Morphological Variation in Adult Chimpanzees (*Pan troglodytes verus*) of the Taï National Park, Côte D'Ivoire

Adrienne L. Zihlman,[1]* Daniel Stahl,[2] and Christophe Boesch[3]

[1]*Anthropology Department, University of California, Santa Cruz, Santa Cruz, CA*
[2]*Department of Biostatistics and Computing, Institute of Psychiatry, Kings College, London, UK*
[3]*Max-Planck Institute for Evolutionary Anthropology, Liepzig, Germany*

ABSTRACT   Twenty five adult chimpanzee skeletons (*Pan troglodytes verus*) of known age and sex (15 females, 10 males) from a long-term study site in Taï National Park, Cote d'Ivoire present new data on variation. These skeletons provide a rare opportunity to measure the cranium and postcranium from the same individuals. We compare measurements and indices of the Taï sample with those of relatively complete *Pan troglodytes schweinfurthii* skeletons from Gombe National Park, Tanzania. Measurements of *Pan paniscus* are included as an outside comparison. The Taï and Gombe samples are analyzed by sex; combined sex samples are compared between the two groups, and the two sexes to each other. Taï females and males do not differ in most long bone lengths or in pelvic dimensions, but do differ significantly in cranial capacity, facial measurements, clavicle length, scapular breadth, and femur length. Gombe females and males differ significantly in some facial measurements and in scapular breadth. In combined sex samples, Taï individuals have lower cranial capacity, longer palate and mandible, and greater dimensions in the trunk and limb lengths. Taï females account for most of the variation; males differ from each other only in greater length of humerus and femur. The Taï skeletons provide new data for assessing individual variation and sexual dimorphism within and between populations and species. The combination of cranial and postcranial data provides a clearer picture of chimpanzee intraspecific and interspecific variation than can be gained from either data set alone. Am J Phys Anthropol 135:34–41, 2008.   © 2007 Wiley-Liss, Inc.

Variation in chimpanzee (*Pan*) morphology bears on questions of taxonomy, phylogeny, sexual dimorphism, growth and development, diet and ecology, and locomotion. Schultz (1940, 1956, and 1969), for example, devoted his career to systematically documenting age and sex variation within chimpanzees as part of his broader research interests in ape and human comparisons, in females and males, in the transformation of body proportions during growth, and in the length of life stages. His chimpanzee samples combined captive and wild specimens from several localities "... Liberia, Cameroon, and Guinea;" whenever possible he measured whole skeletons, though he noted that only 143 of his 247 specimens were complete (Schultz, 1969; p 51).

The 25 adult skeletons (*Pan troglodytes verus*) from Taï National Park, Côte d'Ivoire in western Africa are part of a larger sample that includes 22 immature individuals (cf. Zihlman et al., 2007). This local population has been studied for more than 20 years by Boesch and Boesch-Achermann (2000). They have reported new information on stone tool use, hunting techniques, sex differences in behavior, reproductive patterns, and social organization. The sample of individuals of known age and sex with associated cranial and postcranial elements provides new information on morphological variation in sex and subspecies.

Within and between-species variation in *Pan* has tended to focus on one or more aspects of cranial, mandibular, and dental morphology, for example: cranial capacity (e.g. Schultz, 1969; Cramer, 1977); craniometrics (e.g. Shea, 1982; Shea and Coolidge, 1988; Shea et al., 1993; Uchida, 1996; Guy et al., 2003); mandibular morphology (Taylor and Groves, 2003; Taylor, 2006); and dental metrics and morphology (e.g. Johanson, 1974; Kinzey, 1984, Uchida, 1996; Pilbrow, 2006). Skulls are more numerous in museum collections than limb bones and other postcranial elements and are more abundant in the fossil record.

Although chimpanzee postcrania are fewer in number in skeletal collections, they have been the focus of comparative and functional studies (e.g. Schultz, 1969; Zihlman and Cramer, 1978; Coolidge and Shea, 1982; Shea, 1982; Jungers and Susman, 1984; McHenry, 1984; Morbeck and Zihlman, 1989) or of one anatomical region, for example, the pelvis (Schultz, 1949; Morbeck et al., 1992), vertebrae (Schultz, 1961; Galloway et al., 1996); scapula (Inouye and Taylor, 2000), hands and wrist bones (e.g. Tuttle, 1967; Lewis, 1969; Susman, 1979) or ankle and foot bones (e.g. Schultz, 1963; Lewis, 1980; Gebo, 1992). Valuable data on many aspects of chimpanzee morphology and range of variation are derived from these studies.

