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Body Size and Proportions in Chimpanzees, with Special Reference to *Pan troglodytes schweinfurthii* from Gombe National Park, Tanzania

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ABSTRACT. Body weight, cranial capacity, linear and joint area data from ten free-ranging adult chimpanzees from Gombe National Park, Tanzania with known life histories allow study of variation in a local population and comparison to other populations of *Pan troglodytes* and to *Pan paniscus*. Because individuals in the Gombe population are small compared to other common chimpanzees, they provide a useful comparison to *Pan paniscus*. Body weight and some linear dimensions overlap with *Pan paniscus*. However, cranial capacity, tooth size, and body proportions of Gombe individuals lie within the range of other *Pan troglodytes* and are distinct from *Pan paniscus*.

Key Words: Gombe chimpanzees; Body size and proportions; *Pan troglodytes* subspecies; *Pan paniscus*.

INTRODUCTION

The Gombe chimpanzee population in Tanzania consisting of about 50 individuals has been a focus of behavioral research for more than 25 years (GOODALL, 1986). Information is available on individual kinship, group social relations, diet, range, and habitat, as well as health, life span, and reproduction (GOODALL, 1983). During the course of Gombe research, whenever possible and often through heroic efforts, chimpanzees were located after death and retrieved for skeletal preservation. Complete or partial skeletons of more than 20 individuals, including males and females of different ages, have been made available for study through the cooperation of JANE GOODALL.

This unique, although limited, sample of skeletons from Gombe allows us to ask questions regarding variation within a local population. It then can be compared to other populations of *Pan troglodytes schweinfurthii*, to other common chimpanzee subspecies, and to *Pan paniscus*. In particular, how do body weight, cranial capacity, linear and joint surface area dimensions of the Gombe individuals compare to other chimpanzees? What is the range of variation in linear dimensions among subspecies of *P. troglodytes* and *P. paniscus*? Are body proportions similar in all adult *P. troglodytes* regardless of size, or do proportions differ in larger or smaller individuals? Answers to these questions have direct application to the delineation of species and subspecies in the genus *Pan* and to the discussion surrounding *P. paniscus* as a distinct species from *P. troglodytes*.

MATERIALS AND METHODS

SAMPLE

Gombe *Pan troglodytes schweinfurthii*

The sample used in this paper includes six reproductively mature females aged 19 to 43, four males including a young adult, a middle-aged, and two old males. One old male consists of a cranium only, whereas the postcranial skeleton is available for the other nine individuals (Table 1a). The unaffected side is measured where the effects of trauma or disease occur.

Other *Pan troglodytes*

The Gombe skeletons are compared to 60 adult common chimpanzees, most with known geographical origin and subspecies classification. The free-ranging sample includes 28 females and 22 males. Of these, 22 are *P. troglodytes troglodytes*, 6 are *P. troglodytes verus*, and 14 are *P. troglodytes schweinfurthii* (Table 1b).

Eight *P. troglodytes* skeletons, which are part of the Schultz collection in Zürich, also are included although their geographical proveniences and subspecific classifications are unknown. GROVES (1986) suggests that most of the chimpanzees in this collection are from Liberia. Therefore, we combine data from these individuals with those of *P. t. verus* in separate analyses. No differences occur between these eight individuals and known *P. t. verus*, whereas other comparisons among *P. troglodytes* subspecies do show significant differences in linear dimensions.[1)] This increases the *P. t. verus* sample to 14 individuals. Finally, seven females and three males of unknown heritage constitute the captive *P. troglodytes* sample (Table 1a).

Table 1a. Sample size and composition, *Pan troglodytes* and *Pan paniscus*.

		Males	Females	Total
Pan troglodytes schweinfurthii	Gombe National Park, Tanzania	4[1)]	6	10
Pan troglodytes, mixed subspecies	Various localities	22	28	50
Captive *Pan troglodytes*, mixed subspecies	Various localities	3	7	10
Pan paniscus	Zaïre	12	10	22
Captive *Pan paniscus*	Various localities	2	1	3
Total		43	52	95

1) One individual consists of only the cranium and mandible.

Table 1b. Sample size and composition, *Pan troglodytes* subspecies.

	Males	Females	Total
Pan troglodytes schweinfurthii[1)]	7	7	14
Pan troglodytes troglodytes	10	12	22
Pan troglodytes verus	2	4	6
Pan troglodytes subspecies not verified	3	5	8
Total	22	28	50

1) This is the comparative sample and does not include Gombe individuals.

