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Dental eruption in East African wild chimpanzees

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ABSTRACT

Knowledge of chimpanzee development has played an essential role in our understanding of the evolution of human ontogeny. However, recent studies of wild ape dentitions have cast doubt on the use of developmental standards derived from captive individuals. Others have called into question the use of deceased wild individuals to infer normative development. We conducted a high resolution photographic study of living known-age subadults in the Kanyawara community (Kibale National Park, Uganda) to generate a comprehensive three year record of dental eruption (including tooth emergence ages). These non-invasive data allow comparisons of captive and wild chimpanzees, establish accurate developmental standards for relatively healthy wild individuals, and facilitate direct assessments of primate-wide associations between dental development and life history. Emergence ages in the Kanyawara chimpanzees are very similar to living Gombe chimpanzees, and are broadly comparable to deceased Taï Forest chimpanzees. Early-emerging teeth such as the deciduous dentition and first molar (M1) appear during a time of maternal dependence, and are almost indistinguishable from captive chimpanzee emergence ages, while later forming teeth in the Kanyawara population emerge in the latter half of captive age ranges or beyond. Five juveniles whose lower M1s emerged by or before 3.3 years of age continued to nurse for a year or more beyond M1 emergence, and their mothers showed considerable variation in reproductive rates. The third molars of two adolescent females emerged several months to several years prior to the birth of their first offspring. Given that broad primate-wide relationships between molar emergence and life history do not necessarily hold within this population of chimpanzees, particularly for variables that are reported to be coincident with molar emergence, we suggest that further study is required in order to predict life history variables in hominins or hominoids.

Introduction

In humans and other primates, subadults are routinely aged by comparing tooth eruption[1] patterns with those of known-aged individuals (Smith et al., 1994; Hillson, 2005; AlQahtani et al., 2010). Among chimpanzees, early studies of tooth development reported emergence ages for small numbers of captive animals or museum specimens (reviewed in Smith et al., 2007). This includes a longitudinal study by Nissen and Riesen, who presented the first data on gingival (gumline) emergence in several individuals of known age (Nissen and Riesen, 1945, 1964). In 1945, they reported emergence ages for the deciduous (primary) dentition of 16 captive individuals, followed by a 1964 report on the emergence of the permanent dentition of 15 of the original 16 chimpanzees. Subsequently Conroy and Mahoney (1991) conducted intraoral exams of 58 known-age captive chimpanzees in a 'mixed' longitudinal study (enrolling different-aged subadults who were followed for one to nine years), yielding a somewhat larger data set on deciduous and permanent emergence ages in captive individuals (also see Kuykendall et al., 1992). These data have been used as the basis for comparisons with fossil hominins, leading to the hypothesis that

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[1] The terms 'eruption' and 'emergence' are defined here as follows: eruption is the process of tooth movement from within the alveolar crypt to the fully occluded position in the dental arcade, while emergence refers to the event within the eruptive process whereby the tooth first becomes visible at the margins of the jaw bone (alveolar emergence) or gumline (gingival emergence). Here we use the term 'emergence' to refer to gingival emergence unless otherwise specified.

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Plio-Pleistocene hominins possessed an ape-like growth pattern, as first molar emergence ages were estimated to be very similar to those of captive chimpanzees (Bromage and Dean, 1985; Smith, 1986; Smith and Tompkins, 1995; Anemone et al., 1996).

Recent studies have called into question the appropriateness of developmental data derived from captive animals for the reconstruction of hominin life history (Zihlman et al., 2004, 2007; Kelley and Schwartz, 2010, 2012). Zihlman et al. (2004) estimated maxillary emergence ages from dry skulls of West African wild chimpanzees (*Pan troglodytes verus*), which appeared to show later ages than captive individuals. However, Smith et al. (2010) reassessed the Taï Forest chimpanzee skeletons and found that ages at death in half of the subadults employed by Zihlman et al. (2004) were not known with accuracy sufficient for precise comparisons with captive chimpanzees. Moreover, one key individual in the former study was misidentified during field recovery, leading to overestimated ages for incisor and second molar emergence. Smith et al. (2010) concluded that emergence ages in two remaining known-aged Taï individuals appear to fall near the middle or latter half of captive emergence ranges, which does not support the "unambiguous pattern" of slower wild chimpanzee tooth formation reported by Zihlman et al. (2004:10541). Smith and Boesch (2011) extended these results to suggest that an important source of developmental variation may be the use of deceased wild individuals, who are more likely to have experienced developmental delay due to stress or pathology. They concluded that tooth emergence ages must be established from living individuals.

Here we present the ages of dental emergence of the deciduous and permanent dentition of East African wild chimpanzees (*Pan troglodytes schweinfurthii*) determined for known-age living subadults from the Kanyawara community in Kibale National Park, Uganda. Tooth eruption stages (absence, initial emergence/first appearance, partial emergence, full occlusion), as well as the duration of eruption from the gumline to the occlusal plane, were assessed from a multitude of high-resolution photographs taken over 39 months. We also provide updated information for our initial assessment of first molar (M1) emergence and life history variables (Smith et al., 2013), including new ages at weaning, resumption of sexual swelling, subsequent pregnancy, and interbirth intervals for multiparous mothers. These data provide important insight into developmental variation within a species, facilitating comparisons with large samples of captive individuals, as well as a few known-aged wild chimpanzees. Knowledge of wild chimpanzee dental development is also important for assessing the age of unknown individuals, including subadult females who routinely immigrate into new communities. Finally, these new developmental standards represent an important comparative sample for the study of juvenile fossil hominins.