A cranium associated with the postcranium is not often available for study. Complete skeletons can reveal information that research on only crania, only postcrania, or one body region cannot, for example: sex differences in skull and body dimensions of the same individual; an individual's dimensions relative to its population; and relative body size and sexual dimorphism among populations; and the changes in an individual's cranium, dentition, and limb bones at different ages (Zihlman et al., 2007). Uchida (1996) notes that body size variation and degrees of sexual dimorphism are often estimated from either dentition or isolated postcranial materials; she goes on to caution that "the correlation between dimensions of skull, teeth, and postcranials, and overall body size can vary markedly within a species by character, sex, and population as well as between species" (Uchida, 1996; p 125).

On the basis of geographic distribution, three subspecies have been proposed in chimpanzees: eastern (*Pan troglodytes schweinfurthii*), central (*Pan troglodytes troglodytes*), and western (*Pan troglodytes verus*) groups (Napier and Napier, 1967). Early genetic studies supported such a distinction and later even suggested a fourth subspecies: eastern, central, Nigerian (*P.t. vellorosus*) and western chimpanzees (Morin et al., 1994; Gonder et al., 1997). More recent studies provide another picture. Although they concur by showing the western chimpanzees (*P.t. verus*) distinct from the others, they generally fail to distinguish the eastern from the central chimpanzees (Gagneux et al., 2001; Kaessmann et al., 2001; Bradley and Vigilant 2002; Fischer et al., 2004; Fischer et al., 2006).

The degree to which subspecies can be distinguished morphologically has been the focus of a number of recent studies on cranial, dental, and facial features but notably without postcrania (e.g. Shea et al., 1993; Uchida, 1996; Guy, 2003; Taylor and Groves, 2003; Lockwood et al., 2004; Pilbrow, 2006). There are few studies on postcrania of *P.t. verus*. This study provides data on skeletal variation in cranial and postcranial features of individuals of *P.t. verus* from Taï National Park whose age, sex, and locality are known and compares results with a smaller sample of individuals, also of known age and sex from Gombe National Park, Tanzania, *Pan troglodytes schweinfurthii*. The data based on entire skeletons contribute to discussions of chimpanzee sexual dimorphism, population variation, and subspecies distinctions.

MATERIALS AND METHODS
Sample

The adult sample is represented by remains of 15 females and 10 males and ranges from nearly complete skeletons to a few bones or a single bone, such as a cranium, mandible, or humerus. Adults are defined as having all teeth fully erupted and in occlusion with the epiphysis of the proximal humerus fused (after Bolter and Zihlman, 2003; Zihlman et al., 2007). Long bone lengths, pectoral and pelvic dimensions, and cranial-facial measurements are analyzed for this adult sample. The sample size for cranial capacity means is larger than for other measurements because 10 immature individuals (7 females, 3 males) with second permanent molars (M2) were added to the adult sample; brain size is relatively complete by this dental age (Schultz, 1969; Smith, 1989, 1991; Zihlman et al., 2007).

Whenever possible remains of Taï chimpanzees were retrieved for study and the cause of death determined. During daily follows of targeted individuals from the habituated communities (Boesch and Boesch-Achermann, 2000; Herbinger et al., 2001), a dead chimpanzee body might be encountered. If not too decomposed, the individual was identified and its absence in the study group confirmed. At the same time, the cause of death was determined as precisely as possible (Boesch and Boesch-Achermann, 2000; Leendertz et al., 2006). Some animals died from accidents such as falls or were killed by leopards, but in the majority of instances the cause of death is unknown.

If the death was recent, the carcass was left undisturbed to observe the reaction of the other chimpanzees' responses to death (see Boesch and Boesch-Achermann, 2000). To speed up decomposition of older carcasses and prevent disease transmission, the bodies were buried and retrieved after decomposition was complete. After Ebola outbreaks (Le Guenno et al., 1995; Formenty et al., 1999), the decomposed bodies were removed months later. For those known to have died from Ebola (nine individuals), the bones were boiled in javel water for 1 h. The sample was collected over a 19-year period, and many individuals were members of social groups under study. Skeletal remains from the forest floor were then labeled and stored in the field research station. All skeletal remains were exported to Zurich with corresponding CITES export permits.

