Brief Communication: Dental Development Timing in Captive *Pan paniscus* With Comparisons To *Pan troglodytes*

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ABSTRACT Dental eruption provides markers of growth and is one component of a chimpanzee's physical development. Dental markers help characterize transitions between life stages, e.g., infant to juvenile. Most of what we know about the timing of development in chimpanzees derives from *Pan troglodytes*. Much less is known about the sister species, *Pan paniscus*, with few in captivity and a restricted wild range in central Africa. Here we report on the dental eruption timing for female captive *P. paniscus* ($n = 5$) from the Milwaukee and San Diego Zoos whose ages are known and range from birth to age 8.54 years. Some observations were recorded in zoo records on the gingiva during life; others were made at death on the gingiva and on the skeleton. At birth, *P. paniscus* infants have no teeth emerged. By 0.83 years, all but the deciduous second molars (dm^2) (when both upper and lower dentitions are referenced collectively, no super or subscript notation is used) and canines (dc) are emerged. For permanent teeth, results show a sequence polymorphism for an early P4 eruption, not previously described for *P. paniscus*. Comparisons between *P. paniscus* and *P. troglodytes* document absolute timing differences of emergence in upper second incisors (I^2), and upper and lower canines (C) and third molars (M3). The genus *Pan* encompasses variability in growth not previously recognized. These preliminary data suggest that physical growth in captive *P. paniscus* may be accelerated, a general pattern found in captive *P. troglodytes*. Am J Phys Anthropol 145:647–652, 2011. © 2011 Wiley-Liss, Inc.

Dental eruption provides markers of growth and is one component of a chimpanzee's physical development. Dental markers help characterize life stages and transitions between them, e.g., infant to juvenile to adult. Typically captive *Pan troglodytes* have been used to represent the *Pan* pattern when hypothesizing about growth, development, and life history during human evolution (e.g., Schultz, 1973; Bogin and Smith, 1996; Godfrey et al., 2003). Little is known of dental development in *P. paniscus*. One report on captive *P. paniscus* infants records the first deciduous dentition emergence through the gingiva between 1 and 1.5 months, and states that "temporary dentition is complete at 10 months" (Neugebauer, 1980; p 67). A second study based on histological analysis from a wild-born specimen concludes that the upper first molar (M^1) partially erupts by 4.77 years (Ramirez-Rozzi and LaCruz, 2007).

Boughner and Dean (2008) propose that dental emergence timing is a genus level pattern that encompasses both species of *Pan*. They base this on the histology of molar crown formation times of *P. troglodytes* (i.e., Reid et al., 1998) and *P. paniscus* (i.e., Ramirez-Rozzi and LaCruz, 2007). However, this proposal reinterprets the original study of Ramirez-Rozzi and LaCruz (2007) that relied on one wild *P. paniscus* individual. From it Ramirez-Rozzi and LaCruz argue that dental growth in the two species of *Pan* is distinct based on differences they found in the appositional rates of the maxillary first incisor (I^1) and M^1, and the packing pattern of the perikymata in the I^1. They concluded that the I^1 required a shorter formation time and that the M^1 crown formation is "similar or slightly shorter than values for *P. troglodytes*" (2007; p 174).

In craniofacial and postcranial morphology, researchers disagree on the allometric modeling of *Pan*. When Coolidge gave *P. paniscus* species status, he argued that they were a juvenilized form of *P. troglodytes* (1933). Other views are that the two species represent "scaled variants of the same animal" (McHenry and Corruccini, 1981; p 355). And others find more than one ontogenic pattern (e.g., Cramer, 1977; Shea, 1983; Daegling, 1996; cf Boughner and Dean, 2008). Behavioral studies also support differences in social development within *Pan* (e.g., Kuroda, 1980; Neugebauer, 1980; Brakke and Savage-Rumbaugh, 1991; De Lathourwers and Van Elsacker, 2006).

This study provides new data on the timing and sequence of dental development in female captive *P. paniscus* ($n = 5$) from the Milwaukee and San Diego Zoos, and compares them to findings on captive *P. troglodytes* to test the hypothesis that the two species of *Pan* have the same timing of dental emergence.

