Skeletal Development in *Pan paniscus* with Comparisons to *Pan troglodytes*

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ABSTRACT   Fusion of skeletal elements provides markers for timing of growth and is one component of a chimpanzee's physical development. Epiphyseal closure defines bone growth and signals a mature skeleton. Most of what we know about timing of development in chimpanzees derives from dental studies on *Pan troglodytes*. Much less is known about the sister species, *Pan paniscus*, with few in captivity and a wild range restricted to central Africa. Here, we report on the timing of skeletal fusion for female captive *P. paniscus* (*n* = 5) whose known ages range from 0.83 to age 11.68 years. Observations on the skeletons were made after the individuals were dissected and bones cleaned. Comparisons with 10 female captive *P. troglodytes* confirm a generally uniform pattern in the sequence of skeletal fusion in the two captive species. We also compared the *P. paniscus* to a sample of three unknown-aged female wild *P. paniscus*, and 10 female wild *P. troglodytes* of known age from the Taï National Park, Côte d'Ivoire. The sequence of teeth emergence to bone fusion is generally consistent between the two species, with slight variations in late juvenile and subadult stages. The direct-age comparisons show that skeletal growth in captive *P. paniscus* is accelerated compared with both captive and wild *P. troglodytes* populations. The skeletal data combined with dental stages have implications for estimating the life stage of immature skeletal materials of wild *P. paniscus* and for more broadly comparing the skeletal growth rates among captive and wild chimpanzees (*Pan*), *Homo sapiens*, and fossil hominins. Am J Phys Anthropol 147:629–636, 2012.   © 2012 Wiley Periodicals, Inc.

Skeletal development is important in growth studies because the skeleton serves as part of the infrastructure for the whole body. Skeletal fusions can also help characterize transitions between life stages (Bolter and Zihlman, 2003; Zihlman et al., 2007). The order of epiphyseal fusion by joint (e.g., hip, shoulder) is broadly uniform among primates (Schultz, 1970; Shigehara, 1980; King et al., 2001). Typically, the distal humeral epiphyses fuse first, followed by the hip, knee, and ankle, with the wrist and proximal humerus last. Synchronized fusion at joint elements (e.g., distal femur and proximal tibia) suggests a load-bearing, locomotor contribution to the initiation of epiphyseal closure (Washburn, 1943; King et al., 2001; Bolter, 2004, 2011).

For the genus *Pan*, studies on captive and wild populations yield information on dental development and growth patterns (Nissen and Reisen, 1964; Conroy and Mahoney, 1991; Kuykendall et al., 1992; Zihlman et al., 2004; Smith and Boesch, 2010; Smith et al., 2010; Bolter and Zihlman, 2011). However, studies on skeletal fusion in the genus *Pan* are rare, and the few published chimpanzee studies involve the *P. troglodytes* species (e.g., Schultz, 1940; Nissen and Reisen, 1949; Kerley, 1966; Watts, 1993; Zihlman et al., 2007). Little is known about the timing of skeletal development and possible sex differences in *Pan paniscus*. This gap in knowledge is partly due to the relative rarity of members of the species *P. paniscus*.

Much more information is available on dental eruptions in *Pan* (*troglodytes* in particular), and primates in general, particularly eruption of the first molars (M1) as these are well known life history markers (e.g., Smith, 1989; Godfrey et al., 2001; Kelley and Schwartz, 2009).

In growth and development studies, dental eruptions are emphasized in both extant and extinct species because (1) observations can be made on live primates, usually of known ages; (2) teeth are harder than bone and therefore the most frequently preserved part of the body in the fossil record; and (3) dental age classes are used as proxies for life history inferences.

A species life history pattern includes variations in growth periods (e.g., gestation length and length of juvenility), timing of major developmental milestones (e.g., age at weaning, locomotor independence, and first reproduction), and total of life history events (e.g., birth spacing and life span). As an individual within a species matures, each body system—dental, skeletal, muscular, reproductive—develops to meet the survival needs of the organism at each stage. These maturational patterns are not necessarily on the same schedules, so that brain size, muscle mass, dental eruptions, limb proportions, and epiphyseal unions develop in a mosaic pattern, and this pattern of development may represent a unique profile for a genus or species (Bolter and Zihlman, 2003; King, 2004).