Methods: data collection

Measurements were taken on the cranium and face, torso, and limb bones. Cranial capacities were determined by filling the braincase with mustard seed through the foramen magnum. Cotton was placed in the eye orbits, and other foramina were blocked. The skull was tilted to distribute the seed throughout, tapped twice to settle its contents, and then filled to the plane of the foramen magnum rim. The seed was then poured into a graduated cylinder and recorded to the nearest milliliter. The measurement was performed thrice and the average taken (Bolter and Zihlman, 2003).

Cranial-facial measurements were taken with spreading and digital calipers and recorded to the nearest tenth of a millimeter: interorbital breadth, bizygomatic breadth, upper facial height, palatal length, mandibular length, and mandibular height (landmarks defined in Cramer 1977). These measurements were chosen for analysis because they are frequently recorded as indicators of facial and skull construction.

Measurements taken on the upper torso include scapular breadth and clavicle length. Pelvic dimensions include innominate length, iliac breadth, and acetabular (hip joint) diameter. No individual body weights were available.

Linear measurements of the long bones (e.g., maximum lengths of humerus, radius, femur, and tibia) were taken on an osteometric board and recorded in millimeters (Schultz, 1930, 1937). Lengths on limb bones for each individual provide a basis for calculating indices that reflect proportions within and between limb segments of each individual. The intermembral index or ratio is the humerus length + radius length $\times$ 100/femur length + tibia length; the humero-femoral index is humerus length as a percent of femur length; brachial and crural indices are the ratio of lengths within the limbs:

brachial = radius length × 100/humerus length; crural = tibia length × 100/femur length (Schultz, 1969; Aiello and Dean, 1991).

Comparative sample

Chimpanzee skeletons from Gombe National Park, Tanzania (*Pan troglodytes schweinfurthii*) from individuals known during life provide a comparable sample to Taï. Measurements on 14 relatively complete adult skeletons are expanded from earlier studies (Morbeck and Zihlman, 1989; Zihlman et al., 1990; Morbeck, 1999). The Gombe skeletons from the same local population comprise the only other available sample of individuals of known age and sex (Goodall, 1986). Calculation of cranial capacity includes immature individuals with M2s erupted.

The *Pan paniscus* sample provides a species comparison of cranial and postcranial dimensions against the two *Pan troglodytes* populations (Cramer, 1977; Zihlman and Cramer, 1978; Zihlman, 1984; Morbeck and Zihlman, 1989).

Methods: data analysis

Means, standard deviations, and analysis of variance (ANOVA) are calculated for cranial capacities, facial dimensions, limb, and trunk measurements (a) by sex within the Taï group; (b) by sex within Gombe; (c) by combined sex samples; (d) between the sexes of each group. $P < 0.05$ is taken as significant.

RESULTS

Sample sizes, means, and ranges of cranial, facial, mandibular, trunk, and limb measurements for Taï and Gombe females, males, and combined sexes are presented in Table 1a–c.

Cranial capacity

The cranial capacities of Taï females and Taï males (349.8 vs. 379.2 ml, respectively) differ significantly (ANOVA: $F_{1,\,30} = 7.89$, $P = 0.009$). Gombe females and males are very similar to each other in average cranial capacity (379.4 ml, 379.6).

Comparison in cranial capacities between Taï and Gombe populations in combined sex samples shows significant differences (ANOVA: $F_{1,\,46} = 4.29$, $P = 0.044$). Average cranial capacity for Taï females is statistically lower than that for Gombe females (ANOVA: $F_{1,\,26} = 6.47$, $P = 0.017$), whereas the averages of the two male samples are similar.

Cranial-facial measurements

In cranial-facial dimensions, Taï females compared to Taï males show significant differences in bizygomatic breadth (ANOVA: $F_{1,14} = 22.67$, $P = 0.0003$); palatal length (ANOVA: $F_{1,19} = 7.43$, $P = 0.013$); interorbital breadth (ANOVA: $F_{1,19} = 7.26$, $P = 0.014$); mandibular length (ANOVA: $F_{1,16} = 7.19$, $P = 0.016$) and facial height (ANOVA: $F_{1,19} = 5.53$, $P = 0.029$).