MATERIALS

The sample comprises five captive-born immature female *P. paniscus* whose ages are known (Table 1). None had reproduced.

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TABLE 1. Sample

Specimen	Life stage	Age (yr)	Cause of death
Lannie's Baby	Infant	Newborn	Stillborn
Yatole	Infant	0.83	Head injury from a fall
Leslie	Juvenile	6.74	Acute illness; pneumonia
Eliya	Juvenile	7.30	Acute illness; pneumonia
Naomi	Subadult	8.54	Complications from perforated bowl

TABLE 2. Status of emergence of deciduous dentition: 0 is unemerged, 1 is emerged

	Age (yrs)	i^1/i_1	i^2/i_2	dm^1/dm_1	dm^2/dm_2	c^1/c_1
L. Baby	Newborn	0/0	0/0	0/0	0/0	0/0
Yatole						
Live obs	0.21	0/1	0/1	0/0	0/0	0/0
Live obs	0.29	1/1	1/1	0/0	0/0	0/0
Death	0.83	1/1	1/1	1/1	0/0[a]	0/0[b]
Leslie	6.74	–[c]	1/–[c]	–/1[c]	–[c]	1/1

[a] Deciduous second molars could be palpated through gum, but had not yet broke through. Lower second molars could also be visually seen through the gum line, but had not yet emerged through the gingiva.
[b] Upper and lower canines could be palpated through gum but had not yet broke through.
[c] Denotes presence of permanent teeth.

TABLE 3. Status of emergence of permanent dentition: 0 is unemerged, 1 is emerged

	Age	M1	I1	I^2	I_2	M2	P3	P4	C	M^3	M_3
Leslie	6.74	1	1	0	1	1	1[a]/1	1	0	0	0
Eliya	7.30	1	1	1	1	1	1	1	1[b]	0	0
Naomi											
Live obs	7.85	1	1	1	1	1	1	1	1	0	0
Death	8.54	1	1	1	1	1	1	1	1	1[c]	1[d]

[a] For upper and lower P3, left side fully erupted, right upper side partially emerged, while lower right side is just emerging into gingiva with right dm_1 still in place.
[b] Tips of upper canines are just emerging into the gingiva. Lower canines near full occlusion.
[c] M^3s are just emerging into gingiva with three cusps past gumline.
[d] M_3s almost into full occlusion but torqued medially (bumping laterally against ascending ramus) and so crown surface not flat.

Methods

Three observation bouts of tooth emergence were made during life; the others were made at death, either gingivally or later on the skull. Teeth were considered newly emerged if they pierced through the gingiva (live observation) or surpassed the alveolar bone and showed cuspal discoloration (skeletal observation). If left and right stages of emergence differed, both stages were identified.

The findings cluster into two categories: deciduous teeth ($n = 2$, infants), and later erupting permanent teeth ($n = 3$, late juveniles). The late juveniles already had M1s, second molars (M2s), I1s and lower second incisors (I_2) fully erupted so only minimum estimates can be extrapolated on emergence times for these teeth. Data on the following permanent teeth are presented here: premolars (P3, P4), I^2, and M3.

RESULTS

Tables 2 and 3 record the emergence status of deciduous and permanent teeth for all individuals. Table 4 provides comparisons of emergence times for the deciduous teeth with captive *P. paniscus* and *P. troglodytes*. Tables 5 and 6 compare the emergence times for the permanent teeth of the sample with captive *P. troglodytes*.

Sequence of deciduous tooth eruption is [i^1 i^2] dm^1 [dm^2 *c*]/[i_1 i_2] dm_1 [dm_2 c] and permanent tooth eruption sequence is [M^1 I^1 P^4 M^2] P^3 I^2 *C* M^3/[M_1 I_1 P_4 M_2 I_2] P_3 C M_3.