Whether *P. paniscus* and *P. troglodytes* share a similar pattern of somatic growth is unresolved. Based on linear

measurements of the skeleton, some investigators conclude that the two species share an allometric growth model (McHenry and Coruccini, 1981: 355). Other research on cranio-facial and postcranial morphology suggests different ontogenetic patterns in the two species of *Pan* (e.g., Cramer, 1977; Shea, 1981; Daegling, 1996).

This study tests three hypotheses: that females of the two species of *Pan* share the same (1) sequence of fusion; (2) ages at fusion calibrated by dental stage; and (3) timing of fusion by chronological age. Our analysis controls for potential sex differences in developmental timing by studying only females. Sex differences in fusion times are apparent in some but not all catarrhine species and may be a pattern in the genus *Pan* (e.g., Randall, 1944; Kerley, 1966; Cheverud, 1981; Bolter and Zihlman, 2003; King, 2003; Zihlman et al., 2007). However, because our study is restricted to females, we cannot address skeletal development in male *P. paniscus*.

MATERIALS

We studied 18 skeletal specimens from the genus *Pan*: eight *P. paniscus*, five from captivity and of known age; three from the wild of unknown age; and 10 *P. troglodytes* from the wild, including nine of known age. We add from the literature skeletal growth data on 10 captive *P. troglodytes* females of known age from Yerkes National Primate Center (Kerley, 1966). When the genus

Pan is referenced in the text, it includes all 28 individuals from *paniscus* and *troglodytes*.

The five captive *P. paniscus* females were born either in the San Diego or Milwaukee Zoos, four immature and one young adult. Chronological ages to the day are known. All died of natural causes, and none suffered chronic illnesses (Table 1).

The three wild-caught immature female *P. paniscus* with postcrania are of unknown age, one from the Adolph Schultz collection in Zurich, and two specimens from the Royal Museum of Central Africa collection. These three individuals were studied for the order of fusion of the available skeletal elements and for the timing of fusion by dental complement. However, because their ages are unknown, these three specimens cannot be used in the analysis of chronological fusion ages in *P. paniscus*.

The bone fusion times of 10 wild *P. troglodytes* immature and young adult skeletons from the Taï National Park (Zihlman et al., 2007 and unpublished data) are evaluated for comparison with their sister species *P. paniscus*. The Taï females are listed by name, ages at death, and skeletal elements in Table 2.

The data on the 10 *P. troglodytes* females from Yerkes are taken from one publication by Kerley (1966). He radiographed the stripped joints to ascertain the age of skeletal fusions, and those 10 individuals' ages were reported to the nearest whole year: 6, 7, 9 ($n = 2$), 10, 12, 13 ($n = 2$), 14, and 18 years old respectively.

METHODS

Observations were made on bones of captive *P. paniscus* after the bones were cleaned by dermestid beetles. The ends of long bones were soaked in soapy water to dissolve any cartilage uniting epiphyses to bone shafts. Epiphyses were considered unfused if the ends were unattached, fully fused if bones were completely grown together, and partially fused if bones were united but still partially open.

For captive Yerkes *P. troglodytes*, the method of scoring fusion differs in that radiographs were used to assess unions of the epiphyses to the bone shafts by the author

TABLE 1. Captive sample of immature and young adult Pan paniscus with known ages

Specimen	Life Stage	Age (years)	Cause of death
Yatole	Infant	0.83	Head injury from a fall
Leslie	Juvenile II	6.74	Acute illness; pneumonia
Eliya	Juvenile III	7.30	Acute illness; pneumonia
Naomi	Subadult	8.54	Complications from perforated bowl
Zalia	Young adult	11.68	Complications from anesthesia