Gombe female and male chimpanzees differ in bizygomatic breadth (ANOVA: $F_{1,8} = 16.30$, $P = 0.004$); mandibular length (ANOVA: $F_{1,11} = 11.98$, $P = 0.003$); and facial height (ANOVA: $F_{1,11} = 5.72$, $P = 0.036$), but not in palate length.

The Taï and Gombe samples differ in palatal length (ANOVA: $F_{1,32} = 21.14$, $P = 0.00006$); mandibular length (ANOVA: $F_{1,29} = 20.88$, $P = 0.00005$); and mandibular height (ANOVA: $F_{1,29} = 10.21$, $P = 0.003$). Bizygomatic breadth does not reach significance ($P = 0.052$).

Taï females have significantly longer palates than do Gombe females ($P = 0.0001$) Similarly, Taï males also differ from Gombe males in palatal length, though less than do females ($P = 0.03$).

Table 2 summarizes sex differences in cranial-facial measures in the two populations where adult female mean is represented as % of adult male mean. *Pan paniscus* provides a comparison.

Trunk measurements

In trunk dimensions, Taï female and male chimpanzees show significant differences in clavicle length (ANOVA: $F_{1,10} = 9.32$, $P = 0.012$) and scapular breadth (ANOVA: $F_{1,13} = 8.18$, $P = 0.013$), but pelvic measurements are not significant.

Sex differences in Gombe females and males are significant only in scapular breadth (ANOVA: $F_{1,9} = 11.71$, $P = 0.008$). Clavicle length does not reach significance (ANOVA: $F_{1,11} = 4.40$, $P = 0.06$).

When the Taï and Gombe combined sex samples are compared, there are no significant differences between them in clavicle length or scapular breadth, but they do differ in iliac breadth (ANOVA: $F_{1,24} = 7.91$, $P = 0.001$); innominate length (ANOVA: $F_{1,25} = 6.31$, $P = 0.019$); and acetabular diameter (ANOVA: $F_{1,25} = 16.98$, $P = 0.0004$).

These differences also show up when the females are compared; Taï females have a broader ilium ($P = 0.04$); longer innominate ($P = 0.015$); and larger acetabulum diameter ($P = 0.028$). The males differ only in a larger acetabulum diameter in Taï ($P = 0.033$).

Both of these populations of *Pan troglodytes* have larger trunk dimensions than averages for *Pan paniscus*, although there is overlap (see Table 1b).

Long bones and limb proportions

Taï females and males differ statistically only in femur length (ANOVA: $F_{1,12} = 6.25$, $P = 0.03$). Gombe chimpanzee females and males do not differ significantly in any limb length.

However, with combined sex samples, the two groups differ significantly and Taï limb lengths are longer than those of Gombe: humerus (ANOVA: $F_{1,26}$ 34.67, $P = 0.00003$); radius (ANOVA: $F_{1,24} = 18.94$, $P = 0.0002$); and femur (ANOVA: $F_{1,23} = 35.25$, $P = 0.000005$), but not in the tibia. See Table 1c.

Taï females have a significantly longer humerus ($P = 0.003$), radius ($P = 0.007$), femur ($P = 0.004$) and tibia ($P = 0.015$) compared to Gombe females. Taï males are significantly different from Gombe males in the humerus ($P = 0.006$) and femur ($P = 0.002$) but do not differ in radial or tibial lengths.

Table 3 summarizes sex differences in trunk and limb dimensions in the two populations where adult female mean is represented as % of adult male mean.

Limb indices

Limb indices reflect proportions of long bone lengths within and between segments, rather than absolute lengths. Limb proportions, as measured by intermem-

TABLE 1. *Sample sizes, means, and ranges of cranial, pectoral and pelvic, and limb bone measurements for Taï and Gombe populations*