1) Results using this procedure are tentative since museum records indicate that some of the free-ranging individuals in Schultz's collection with known geographical localities come from areas inhabited by *Pan troglodytes troglodytes*. In addition, SCHULTZ (1937) states that many individuals are from French Cameroons. Later, with an increased sample size, he indicates that the free-ranging sample in the "writer's series" is "composed chiefly of specimens from Liberia, Cameroon, and Guinea..." (SCHULTZ, 1969). This also suggests that both *P. t. verus* and *P. t. troglodytes* are included in the Schultz collection housed in Zürich.

Pan paniscus

Twenty-five adults, including three captive individuals (one female and two males), make up the *P. paniscus* sample. Of the 22 free-ranging individuals 10 are females and 12 are males (Table 1a).

Age and Sex

Adults are defined by eruption of the third molars and fully formed joint epiphyses with at least some epiphyseal fusion. Only individuals with known sex determined in the field or laboratory are used in this study.

Measurements

Quantitative data that describe body size and are used to calculate body proportions include body weight (in kg), cranial capacity (in ml), tooth size (in mm), postcranial long bone linear (in mm) and joint surface area (in mm^2) dimensions (Table 2). The comparative sample for linear dimensions is based on our measurements of free-ranging *P. troglodytes* and *P. paniscus*. Joint surface area comparisons with Gombe chimpanzees are primarily with captive chimpanzees. Cranial capacity and dental measurements are compared to those published for *P. troglodytes* and *P. paniscus*.

Body weights taken during life are available for five Gombe chimpanzees in our skeletal sample. Researchers used a hanging scale with the lure of bananas to weigh chimpanzees during the course of field observations (Pusey, 1978; Wrangham & Smuts, 1980). Several body weights are available on the same individual, taken over a period of months or years (see also Goodall, 1983).

Table 2. List of measurements.*

Body weight	
Cranio-dental features	
	Cranial capacity
	Canine length
	M2 length
Postcranial skeletal linear dimensions	
	Clavicle length
	Scapular morphological length
	Humerus length
	Radius length
	Femur length
	Tibia length
	Innominate length
	Iliac breadth
Postcranial skeletal joint surface areas	
	Scapula, glenoid fossa
	Humerus, humerus head
	Innominate, acetabulum
	Femur, femur head
Body proportions	
	Humero-femoral index
	Intermembral index
	Brachial index
	Crural index

*Standard linear measurements and indices are used in this study. Joint surface area dimensions are measured from latex templates as described in the text.

Each individual in the captive *P. troglodytes* and *P. paniscus* samples was weighed prior to or at the time of death. In addition, body weight obtained from museum records is known for five *P. troglodytes* and ten *P. paniscus* free-ranging individuals.

Cranial capacity is measured in each individual in the Gombe series. Volume is determined by pouring mustard seed into the cranium and then into a graduated cylinder. Most techniques for measuring cranial capacity physically may involve considerable measurement error (CRAMER, 1977). Therefore, an average of three measurements on each cranium is used here.

Linear values are measured using Gneupel sliding or spreading calipers and, for maximum long bone lengths, a bone board. Maxillary and mandibular canine and second molar mesio-distal lengths are measured on Gombe individuals. Lower canines are measured so that mesio-distal lengths are greater than bucco-lingual lengths as defined by JOHANSON (1974), who is concerned with the effects of canine rotation. Extremely worn teeth of old individuals are not included. Standardized long bone, shoulder and pelvic measurements, as listed in Table 2, include linear dimensions of the humerus, radius, femur and tibia, and the clavicle, scapula, and innominate.

Joint surface areas of the glenoid fossa, humerus head, acetabulum and femur head are measured using a Zeiss MOP 3 Image Analyzer from latex templates taken on dry bone (technique modified from GOMBERG, 1981; GOMBERG & MORBECK, 1983; MORBECK & ZIHLMAN, 1988).

Gombe values also are compared to published data on body weights (RAHM, 1967; SCHULTZ, 1968; ZIHLMAN, 1984; UEHARA & NISHIDA, 1987); on cranial capacity (SCHULTZ, 1968; TOBIAS, 1975; CRAMER, 1977); dentition (ALMQUIST, 1974; JOHANSON, 1974; SHEA, 1982); and linear measurements (MORBECK, 1972; ZIHLMAN & CRAMER, 1978; JUNGERS & SUSMAN, 1984).