TABLE 2. Sample of wild Pan troglodytes females from Taï National Park

Taï individual and catalog number[a]	Life stage	Age (years)[b]	Skeletal elements available for this study
Ophelia No. 14993	Infant	0.74	Innominates
Piment No. 11788	Juv I	3.76	Innominates
Manon No. 11783	Juv I	5.19	Innominates
Endora No. 14991	Juv II	7.96	R Humerus
— No. 11791[c]	Juv II	—	Innominates, Humeri, Radii, Ulnae, Femora, Tibae, L Scapula
Tina No. 11790	Juv III	10	Humeri, R Radius, Scapulae
Kana No. 13437	Juv III	11.38	Innominates, Humeri, Radii, Ulnae, Femora, Tibae, Scapulae
Ariane No. 11776	Juv III	12	Innominates, R Humerus, Radii, Ulnae, R Femur, Tibae, Scapulae
Zerlina No. 11792	Subadult	12	Innominates, Humeri, Radii, Ulnae, L Femur, L Tibia, L Scapula
Agatha No. 11775	Young adult	16	Humeri, R Radius, Femora, R Tibia

[a] Some data from Zihlman et al. (2007). Additional unpublished skeletal data from Taï Park individuals Cat. No. 13437 "Endora" and 14991 "Kana" aged using known birth and death dates from Smith et al. (2010).
[b] For four individuals, Cat. Nos. 11792 "Zerlina," 11776 "Ariane," 11790 "Tina," and 11775 "Agatha" ages were rounded to nearest year as birth dates were unknown, but year of birth estimated. Month and year of death are known for each.
[c] For no. 11791, only the age class assignment of Juvenile II is used due to questions regarding her identity. We identified her as "Xindra" who died at 8.3 years old, cause of death unknown (Zihlman et al., 2004, 2007), but Smith et al. (2010) identify the individual as "Goshu" at 6.4 years who died of a leopard attack. See also Figure 1(b).

TABLE 3. Pan paniscus compared with Pan troglodytes in maxillary dental emergence and skeletal element fusion initiating in each stage, females only (see also Figs. 1–4)

Life stage	Teeth emerg.	Pan paniscus (n = 8)		Pan troglodytes (n = 10)[a]	
Infant	Decid.	1 captive 0.83 years	Pubic ramus	1 wild 0.74 years	Pubic ramus
Juv I	M1	1 wild unk	No change	2 wild 3.76 and 5.19 years	No change
Juv II	M2	1 captive 6.74 years 1 wild unk	Elbow (humerus) and hip (acetabulum)	2 wild 7.96 and 8.3[b] years	No change
Juv III	C	1 captive 7.30 years	Elbow (radius)	3 wild 10, 12, and 12 years	Elbow and hip (acetabulum and femoral head)
Subadult	M3	1 captive 8.54 years 1 wild unk	Hip (femoral head*), knee*, and ankle	1 wild 12 years	Knee (fibula) and ankle
Young adult	All	1 captive 11.68 years	Elements fused: shoulder, wrist, and iliac crest	1 wild 16 years	Elements fused: knee (tibia, femur), shoulder, and wrist (radius)

[a] *Pan troglodytes* data all from wild individuals (Zihlman et al., 2007). Kerley (1966) did not publish the stage of dental development for the 10 females for which he reported fusion data, and so they were excluded from this table.
* denotes fused in captive but unfused in wild specimens; for captive specimen only one proximal tibia (R) partially fused.
[b] As aged in Zihlman et al. (2007).

TABLE 4. Dental emergence and bone fusion in Pan paniscus and Pan troglodytes

Skeletal element	Pan paniscus Captive, age in years, n = 5	Pan troglodytes Captive from Yerkes, age in years, n = 10 (Kerley, 1966)	Pan troglodytes Wild from Taï National Park[a]; age in years, n = 9
Ischio-pubic ramus	<0.83 years	n/a	$0.74 < x < 3.76$ years
Distal humerus	<6.74	≈6–7 years	$7.96^{b} < x < 10$
Acetabulum	<6.74	≈7 years	$5.19 < x^{c} < 11.38$
Proximal radius	7.3[d]	≈9 years	$11.38 < x < 12$
Coracoid process	$7.3 < x < 8.54$	≈9 years	$10 < x < 11.38$
Proximal femur	$7.3 < x < 8.54$	≈9 years	$11.38 < x < 12$
Distal tibia	<8.54	≈9 years	$11.38 < x < 12$
Proximal tibia	≈8.54[e]	≈9–14 years	>12
Humeral head	$8.54 < x < 11.68$	≈9–14 years	>12
Acromial process	$8.54 < x < 11.68$	<10 years	>12
Iliac crest	≈11.68	≈9–14 years	>12

