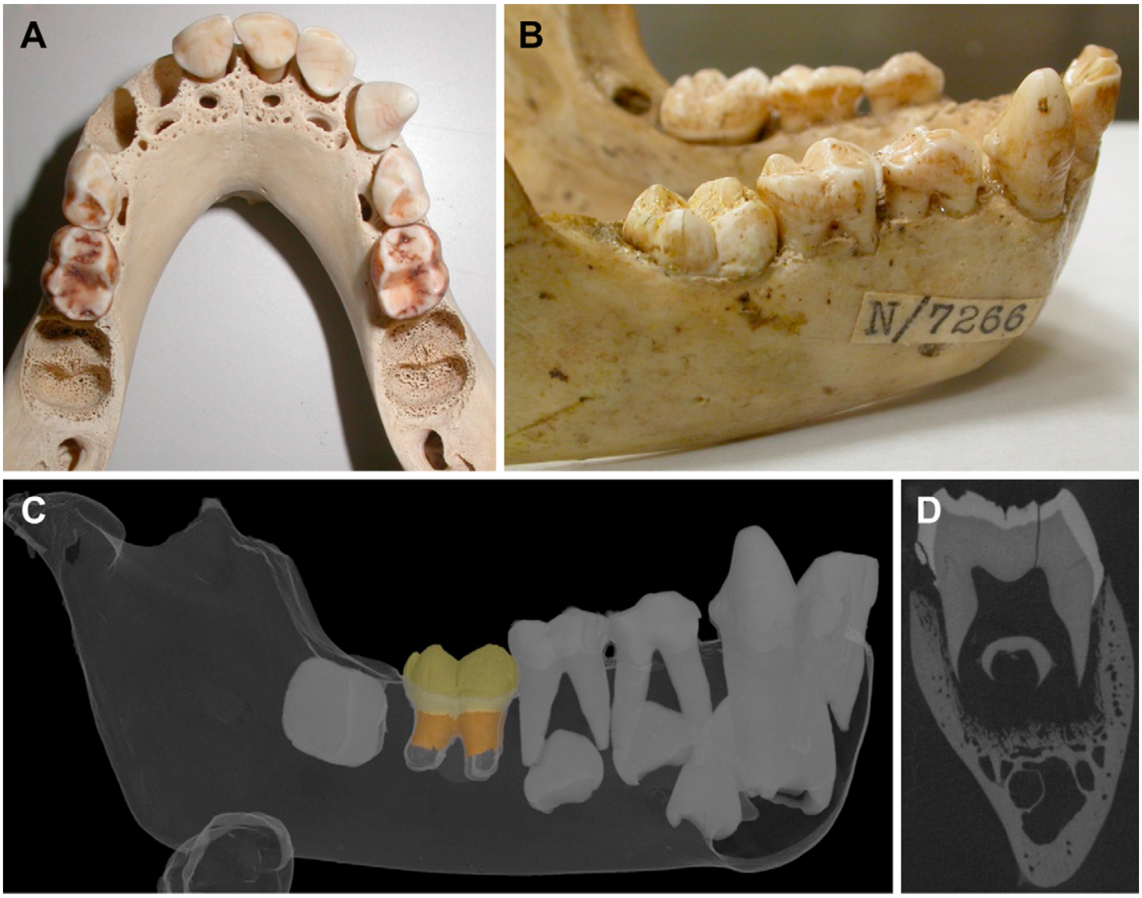

Fig. 6. A) The mandible of Piment (11788), the single case supporting recent statements that wild chimpanzees erupt M1s at 4 years of age. Although the maxillary M1s were unerupted, the mandible suggests otherwise. Alveolar root impressions of M1s are past the formation of the root clefts and bony margins were actively resorbing. B) Mandible of wild-shot *Pan troglodytes verus* (Peabody Museum N/7266) showing late-stage eruption of the right mandibular M1. C) Virtual model of N/7266 following microCT scanning (39 micron resolution), with the erupting M1 segmented to display the degree of root formation. D) Virtual cross-section though the mesial roots of right mandibular M1 of N/7266, revealing a mesial crypt depth of 7.5–7.6 mm (from alveolar margin). Equivalent measurements of Piment's lower molar root depths are 6.2–7.2 mm (left), and 6.2–6.7 mm (right). The depth of the bifurcation is nearly identical in the two mandibles; for Piment, depth from the alveolar margin is 3.6 mm (left) and 4.8 mm (right); N/7266 shows a depth of 4.1 mm (right). This comparison suggestst that one or both of Piment's mandibular M1s were likely at or just through the gingiva by 3.76 years of age.

history of later hominins. Both Wolpoff and Caspari (2006) and Monge et al. (2007) recently highlight similarities between the growth and development of chimpanzees and members of the genus *Homo* in terms of pattern and timing. Wolpoff and Caspari (2006) compared the developmental status of Krapina Maxilla B (*Homo neanderthalensis)* with the 11791 maxilla, noting that the development was so similar they could have come from the same population. If true, such a comparison raises questions, given that Wolpoff (1979) and Wolpoff and Caspari (2006) have aged the Krapina B maxilla at 7–8 years of age, and that chimpanzee 11791 was said to be 8.3 (Zihlman et al., 2004). Our reassessment of 11791 finds her to be 6.4 years of age, occupying a more advanced state of maturation than the Krapina individual. Many young primates look similar when M1s are erupted with a deciduous dentition, as in Maxilla B. Fine-scaled comparisons, however, show differences in developmental patterns between Neanderthals and great apes (e.g., Smith, 1994). Current evidence suggests that both *H. erectus* and Neanderthals exhibit a more prolonged pattern of growth and development than that seen in chimpanzees and australopiths (e.g., Dean et al., 2001; Smith et al., 2007b).

Conclusions