Measurement		Taï chimpanzees			Gombe chimpanzees			*Pan paniscus*[a]		
		N	Mean	Range	N	Mean	Range	N	Mean	Range
(a) Cranium										
Cranial capacity[b] (ml)	F	21	349.8	300–395	8	379.4	337.2–406.0	56	350.1	
	M	10	379.2	345–415	8	379.6	325.6–420.0			
	Total	31	364.5		16	379.5				
Interorbital breadth (mm)	F	14	18.6	14.3–22.7	8	18.4	10.8–21.9	56	14.5	
	M	7	21.6	18.9–25.5	5	17.3	14.1–21.5			
	Total	21	20.1		13	17.8				
Bizygomatic breadth (mm)	F	9	119.6	110.0–125.6	8	114.7	108.0–121.0	56	110.9	
	M	7	131.5	124.0–137.2	4	127.3	117.0–131.0			
	Total	16	125.6		12	121.0				
Facial height (mm)	F	14	83.1	74.6–94.3	8	78.5	72.5–85.1	56	73.0	
	M	7	89.4	83.8–99.4	5	86.7	77.1–95.5			
	Total	21	86.3		13	82.6				
Palatal length (mm)	F	14	64.8	61.5–71.0	8	71.6	66.9–79.4	56	58.1	
	M	7	68.3	65.0–72.8	5	77.8	68.7–91.8			
	Total	21	66.6		13	74.7				
Mandibular length (mm)	F	11	129.7	119.7–137.9	8	117.2	112.8–123.0	56	102.4	
	M	7	135.7	130.3–140.8	5	128.4	121.5–138.4			
	Total	16	132.7		13	122.8				
Mandibular height (mm)	F	11	63.6	57.3–73.8	8	57.7	53.1–65.8	56	55.4	
	M	7	65.8	58.2–69.9	5	59.6	50.9–68.4			
	Total	16	64.7		13	58.7				
(b) Pectoral and Pelvic bones										
Clavicle length (mm)	F	9	111.5	102.8–117.7	8	107.0	95.5–115.2	20	105.0	84.5–113
	M	3	121.2	116.7–123.6	5	116.6	102.5–127.0			
	Total	12	116.3		13	111.8				
Scapular breadth (mm)	F	10	70.2	61.0–83.5	8	73.0	67.5–77.2	21	72.0	59–84
	M	5	80.2	73.6–86.5	3	83.4	77.4–88.8			
	Total	15	75.2		11	78.2				
Innominate length (mm)	F	7	263.3	255.0–270.5	8	252.8	243.0–259.0	17	256.7	223–274
	M	6	271.9	260.0–280.0	5	263.7	249.0–276.3			
	Total	13	267.6		13	258.2				
Iliac breadth (mm)	F	7	113.3	104.0–126.0	8	104.1	91.0–120.0	21	99.0	79–118
	M	5	121.8	114.0–130.0	6	114.0	105.0–122.0			
	Total	12	117.5		14	109.0				
Acetabulum diameter (mm)	F	8	37.8	34.8–41.8	8	34.1	30.7–37.5	21	36.0	32.8–42.5
	M	6	39.1	37.0–43.0	5	35.9	34.3–37.0			
	Total	14	38.4		13	35.0				
(c) Limb Bone										
Humerus length (mm)	F	9	296.8	282.0–310.0	8	271.7	258.0–295.0	21	284.9	256–308
	M	5	297.9	293.0–306.5	6	277.0	260.0–291.1			
	Total	14	297.4		14	274.4				
Radius length	F	9	268.9	253.0–281.5	8	246.3	237.0–264.5	21	261.7	235–284
	M	4	272.1	259.0–278.5	5	256.8	242.0–278.2			
	Total	13	270.5		13	251.6				
Femur length	F	8	288.9	277.0–297.0	7	266.8	253.0–284.0	15	293.3	275–316
	M	6	297.0	293.5–300.0	4	274.3	261.0–287.0			
	Total	14	292.9		11	270.5				
Tibia length	F	7	239.6	228.0–246.0	7	222.7	211.0–237.2	21	242.2	225–271
	M	6	243.3	235.0–248.0	5	230.8	215.0–245.0			
	Total	13	241.5		12	226.7				

[a] Cranial measurements are from Cramer (1977) and ranges are not available.
[b] Cranial capacity calculations include individuals with second permanent molars (M2). See Text.

bral, humero-femoral, brachial, and crural indices, do not differ significantly between Taï and Gombe, even though the averages of the long bone lengths do differ significantly. In contrast, humero-femoral and intermembral indices in all populations of *Pan troglodytes* differ significantly from *Pan paniscus*, (P < 0.01) but the brachial and crural indices do not (Zihlman and Cramer, 1978; Jungers and Susman, 1984; Morbeck and Zihlman, 1989). See Table 4.