Partial fusion indicated by ≈.
[a] From Zihlman et al. (2007) and unpublished data.
[b] Distal end damaged by leopard attack and therefore fusion stage is tentatively diagnosed using the following conditions: (1) thinness of bone at distal ends, indicative of termination of bone without epiphysis and (2) unfused medial epicondyle which is reported to associate with unfused distal epiphyses in chimpanzees (Humphrey, 2011).
[c] No data on 7.96 and 10 years old.
[d] Proximal radius: L-partially fused; R-still unfused.
[e] Proximal tibia: R-partially fused; L-still unfused.

of that study, confirmed by histological examination of the growth plates (Kerley, 1966). These analyses record fusion as occurring earlier than methods assessing bones directly (e.g., Krogman and Işcan, 1986), as employed for the captive *P. paniscus* and wild *P. troglodytes* in this study.

P. paniscus specimens were organized by stage of dental eruption into age classes, following the methods outlined for *P. troglodytes* (Zihlman et al., 2007). Maxillary teeth were scored as follows: no emergence, partial emergence, and full emergence. If the two sides differed, the less developed dentition was used to establish age class. The age classes were as follows: Infant (no permanent teeth emerged), Juvenile I (M^{1} emerged), Juvenile II (second molar or M^{2} emerged), Juvenile III (canines or C̲ emerged), and subadult (third molar or M^{3} emerged). An individual was classified as Adult if all teeth were fully emerged and the proximal humerus fully fused (see below).

Fusion times of 22 skeletal elements on both left and right sides were assessed: long bones, proximal, and distal ends (12 elements); medial epicondyle of the humerus, greater and lesser trochanters (three elements); pelvis: acetabulum (three elements), ischio-pubic ramus (one element), iliac crest (one element); scapula: coracoid and acromial processes (two elements).

RESULTS

Order of fusion

Skeletal fusions occur in generally the same sequential order in captive *P. paniscus*, wild *P. paniscus*, captive *P. troglodytes*, and wild *P. troglodytes* (Tables 3 and 4). Two exceptions are noted. In *P. paniscus*, the acetabulum fuses earlier in sequence than *P. troglodytes*, whereas the long bones of the hip and knee may fuse later in sequence.

Timing of fusion by age class (dental emergence)