DISCUSSION

P. paniscus has been characterized as erupting deciduous teeth early: "preliminary data on *Pan pansicus* suggest that the bonobo matures more rapidly than the common chimpanzee, completing the deciduous dentition a half-year earlier" (Smith et al., 1994; p 191). The findings presented here suggest *P. paniscus* develops deciduous dentition like *P. troglodytes* (common chimpanzees) but the permanent dentition departs from that pattern.

Maxillary teeth

Left and right I^2s emerge later in absolute time and sequence when *P. paniscus* is compared with the longitudinal sample reported for 58 captive *P. troglodytes* from LEMSIP (Kuykendall et al., 1992). In our study, the 6.74-year-old "Leslie" still had deciduous left and right second incisors (di^2) with permanent I^2s encapsulated below the alveolus (see Figs. 1a and 2a) whereas the 7.30-year-old "Eliya" had her I^2s fully erupted. Because 90% of *P. troglodytes* individuals in the LEMSIP study had emerged I^2s by 6.9 years and 95% by 7.30 years, we conclude that *P. paniscus* falls at the edge or outside of the range of variation in I^2 eruption for this population. Note that the LEMSIP values reflect a mixed sex sample, and the 36 females consistently erupted the maxillary I^2s about 6 to 9 months earlier than the 22 males (Conroy and Mahoney, 1991). This sex difference in eruption timing of the I^2s further supports the placement of the female *P. paniscus* outside of the range of variation of LEMSIP female *P. troglodytes*. However, I^2s emerged as late as 8.25 years in a captive *P. troglodytes* population from Yerkes ($n = 7$ females) so that these *P. paniscus* fall into their range.

The canines of "Eliya" were just emerging into the gingiva at 7.30 years, which fits into the range of 6.78 to 8.75 years for the LEMSIP *P. troglodytes* ($n = 2$ females, $n = 1$ male) (Kuykendall et al., 1992). However, the seven Yerkes females emerged their canines later at 7.58 to 10.1 years (Nissen and Riesen, 1964). The sample of two populations show a contradictory pattern: in the upper canines *P. paniscus* is distinguished from the Yerkes *P. troglodytes* in accelerated development and is more allied with the LEMSIP population, whereas the I^2s fit better with the Yerkes group in late emergence and not with the LEMSIP chimpanzees.

Emergence times of M^3s are only available for the Yerkes population, and in females the earliest emergence time reported in *P. troglodytes* is 9.75 years. In *P. paniscus*, based on two separate observations of "Naomi" (8.54 years old), the M^3s were unemerged into the gingiva at 7.85 years, but in a later observation were partially emerged at 8.54 years (see Figs. 1b and 2b). Captive

TABLE 4. Timing in years of decidious tooth eruption in Pan paniscus and Pan troglodytes

Deciduous maxillary and mandibular teeth	*Pan paniscus* This study; N(ind) = 2 (F)	*Pan paniscus* Neugebauer (1980); N(ind) = 4 (2 F; 2 M)	*Pan troglodytes* Kuykendall et al. (1992); 50th percentiles[a] N(ind) = 58 (36 F; 22 M)
di1,2	$0 < x < 0.29$ yrs	0.083–0.125 yrs	0.25, 0.33 yrs
dm1	≈0.83	0.33–0.50[b]	0.38
dm2	>0.83	0.50–0.83[b]	0.77
dC	>0.83	0.50–0.83[b]	1.07

[a] Left and right, maxillary and mandibular ages averaged.
[b] Approximate ages in months reconstructed from Fig. 2 in text.

TABLE 5. Timing in years of permanent maxillary tooth eruption in captive Pan paniscus and Pan troglodytes