DISCUSSION

Individuals within the Taï and Gombe groups, and the differences between females and males illustrate a mosaic of differences: in the cranium and postcranium of individuals; in the pattern of sex differences within and between Taï and Gombe samples, and between *Pan troglodytes* and *Pan paniscus*. In combined sex samples there are significant differences in cranial capacity and limb lengths, and pelvic dimensions. Most of the differ-

ence between the two groups can be attributed to variation between females: Gombe females are higher in cranial capacity, whereas Taï females have longer limbs and larger pelvises. Table 5 summarizes the five pair-wise comparisons. *Pan paniscus* overlaps the ranges in some dimensions of the two *Pan troglodytes* populations, but is distinct in its absence of sexual dimorphism in cranial capacity, trunk, or limb dimensions and in its intermembral and humero-femoral indices.

Individuals

An individual is transformed into a mosaic when specific bones from the cranium and postcranium of one skeleton are measured (Morbeck cited in Pusey, 2005); that is, a large cranium may not correlate directly with long limb bones, or a small cranium with shorter ones. Even though a Taï female has the lowest female cranial capacity (300 ml), she falls above the female average in length of the humerus (300 mm), radius (277 mm), femur (297 mm), tibia (242 mm), clavicle (112.8 mm), and innominate (270.5 mm), and in scapular breadth (77 mm), iliac breadth (120 mm) and acetabulum diameter (38.1 mm).

TABLE 2. *Sex differences in cranial-facial measurements: adult female mean as % of adult male mean*

Measurement	Taï *Pan troglodytes*	Gombe *Pan troglodytes*	*Pan paniscus*[a]
Cranial capacity	92.2*	99.9	99.2
Interorbital breadth	86.0*	105.8	98.3
Bi-zygomatic breadth	90.9*	90.1*	95.3
Facial height	92.9*	90.5*	100.6
Palatal length	94.8*	92.0	96.3
Mandibular length	95.6*	91.3*	98.6
Mandibular height	96.7	96.7	92.9

* Statistically significant at $P < 0.05$. See Text.
[a] Data from Cramer (1977).

TABLE 3. *Sex differences in limb and trunk measurements: adult female mean as % of adult male mean*

Measurement	Taï *Pan troglodytes* (%)	Gombe *Pan troglodytes* (%)
Humerus length	99.6	98.1
Radius length	98.8	95.9
Femur length	97.3	97.3
Tibia length	98.5	96.5
Clavicle length	92.0*	91.7
Scapular breadth	87.8*	87.5*
Innominate length	96.8	95.9
Iliac breadth	93.0	92.3
Acetabulum diameter	96.7	95.0
Overall Average	95.6	94.5

* Statistically significant at $P < 0.05$.

On the other hand, a Taï male with a similar humeral length as this female (300 mm) has a cranial capacity of 402 ml. The Gombe male with the shortest humerus, radius, femur, tibia, and innominate lengths of the males has a cranial capacity at 408 ml, one of the highest (Zihlman et al., 1990). Two Gombe females have limb bone lengths above the female average, but their cranial capacities differ (406 ml and 350 ml). It is misleading to extrapolate trunk and limb size from only cranial capacity, or to head size from trunk and limb measurements.

Females and males

Morphological differences between female and male *Pan troglodytes* have been documented in numerous studies, for example, in body mass, cranial capacity, long bone dimensions, and dentition (e.g., Schultz, 1969; Cramer, 1977; Jungers and Susman, 1984; Oxnard et al., 1985; Smith and Jungers, 1997; Pusey et al., 2005). However, information for all these morphologies are not available from the same individuals. The Taï and Gombe adult samples demonstrate that sexual dimorphism in the genus *Pan* is not a uniform feature and that to some extent, cranial and postcranial dimensions and body mass vary independently due in part to the order in which body parts reach maturity (e.g., Zihlman, 1997; Bolter and Zihlman, 2003; Zihlman et. al., 2007).