In female specimens sorted by life stages based on dental emergence, it appears that the timing of fusion in some skeletal elements may occur during different age classes in *P. paniscus* than in *P. troglodytes* (Table 3). (Note that in the Yerkes study, the captive *P. troglodytes* individuals were not assessed for both skeletal and dental
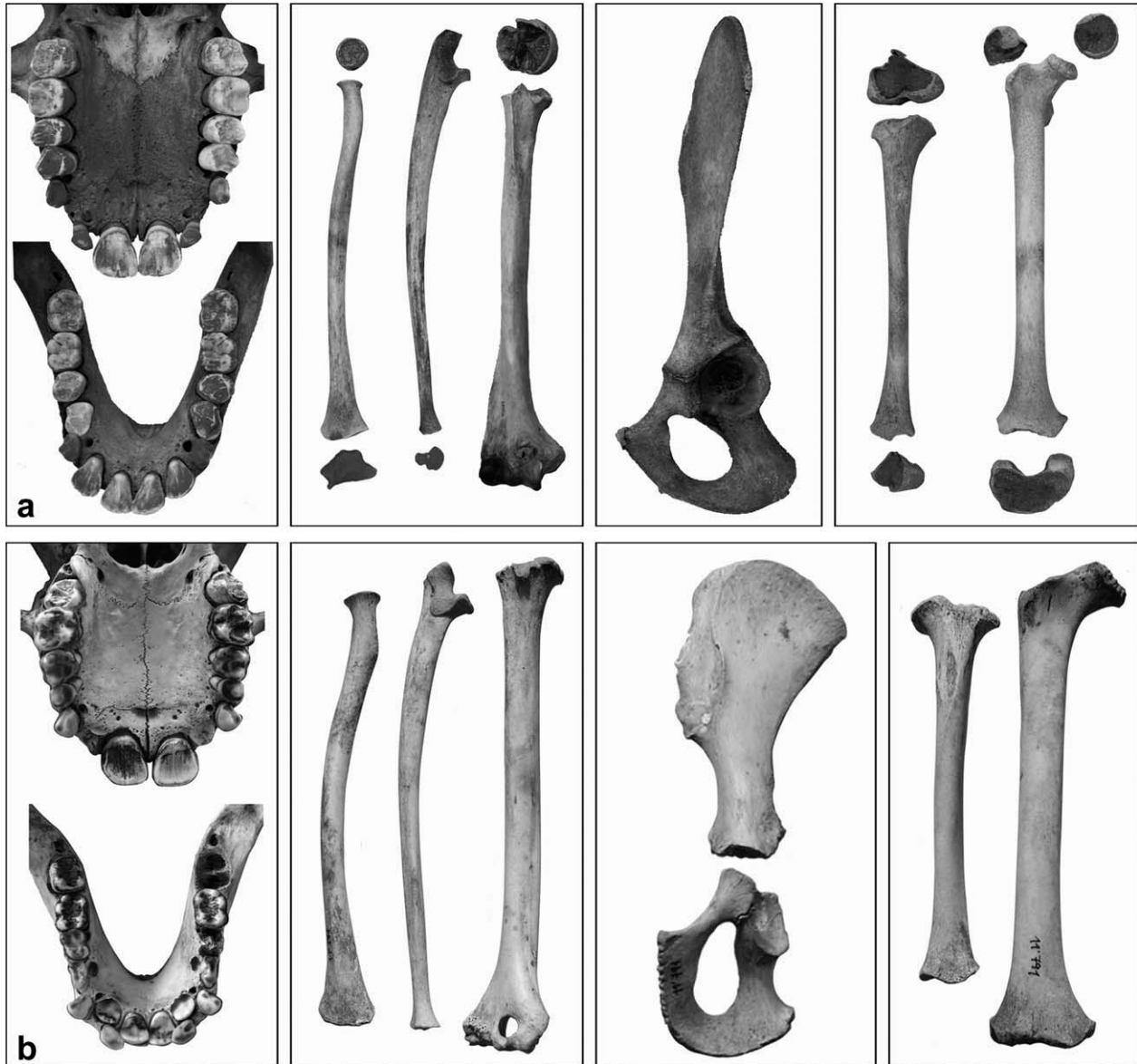
Fig. 1. Juvenile II: dentition, upper limb bones, innominate, and lower limb bones. (**a**) Captive *Pan paniscus*, 6.74 years old "Leslie" and (**b**) Wild *Pan troglodytes* Taï specimen No. 11791.

development and cannot be compared in this category.) For example, the distal humeral epiphysis appears to fuse before canine eruption in female *P. paniscus*, whereas the fusion occurs after canine emergence in wild *P. troglodytes*. These data are merely suggestive because the sample size is small. Both dental and skeletal development can rarely be assessed on the same individual.

Additionally, data from *P. paniscus* subadults (one captive 8.54 years, and one wild specimen of unknown age) indicate that captive *P. paniscus* may fuse portions of their postcranial anatomy earlier than their wild counterparts given similar stages of dental emergence (Table 3).

Timing of fusion by chronological age

Data on timing of fusion in the Yerkes captive *P. troglodytes* are limited. The ages are given in whole years in Kerley's study (1966), and no indication is given as how

the years were calculated (for example, did an 8.5 years old get counted as a 9 years old?). Thus, the timing results are less accurate than the captive *P. paniscus* data to which they are compared. Additionally, there are gaps in the age groups when a considerable amount of skeletal growth is occurring; for example, there are no 8 years old in the Yerkes dataset and many of the fusions occur in the 7–9 years range (Table 4). Furthermore the methods used by Kerley do not elaborate how cases of asymmetry in individuals were recorded—did both sides need to be partially fused to score the individual as such, or was at least one side partially fusing enough? And as noted above, the radiographic method assigns partial fusion earlier than the observations directly on the skeleton and therefore the fusion timings for captive *P. troglodytes* are conservative.