	Pan paniscus	*Pan troglodytes*	
	This study; interval of emergence females only; N(ind) = 3	Nissen and Riesen (1964); mean (ranges) females only; Yerkes; N(ind) = 7	Kuykendall et al. (1992); probit median, min-max; mixed sex sample[a] LEMSIP; N(ind) = 58
M^1	<6.74 yrs	3.27 (2.75–3.75) yrs	3.18 (2.26–4.38) yrs
I^1	<6.74	5.63 (4.50–6.75)	5.55 (4.47–6.43)
P^4	<6.74	7.47 (6.25–8.33)	6.50 (4.86–7.60)
M^2	<6.74	6.76 (5.92–7.58)	6.74 (5.23–7.37)
P^3	≈6.74	6.96 (6.08–8.08)	6.67 (4.86–7.97)
I^2	$6.74 < x < 7.30$	6.79 (5.83–8.25)	6.22 (4.67–6.83)
C	≈7.30	9.03 (7.58–10.08)	8.11 (6.52–8.74)
M^3	≈8.54	11.33 yrs (9.75–13.08)	ND

[a] LEMSIP females had statistically significant earlier eruption of maxillary I2, P3, and P4. However, the data in Kuykendall et al. (1992) were not reported by sex [only median values were divided out by female and male in Conroy and Mahoney (1991)], so the ranges listed here may reflect slightly older values (6–12 months) than if female-only values were available. When left and right sides differed, the two were averaged.

TABLE 6. Timing in years of permanent mandibular tooth eruption in captive Pan paniscus and Pan troglodytes

	Pan paniscus	*Pan troglodytes*	
	This study; interval of emergence; N(ind) = 3; females only	Nissen and Riesen (1964); mean (ranges) females only; Yerkes; N(ind) = 7; N(obs) = 217	Kuykendall et al. (1992); probit median, min-max; mixed sex sample[a] LEMSIP; N(ind) = 58
M_1	<6.74 yrs	3.27 (2.75–3.75) yrs	3.15 (2.14–3.96) yrs
I_1	<6.74	5.63 (4.50–6.75)	− (4.81–6.29)
P_4	<6.74	7.47 (6.25–8.33)	6.76 (4.86–7.97)
M_2	<6.74	6.76 (5.92–7.58)	6.66 (4.81–6.96)
P_3	L ≈ 6.74; R > 6.74	6.96 (6.08–8.08)	7.40 (4.86–8.74)
I_2	<6.74	6.79 (5.83–8.25)	5.88 (4.81–6.69)
C	<7.30	9.03 (7.58–10.08)	− (6.52–8.74)
M_3	$7.85 < x < 8.54$	10.71 (9.00–13.08)	ND

[a] LEMSIP females had statistically significant earlier eruption of mandibular I1, I2, P3, P4, and M2. However, the data in Kuykendall et al. (1992) were not reported by sex [only median values were divided out by female and male in Conroy and Mahoney (1991)], so the ranges listed here may reflect slightly older values (4–12 months) than if female-only values were available. When left and right sides differed, the two were averaged.

P. paniscus M^3 emergence times are earlier than any published report for *P. troglodytes.*

Mandibular teeth

On the data available (P_3, P_4, *C*, and M_3), the only teeth that distinguish the two species of *Pan* are the canines and M_3s.

The lower canines as well as the upper canines in *P. paniscus* fall into the range of variation of the *P. troglodytes* from the LEMSIP population, though outside of the range of variation of the Yerkes *P. troglodytes* (Table 6).

Emergence times of M_3s are only available for the *P. troglodytes* Yerkes group; the earliest emergence time reported in females is 9.00 years. In *P. paniscus*, "Naomi's" M_3s were unemerged into the gingiva at 7.85 years and by 8.54 years were near full occlusion (Figs. 1b and 2b).

Sequence

P^4 erupts very early in this sample and before the I^2s. This polymorphism has not previously been reported for *P. paniscus*. The late eruption of the I^2s after both P^3