STATISTICS

Descriptive statistics (means, ranges, and standard deviations) are determined for metric variables, selected within and between limb segment indices. "Size adjusted" variables are calculated for each group, for males and females in each group, and for each recognized subspecies of free-ranging common chimpanzees. (Discussion of results on the mosaic pattern of sex differences will be published separately.) "Size-adjusted" linear variables for humerus, radius, femur, and tibia are calculated in three ways. These include: (1) the ratio of each long bone length to the sum of the lengths of these elements; (2) the ratio of each long bone length to the average of the lengths of these elements; and (3) a "weighted average" in which each long bone length is "weighted with the reciprocal of its within taxon, pooled-sex mean" (WOOD & CHAMBERLAIN, 1986).

Analyses of variance combined with a series of students *t*-tests show levels of statistically significant differences within and between groups. The statistical Package for the Social Sciences is used to analyze data (NIE et al., 1975; NORUŠIS, 1984).

RESULTS AND DISCUSSION

Results indicate that most ranges for body weight and long bone linear measurements overlap. However, the means show that the Gombe individuals weigh less and, in most

postcranial features, are smaller than either pygmy chimpanzees or other common chimpanzees.

Unlike limb bone lengths, the glenoid fossa, humeral head and acetabular surface areas are intermediate between *P. paniscus* and *P. troglodytes*. The femoral head, however, is smaller than in both *Pan* species. Cranial capacity, canine and molar tooth size are similar to other common chimpanzees and larger than in pygmy chimpanzees.

Body Weight

Mean weights of Gombe females (29.8 kg) and Gombe males (39.5 kg) reported by Wrangham and Smuts (1980) are lower than those published for both *P. troglodytes* and *P. paniscus* (e.g., Schultz, 1968; Zihlman & Cramer, 1978; Zihlman, 1984). The Gombe chimpanzee weights are the lowest reported for *P. troglodytes*, including weights published for other *P. t. schweinfurthii* (Rahm, 1967; Uehara & Nishida, 1987). Gombe chimpanzee body weights approach those recorded for *P. paniscus* (Table 3).

Cranial Capacity

The average cranial volume for ten Gombe adults is 388 ml. This value equals the mean of 389 ml for 67 adult common chimpanzees measured by Cramer (1977). The Gombe female average of 389.5 ml is greater than female sample means published by Cramer (1977) of 375 ml; Tobias (1975) of 371 ml; and Schultz (1968) of 355 ml. The mean for four Gombe males (386 ml) is less than that of the females and smaller than other male averages reported in the literature (404 ml, Cramer, 1977; 399 ml, Tobias, 1975; 396 ml, Schultz, 1968) (see Table 4).

The cranial volumes for Gombe individuals are greater than the published capacities for

Table 3. Means, ranges, and sample sizes for chimpanzee body weight (kg).

	Gombe *Pan troglodytes*[1)]	Other *Pan troglodytes*[2)]	*Pan paniscus*[3)]
Females	29.8 (6)	42	33.4 (6)
	26.4–32.3		27.0–38.5
Males	39.5 (9)	48	45.5 (4)
	33.6–47.3		38.0–61.0

1) Means and ranges from Wrangham and Smuts (1980). Also see Goodall (1983); 2) Schultz (1968), sample sizes and ranges not given. Museum records for two females (*P.t. verus*, 21.1 kg; *P.t. schweinfurthii*, 31.3 kg) and three males (*P.t. troglodytes*, 46.0 kg; two *P.t. verus*, 46.3 kg and 48.5 kg) in our free-ranging sample indicate that Schultz's female mean may be too high; 3) data from museum records are from ten free-ranging individuals used in this study.

Table 4. Means, ranges, and sample sizes for chimpanzee cranial capacity (ml).

	Gombe *Pan troglodytes*	Other *Pan troglodytes*[1)]	*Pan paniscus*[1)]
Females	389.5 (6)	374.8 (34)	348.7 (30)
	354.0–406.0	260	160
Males	385.8 (4)	404.2 (33)	351.6 (29)
	323.0–408.0	140	140
Females and males	388.0 (10)	389.3 (67)	350.1 (59)
combined	323.0–408.0	255	180

1) Data are taken from Cramer (1977). Ranges are cited here; minimum and maximum values are not available.