Even given these conservative age assessments for captive *P. troglodytes*, the timings of fusion in captive
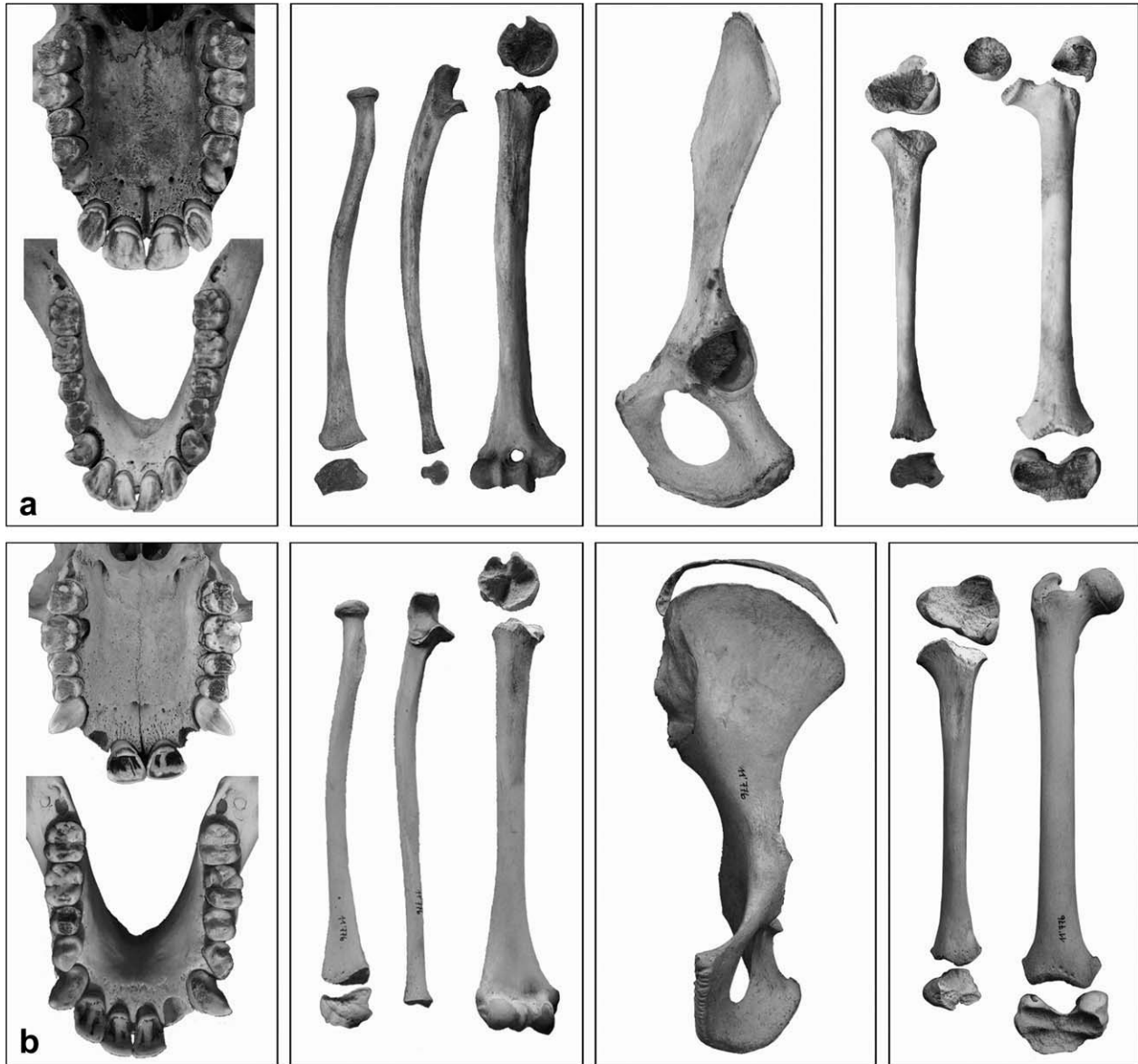
Fig. 2. Juvenile III: dentition, upper limb bones, innominate, and lower limb bones. (**a**) Captive *Pan paniscus*, 7.30 years old "Eliya" and (**b**) Wild *Pan troglodytes* Taï specimen 12-year old "Ariane."

P. paniscus are earlier than *P. troglodytes* for seven out of the 10 comparisons in Table 4 and are never later. More information is clearly needed on individuals of known ages, and through standardized growth assessment methods.