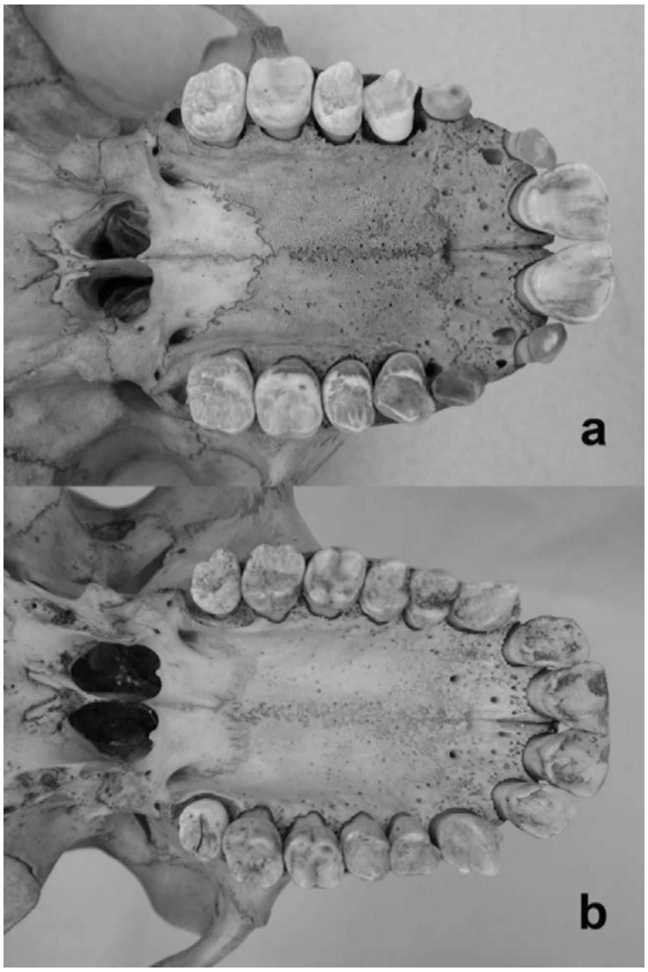

Fig. 1. Maxillary view of teeth in 6.74-year-old "Leslie" (**a**) and 8.54-year-old "Naomi" (**b**). Note in the 6.74-year-old the permanent I^2s are still encapsulated below the alveolus, visible through a small hole behind the di^2s. In the 8.54-year-old only three of the four cusps of the M^3s have emerged passed the gumline.

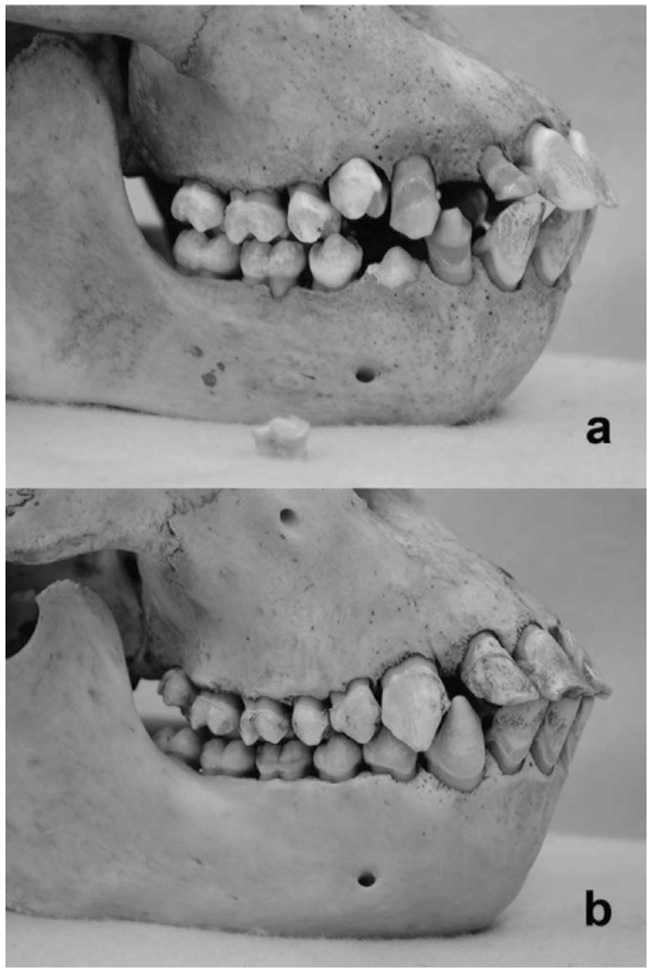

Fig. 2. Right side view 6.74-year-old "Leslie" (**a**) and 8.54-year-old "Naomi" (**b**). Note in the 6.74-year-old, the P_3 is just emerging; the dm_1 still present in gum tissue has been removed and set in front of the mandible for this photo. I^2 and canines are deciduous and M3s unemerged. In the 8.54-year-old all permanent teeth have emerged, although the M3s are not in full occlusion.

and P^4 in the present sample is common in the Tervuren *P. paniscus* sample (Kinzey, 1984), but is not common in *P. troglodytes* (Kuykendall et al., 1992).