P. paniscus. The average for male and female *P. paniscus* is 350 ml with no sexual dimorphism (females 349, males 352; CRAMER, 1977).

DENTITION

Gombe chimpanzee tooth size, as expressed in maxillary canine and second molar mesio-distal length is similar to other common chimpanzees but larger than pygmy chimpanzees (Table 5). Lower canine size of Gombe chimpanzees also is larger than that reported by JOHANSON (1974) for pygmy chimpanzees. In general, *P. troglodytes* tooth size for both anterior and posterior dentition is significantly larger than *P. paniscus* in much larger samples (e.g., JOHANSON, 1974; ALMQUIST, 1974). The Gombe individuals conform to this pattern of variation.

LIMB BONE LENGTHS

Long bones are shorter in the Gombe skeletons than those in common and pygmy chimpanzees. Mean values for lengths of the humerus, radius, femur, and tibia, as well as lengths of the forelimb and hindlimb, show statistically significant differences when compared to means for other free-ranging *P. troglodytes* (Table 6a).

When size-adjusted values are applied, differences between Gombe and other *P. troglodytes* disappear. Ratios of each element to the sum (method 1), to the average of the four long bones (method 2), or ratios using weighted averages (method 3) show no significant differences. Comparisons between Gombe and captive chimpanzees exhibit significant differences in size-adjusted humerus lengths ($p<.05$). However, the overall pattern of raw data and size-adjusted values suggests that proportions are similar in all *P. troglodytes*.

Variation among subspecies of *P. troglodytes* is reflected in comparisons of Gombe long bone lengths with those of each common chimpanzee subspecies (Table 6b). Compared to other *P. t. schweinfurthii* and *P. t. troglodytes*, Gombe chimpanzee long bones are significantly shorter. In contrast, compared to both samples of *P. t. verus*, the means of the Gombe humerus and tibia lengths are similar, whereas the radius and femur means are significantly different.

Average limb bone lengths in the *P. t. schweinfurthii* comparative sample (that is, localities other than Gombe) are longer than those of *P. t. troglodytes*, which in turn, are longer than those of *P. t. verus* (Table 6b). That *P. t. schweinfurthii* has the longest limb bones and the

Table 5. Means, ranges, and sample sizes for chimpanzee tooth size (mm).

	Gombe *Pan troglodytes*	Other *Pan troglodytes*[1)]	*Pan paniscus*[1)]
Maxillary M2 mesio-distal length			
Females	10.0 (6)	9.7 (30)	8.7 (20)
	9.0–10.5	8.4–10.9	8.0–9.8
Males	10.8 (3)	10.2 (26)	8.5 (17)
	10.0–11.5	9.0–11.9	7.0–10.0
Maxillary canine mesio-distal length			
Females	11.3 (4)	11.3 (30)	8.8 (19)
	10.5–12.0	10.3–12.8	7.8–9.7
Males	13.3 (2)	14.8 (26)	11.2 (17)
	13.0–13.5	12.2–19.2	10.0–13.4

1) Data are from SHEA (1982).

Table 6a. Means, ranges, and sample sizes for chimpanzee limb segment lengths (mm) for combined sex samples.

	Gombe *Pan troglodytes*	Other *Pan troglodytes*	*Pan paniscus*
Forelimb length[1)]	516.2 (9)	564.4 (50)***[2)]	546.6 (22)**
	494.5–559.5	485.0–626.0	485.0–600.0
Humerus length	270.2 (9)	292.7 (50)***	284.0 (22)*
	258.0–295.0	251.0–325.0	250.0–309.0
Radius length	246.1 (9)	271.6 (50)***	262.6 (22) **
	230.0–264.5	234.0–305.0	235.0–291.0
Hindlimb length[1)]	484.9 (7)	534.0 (50)***	540.0 (17)***
	464.0–521.0	464.0–617.0	482.0–582.0
Femur length	264.2 (7)	290.1 (50)***	293.3 (17)***
	253.0–284.0	251.5–337.0	264.0–319.0
Tibia length	221.9 (8)	244.0 (50)***	245.1 (22)***
	211.0–237.0	212.5–280.0	218.0–274.6

1) Forelimb length equals humerus length plus radius length; hindlimb length equals femur plus tibia length; 2) difference in mean values for Gombe *P. t. schweinfurthii* series and comparative sample: $*p<.05$; $**p<.01$; $***p<.001$.