In cranial capacity, face, and mandible size, Taï females and males differ significantly. A study of Liberian chimpanzee skulls (*Pan troglodytes verus*, $n = 99$; 56 females, 43 males) found statistical differences in bizygomatic breadth, face height, and palatal length attributed to the clear sexual dimorphism of the canines (Dierbach, 1986). Overall, Dierbach concluded that sexual dimorphism on the skull based on 24 skull measurements was slight, with males on average 3.7% larger than females. Dierbach did not determine cranial capacity. However, from a small sample of the same collection, Protsch et al., (1987) determined cranial capacities using mustard seed and calculated an average of 351.6 ml ($n = 18$); females, 343.6 ml ($n = 9$) and males, 360 ml ($n = 9$). They concluded that *P. troglodytes verus* has little sexual dimorphism and has the smallest cranial capacities of *P. troglodytes*. Taï cranial capacity based on a larger sample ($n = 31$) shows a higher average (364.5 ml) and significant cranial-facial differences between females and males.

In contrast to Taï, Gombe individuals do not show sex differences in cranial capacity. Gombe females and males do differ significantly in bizygomatic breadth, facial height, and palatal, and mandibular lengths.

One variable contributing to sex differences in facial and mandibular measurements for both populations may be attributed to the males' larger canine roots and teeth

TABLE 4. *Indices of limb bones*

Index	Taï (10) Mean	Taï (10) Range	Gombe (11) Mean	Gombe (11) Range	*Pan paniscus* (17)[a] Mean	*Pan paniscus* (17)[a] Range
Intermembral	106.7	104.8–109.6	105.9	104.0–108.0	102[b]	98–106
Humero-femoral	102.2	100.0–106.1	101.4	99–105	97[b]	94–104
Brachial	90.0	85.6–95.4	91.8	87.0–95.6	92	86–99
Crural	81.9	80.1–85.4	83.8	82.0–85.2	84	78–95

Combined sexes. Sample size in bracket.
[a] Morbeck and Zihlman 1989.
[b] Statistically significant, $P < 01$.

TABLE 5. *Summary of significant differences for the pair-wise comparisons*

Measurements	Taï Female/Male	Gombe Female/Male	Combined sex Taï population/ Gombe population	Female/Female	Male/Male
Cranium					
Cranial capacity (ml)	<0.01	–	<0.05	<0.05	–
Interorbital breadth (mm)	<0.05	–	–	–	–
Bizygomatic breadth (mm)	<0.001	<0.01	–	–	–
Facial height (mm)	<0.05	<0.05	–	–	–
Palatal length (mm)	<0.05	–	<0.001	<0.001	<0.05
Mandibular length (mm)	<0.05	<0.01	<0.001	–	–
Mandibular height (mm)	–	–	<0.01	–	–
Trunk					
Clavicle length (mm)	<0.05	–	–	–	–
Scapular breadth (mm)	<0.05	<0.01	–	–	–
Innominate length (mm)	–	–	<0.05	<0.05	–
Iliac breadth (mm)	–	–	0.001	<0.05	–
Acetabulum diameter (mm)	–	–	<0.001	<0.05	<0.05
Limbs					
Humerus length	–	–	<0.001	<0.01	<0.01
Radius length	–	–	<0.001	<0.01	–
Femur length	<0.05	–	<0.001	<0.01	<0.01
Tibia length	–	–	–	<0.01	–

(Schultz, 1969; p 55; Oxnard et al., 1985; Dierbach, 1986).

Taï females and males differ in the clavicle and scapula, but not in the pelvis. Clavicle length is not dimorphic in Gombe individuals, but scapular breadth is. A study on Gombe chimpanzee vertebrae found that the last cervical and almost all thoracic and lumbar vertebrae are significantly larger in males than females (Galloway et al., 1996). The difference in scapular breadth common to both Taï and Gombe samples indicates that the upper torso of chimpanzee males is broader than that of females, an observation reported by Schultz (1956). Schultz showed that male chimpanzees, as in other male anthropoids, have larger chest circumferences. Results of all three studies indicate a broader upper torso in male chimpanzees.

When combining measurements and considering the whole body, sex differences in limb, and trunk dimensions are relatively low in both populations: Taï, 95.6% and Gombe, 94.5%. Table 3.