This study presents an expanded analysis of dental development in the Taï chimpanzee skeletal collection employed by Zihlman et al. (2004), including novel data on crown and root formation, and inclusion of additional juveniles. Currently there are 16 Taï juveniles of known age; radiographic imaging of these individuals reveals almost complete crown formation overlap with captive standards, which is also found for M1 and M2 histological data. Thus, crown formation times derived from captive primates are suitable for comparison with both wild and fossil primates. Root formation shows some differences with advancing age, although comparative samples of older captive individuals are limited. It is known that the variability of tooth formation (i.e., initiation, crown completion, root formation) increases with age (e.g., Garn et al., 1959), which may lead to differences when small sample sizes are compared. Alternatively, differences in root formation may be due to limited alveolar space in wild individuals, potentially leading to slower root growth, later eruption timing, impaction, and/or overcrowding (observed in a small subset of this collection). Captive developmental standards predict age of three out of four wild subjects with reasonable accuracy, representing additional evidence of overall similarities in dental development between young captive and wild individuals.

When the 13 individuals employed by Zihlman et al. (2004) are reconsidered, fewer than half of the original ages employed are of sufficient precision for comparison with captive chimpanzee eruption ages. Two of the individuals were misidentified during field recovery and after accession, including one key individual who was erupting I2 and M2 at death (now 6.4 rather than 8.3 years old), resulting in complete overlap with captive eruption ages. This is the only known-age individual in the collection that shows direct evidence of gingival emergence at death (who appears free of gross dental pathology). The other key Taï individual in the Zihlman et al. (2004) study with unerupted maxillary M1s is likely to have erupted her mandibular first molars by 3.8 years of age, an age more similar to captive ranges than the previous estimate (4.1 years of age from maxillary M1s). These findings are consistent with the paradigm that teeth are more buffered from environmental variation during development than are other skeletal elements. Parallels between environmental variation, hormonal variation, and tooth development represent an interesting area worthy of further study. Finally, revised estimates of eruption ages in these two individuals also reinforce taxonomic differences in dental development between living *Pan* and *Homo*, and are distinct from molar eruption ages estimated for early fossil *Homo*.

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