Captive versus wild timing of emergence

Growth and development differences between wild and captive primates are well documented (e.g., Coe et al., 1979; Phillips-Conroy and Jolly, 1988; Tutin, 1994; Kimura and Hamada, 1996; Boesch and Boesch-Achermann, 2000; De Lathouwers and Van Elsacker 2005; Stevens et al., 2008; Kelley and Schwartz, 2010). On average wild great apes are known to have dental emergence times later than in captivity (Zihlman et al., 2004, 2007; Kelley and Schwartz, 2010; Smith and Boesch, 2010) although the mechanisms of differential growth are not clearly understood (Smith et al., 2010). We suspect that captive *P. paniscus* dental emergence is accelerated compared with their wild counterparts as is found in other hominoids. This hypothesis remains untested until further data on wild dental emergence times becomes available.

Evidence on reproductive development strengthens the hypothesis that compared with populations in the African Congo, developmental timing quickens in captivity (De Lathouwers and Van Elsacker, 2005). In the wild, adolescence begins when females emigrate from their natal groups around 8 years, with first births around 14 to 15 years (Furuichi et al., 1989; Kuroda, 1989; Idani, 1991; Kano, 1992; Hashimoto 1997; Mulavwa et al., 2008). In captivity females reach adolescence by 7 years with average age at first birth between 9 and 10.5 years (Neugebauer 1980; Kuroda, 1989; De Lathouwers and Van Elsacker 2005; Stevens et al., 2008), at least 3 years earlier than in the wild.

Molar emergence timing links developmental systems that are used to model general growth patterns. Captive *Pan troglodytes* and *Pongo pygmaeus* postpone reproduction until after M_3 emergence, unlike the pattern found in cercopithecoids (Dirks and Bowman, 2007). *P. paniscus* in captivity appears to share this life history association between reproductive and dental developmental systems. Although no *P. paniscus* wild data are available on M_3 emergence, one *P. troglodytes* 11.38 wild adolescent female of known birth and death date did not have emerged mandibular M3s ["Kana" from the Taï population, part of the authors' study on wild chimpanzees (Zihlman et al., 2004, 2007); death date as published in Smith et al. (2010)]. Like *P. paniscus, P. troglodytes* in the wild reproduce much later than their captive counterparts at 14.9 years (Tutin, 1994).

We suspect that this link between postponed reproductive development and protracted development in other systems, like dental maturation, holds constant for wild *P. paniscus*. If this hypothesis is supported, then the timing of some or all life stages in captive *P. paniscus* may be shorter than the pattern in the wild.

CONCLUSION

The genus *Pan* encompasses variations in dental development not previously known, reminiscent of the range of variation found in the genus *Homo* (cf. Liversidge et al., 1998). Importantly, these data demonstrate that *P. paniscus* dental timing and sequence show a distinct pattern from that of *P. troglodytes,* specifically in I^2s, canines and upper and lower M3s. Perhaps these polymorphisms are related to differences in facial morphology and growth between the two species, a potential area of study for future researchers. We additionally hypothesize that an accelerated growth pattern in dentition may characterize captive populations of *P. paniscus* compared with their wild counterparts. Information on dental developmental timing from wild populations must be used to test this hypothesis and those data currently do not exist. These data may be available in the near future as field primatologists conduct long-term research on wild populations, and recover specimens for study at death. This present study provides another step towards a more robust database for researchers modeling life history events for chimpanzees, other living apes, and fossil species.

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