Taï and Gombe populations

On the basis of these samples, the two populations vary significantly in two regions. Taï chimpanzees have longer limb bones (humerus, radius, and femur). Gombe individuals, on average, have larger cranial capacities. Taï females account for the difference in cranial capacity between the two populations, whereas means and ranges of the two male groups are nearly identical. Cranial capacity averages for Taï females (349.8 ml) and males (379.2 ml) are similar to averages reported by Schultz (1969) (352 cm^3 and 381 cm^3, n = 116). Gombe females are above Schultz's female average (379.4 ml); males are at the average (379 ml).

Lengths but not indices of the limb bones differ between Taï and Gombe; their intermembral indices are similar to those published by Schultz (1969) based on his combined sex sample of 141 *Pan troglodytes* (intermembral index 106.6). Taï average limb lengths are slightly above the average from Schultz, (humerus, 295.5 mm, Taï, 297.4; femur, 291 mm, Taï, 292.9 mm). Gombe humerus and femur lengths fall within the range reported by Schultz, but the averages of Gombe long bone lengths are over 20 mm lower (e.g., 274.4 vs. 295.5 and 291 vs. 270.4).

Body weights on Gombe individuals from the wild have a median of 31.3 kg for females and 39 kg for males (Pusey et al., 2005), whereas Mahale chimpanzees, a population located only 200 km south along Lake Tanganyika average 35 kg for females and 40 kg for males (Uehara and Nishida, 1987). No body weights for the Taï sample are available; four body weights recorded for *P.t. verus* (41.6 kg for 3 females; 46.3 kg for one male) (Smith and Jungers, 1997) suggest Taï individuals on average are heavier than Gombe.

Species and subspecies

The Taï population represents the western subspecies *P.t. verus,* and Gombe one of the most eastern populations of *P.t. schweinfurthii*. The relationship of these and other populations must include phylogeny, demographic history, and adaptations of *Pan*. Long-term behavioral studies from several field sites across their geographical range document inter-group behavioral differences and help sort out the meaning of variation (e.g., Goodall, 1986; Nishida, 1990;2003; Whiten et al., 1999; Boesch et al., 2002).

Coolidge (1933), before molecular data were available, proposed that *Pan paniscus* was a distinct species based on its cranial and postcranial morphology. Later studies confirmed and elaborated his conclusions: dental size and shape (Johanson, 1974; Kinzey, 1984), cranial-facial dimensions (Cramer, 1977; Shea and Coolidge, 1988); and postcrania (Zihlman and Cramer, 1978; McHenry and Corrucini, 1981; McHenry, 1984). *Pan paniscus* sexual dimorphism in cranial capacity, limb length, and body mass differs from *Pan troglodytes*. Although males are heavier than females, there are no statistical differences in cranial capacity or limb lengths, a contrast with the pattern of sex differences for *Pan troglodytes* (Cramer and Zihlman, 1978; Zihlman and Cramer, 1978).

Early molecular studies showed that *Pan paniscus* was distant from *Pan troglodytes*, but distinctions among

subspecies were not made (Sarich and Cronin, 1976). Genetic variation among chimpanzees consistently shows that *P.t. verus* is distinct, although the central and eastern populations are not so easily distinguished. Furthermore, *P.t. verus* has the least genetic diversity of *Pan troglodytes* based on nucleotides and haplotypes (e.g. Fischer, 2004; Fischer et al., 2006; Gonder, et al., 2006). A number of morphological studies also show that *P.t. verus* can be distinguished from other populations: studies on the cranium (Shea et al., 1993; Uchida, 1996); facial dimensions (Guy et al., 2003); temporal bone (Lockwood et al., 2004); mandible (Taylor, 2006); and dentition (Uchida, 1996). From her study of a sample of 49 *P.t. verus* crania, Uchida (1996; p104) notes that "premolar and molar morphology of *P.t. verus* and *P. paniscus* is plausibly seen as more derived than in the other two subspecies of *P. troglodytes*."

Morphological distinctions in the pattern of sexual dimorphism of the Taï sample is not inconsistent with findings based on other morphological and genetic studies. The morphological findings reported here may be an artifact of sampling, may reflect genetic drift or adaptation to particular ecological conditions, or reflect some combination thereof. Additional studies that evaluate cranial and postcranial material from the same individuals will help resolve questions of population variation. There remains much to learn about chimpanzee morphology which further underscores the need to conserve our closest living relatives.

ACKNOWLEDGMENTS

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