When chronological fusion times of captive *P. paniscus* are compared with those of wild Taï female *P. troglodytes*, captives consistently show an earlier age for maturation of skeletal elements although data are not numerous (Table 4). Photographs of representative individuals are shown in Figures 1–4.

DISCUSSION

Hypothesis 1: Females of the two species share the same sequence of skeletal fusion

This hypothesis is generally supported. The sequence of skeletal fusion in *P. paniscus* and *P. troglodytes*

females is very similar, with two possible exceptions in the hip and lower limb. These subtle variations may be due to locomotor differences (Washburn, 1943; King et al., 2001; Bolter, 2004, 2011). More data are needed to better elucidate the patterns of variation.

Hypothesis 2: Females of the two species share the same ages at fusion calibrated by dental stage

This hypothesis is tentatively supported, albeit slight differences between the two species are expressed in the late juvenile and subadult stages. These two life stages are defined by the eruption of canine and third molars respectively, and in *P. paniscus* these teeth erupt earlier than in their captive *P. troglodytes* counterparts (Bolter and Zihlman, 2011). Therefore, the variations in fusion
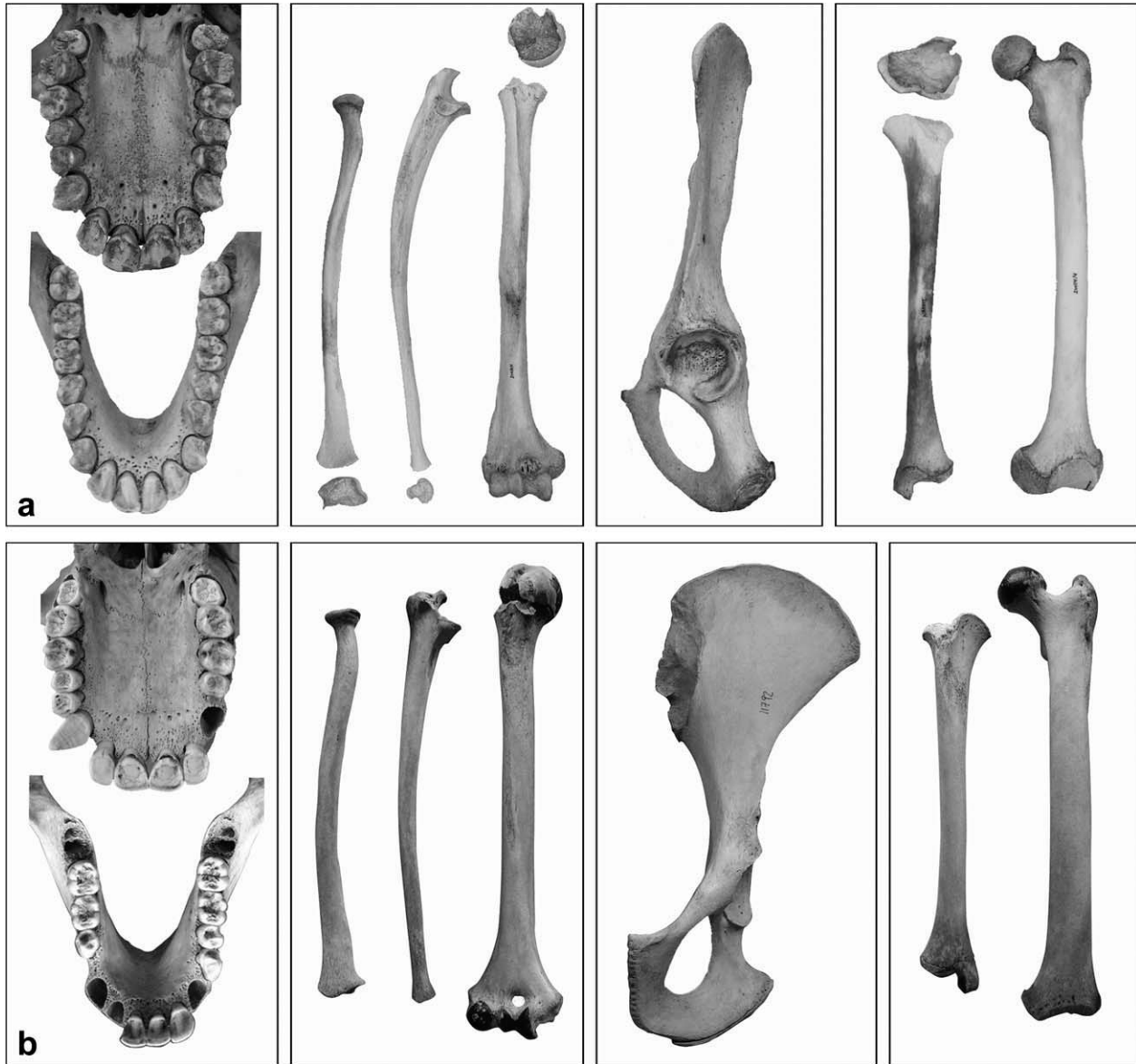
Fig. 3. Subadult: dentition, upper limb bones, innominate, and lower limb bones. (**a**) Captive *Pan paniscus*, 8.54-year old "Naomi" and (**b**) Wild *Pan troglodytes* Taï specimen 12-year old "Zerlina."