Methods

Several dedicated photographers (RMD, ABB, and NFB) accompanied a team of field assistants to locate and photograph subadult chimpanzees from the Kanyawara community in Kibale National Park (Uganda) from March 2011 through June 2014. The Kanyawara community consisted of 53–54 habituated individuals during this time, including more than 25 subadults aged 0–15 years whose births are known to within a month or less (Table 1). Photographic data on dental eruption were collected when chimpanzees were resting, grooming, or playing (Fig. 1). High-resolution photographs were taken using a digital SLR camera with high ISO capability (at least 3200), high frames per second (at least six), and a wide aperture lens (f/4 at 200 mm). Approximately 2,500 photographs of subadult community members taken on a weekly or monthly basis were examined by AP and TMS for information on the presence or absence of teeth. Tooth emergence was assessed from exposed cusp tips at or just above the gumline, which is the standard used in laboratory settings and for living humans. When possible we used subsequent images to confirm that small protein stained regions of postcanine tooth crowns were closely followed by the emergence of the mesial and distal aspects of the crown. We chose not to extrapolate ages when initial emergence was not captured in photographs, thus the only error associated with our emergence

Table 1
Kanyawara wild chimpanzees included in this study.

Name	Sex	Birth date	First photo age (yrs)	Last photo age (yrs)
WZ (Winza)	M	5/25/2012	0.4	1.4
MM (Mango)	F	1/21/2012	0.5	2.3
OB (Tembo)	M	1/20/2012	0.3	2.4
RB (Burma)	M	11/17/2011	0.6	0.8
TR (Thatcher)	F	11/12/2011	0.4	2.5
UK (Buke)	F	4/6/2011	0.2	2.9
LE (Betty)	F	1/2/2011	0.7	1.9
BT (Basuta)	M	6/23/2010	1.2	3.9
AN (Azania)	F	5/1/2009	2.5	4.9
OL (Gola)	F	3/3/2009	2.5	3.6
MN (Moon)	M	12/26/2008	2.6	5.4
WC (Wallace)	M	8/5/2008	3.1	5.8
QV (Quiver)	M	8/3/2008	2.8	4.3
WE (Wenka)	F	6/22/2007	4.3	5.4
OM (Omusisa)	F	6/23/2005	5.9	7.3
TS (Tsunami)	F	1/23/2005	6.6	9.0
AZ (Likizo)	M	12/28/2004	6.4	9.4
UN (Unasema)	M	11/1/2004	7.1	9.2
EU (Euro)	F	5/25/2004	7.2	–
BO (Bono)	M	10/22/2003	7.9	10.6
OG (Tacugama)	M	4/10/2001	9.9	13.2[a]
TT (Tuber)	M	11/1/2000	10.4	13.1[a]
NP (Special)	F	2/9/2000	11.6	14.3[a]
AT (Tuke)	M	11/2/1999	11.5	14.6[a]
OT (Tenkere)	F	2/13/1999	13.6	15.7[a]
MX (Max)	M	1/15/1998	13.4	14.2[b]
PB (Bud)	M	1/20/1995	16.3	19.4[a,b]

[a] All teeth erupted prior to the end of photographic recording.
[b] Third molar teeth erupted later than in other individuals possibly due to tooth impaction.

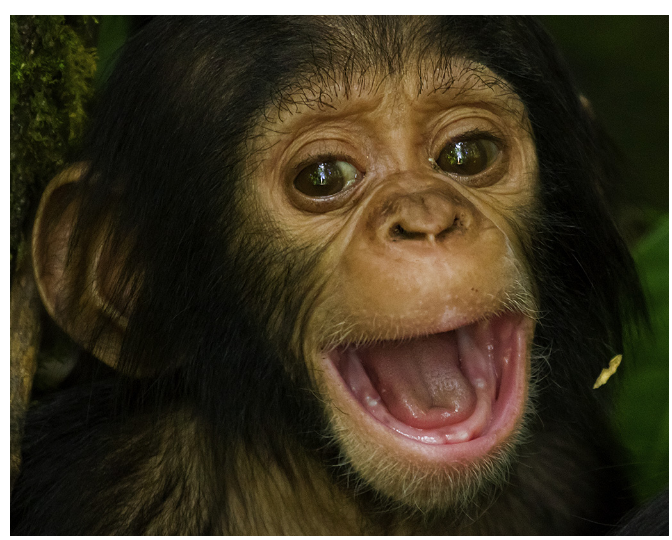

Figure 1. Deciduous tooth emergence in a two-month old wild chimpanzee female infant. The image depicts Buke at approximately 58 days of age showing initial emergence of her deciduous lower central incisors and deciduous third premolars (small white spots in the pink U-shaped dental arcade). Her deciduous lower lateral incisors appeared shortly before 93 days of age, the deciduous lower fourth premolars were first seen fully erupted at 315 days of age, and the deciduous lower canine appeared to cut the gum at 437 days of age. She was estimated to be three weeks old when she was first observed with her mother.