times by dental stage may be due to variations in dental eruption patterns and not variations in skeletal growth.

Hypothesis 3: Females of the two species share the timing of fusion by chronological age

This hypothesis is rejected. It appears that (1) species-level differences may exist in skeletal growth in the genus *Pan* and (2) environmental factors may influence the skeletal growth (captive vs. wild).

Data suggest that female captive *P. paniscus* mature skeletal elements faster than their captive *P. troglodytes* counterparts. These data are consistent with the findings of accelerated dental development in captive *P. paniscus* compared with *P. troglodytes* (Bolter and Zihlman, 2011). The consistency of these two growth studies suggests a regulatory relationship between bone and tooth development in *Pan*.

In regards to the captive/wild dichotomy, results are only speculative that differences occur in development between captive and wild *P. paniscus* populations in the later (subadult) life stage. A maturational dichotomy has been documented for *P. troglodytes* in that skeletal growth matures faster in captivity than in the wild (Kimura and Hamada, 1996; Zihlman et al., 2007). Dental development also proceeds earlier in captivity than in the wild (Zihlman et al., 2004; Smith and Boesch, 2010; Smith et al., 2010). Although no chronological data exist on wild skeletal maturation patterns in *P. paniscus*, we expect it will be slower in free-ranging communities.

CONCLUSIONS

P. paniscus and *P. troglodytes* share a general sequence of skeletal fusion. When *P. paniscus* are compared with *P. troglodytes* for fusion timing and sequence by dental emergence, slight variations emerge. When

Fig. 4. Humeral fusion in four wild *Pan troglodytes* Taï specimens, from left to right: "Tina" 10 years, "Kana" 11.38 years, "Ariane" 12 years, "Zerlina" 12 years.

directly comparing known-aged captive *Pan* populations, the timings of selected skeletal events are often earlier in *P. paniscus.* Development of bones and teeth occur more rapidly in captivity than in the wild for *P. troglodytes*, and we hypothesize this may be the trend for captive versus wild *P. paniscus.*

These data establish a range of developmental variation in the genus *Pan*. The timing of skeletal maturation in *P. paniscus* correlates to dental markers by life stage and provides an expanded comparative framework for estimating age and life history in skeletal collections. It increases the possibility of assigning the life stages of unknown *P. paniscus* skeletons recovered at field sites from the wild, thereby increasing the likelihood of identifying individuals. The applicability of these data highlights another facet of the important contribution that captive animals provide to our understanding of primate anatomy, development and variation.

It is imperative to have a clearly defined model of what constitutes an ape-like growth pattern, particularly when an ape-like pace of growth is used to reconstruct early fossil hominin growth, development, and life history features. For example, *Homo erectus* (*ergaster*) has been characterized as having an ape-like growth pattern (Dean and Smith, 2009; Dean and Lucas, 2009). Here, we provide a more robust dataset for comparing of growth rates across *Pan* species to interpret fossil hominins, and create a better foundation to assess commonalities and differences in maturation schedules among the genus *Pan* and humans. With more data on *Pan* maturation patterns and schedules, we are better positioned to interpret the evolution from an ape-like to more human-like growth, development and life history.

ACKNOWLEDGMENTS

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