Table 6b. Means, ranges, and sample sizes for *Pan troglodytes* subspecies limb segment lengths (mm) for combined sex samples.

	P. troglodytes schweinfurthii[1)]	*P. troglodytes troglodytes*	*P. troglodytes verus*	
			Known cases	Increased sample
Forelimb length[2)]	578.5 (14)***	568.8 (22)***	557.7 (6)*	543.4 (14)*
	485.0–622.0	526.0–626.0	520.0–625.0	513.0–625.0
Humerus length	301.6 (14)***	294.4 (22)***	288.7 (6)	281.2 (14)
	251.0–322.0	273.0–325.0	260.0–325.0	260.0–325.0
Radius length	276.8 (14)***	274.3 (22)***	269.0 (6)**	262.2 (14)**
	234.0–305.0	243.0–302.0	252.0–300.0	246.5–300.0
Hindlimb length[2)]	555.3 (14)***	533.0 (22)***	523.8 (6)*	514.3 (14)*
	464.0–617.0	488.0–586.0	501.0–584.0	478.5–584.0
Femur length	300.8 (14)***	288.6 (22)***	287.3 (6)**	281.8 (14)**
	251.5–337.0	270.0–315.0	275.0–315.0	265.0–315.0
Tibia length	254.5 (14)***	244.5 (22)***	236.4 (6)	232.5 (14)
	212.5–280.0	233.0–271.0	223.5–269.0	213.0–269.0

1) This is the comparative sample and does not include Gombe individuals; 2) definitions in Table 6a; $*p<.05$; $**p<.01$; $***p<.001$.

broadest ranges is interesting since *P. t. troglodytes*, and not *P. t. schweinfurthii*, often is depicted as the largest (at least in body weight) of the currently recognized *P. troglodytes* subspecies (e.g., JUNGERS & SUSMAN, 1984).

When the Gombe sample is combined with other *P. t. schweinfurthii* (Table 7), the ranges show little change, but the shorter limb bones influence the pattern of subspecies size relationships. *P. t. troglodytes* means for humerus, radius, and tibia lengths are greater than those of the combined *P. t. schweinfurthii* sample. These subspecies show significant differences ($p<.05$) in intermembral index and size-adjusted values for the radius and femur lengths, but not in absolute long bone lengths.

Using both the comparative and combined samples of *P. t. schweinfurthii* long bone lengths, no statistical differences separate *P. t. troglodytes* from *P. t. verus*. However, *P. t. troglodytes* ($p<.001$, forelimb; $p<.05$, hindlimb) and the comparative sample of *P. t. schweinfurthii* ($p<.01$) long bone lengths are significantly different from the eight *P. troglodytes* from unknown localities. The combined Gombe-*P. t. schweinfurthii* sample shows a difference only with humerus length ($p<.05$). Differences between size-adjusted long bone lengths of

Table 7. Means, ranges, and sample sizes for *Pan troglodytes schweinfurthii* limb segment lengths (mm) for combined sex samples.

	Gombe *Pan troglodytes schweinfurthii*	Other *Pan troglodytes schweinfurthii*	Combined *Pan troglodytes schweinfurthii*
Forelimb length[1)]	516.2 (9)	578.5 (14)	554.1 (23)
	494.5–549.5	485.0–622.0	485.0–622.0
Humerus length	270.2 (9)	301.6 (14)	289.3 (23)
	258.0–295.0	251.0–322.0	251.0–322.0
Radius length	246.1 (9)	276.8 (14)	264.8 (23)
	230.0–264.5	234.0–305.0	230.0–305.0
Hindlimb length[1)]	484.9 (7)	555.3 (14)	531.8 (21)
	464.0–521.0	464.0–617.0	464.0–617.0
Femur length	264.2 (7)	300.8 (14)	288.6 (21)
	253.0–284.0	251.5–337.0	251.5–337.0
Tibia length	221.9 (8)	254.5 (14)	242.7 (22)
	211.0–237.0	212.5–280.0	211.0–280.0

1) Definitions in Table 6.

Gombe *P. t. schweinfurthii* and other subspecies are not significant in most comparisons. The exception is in size-adjusted tibia length, forelimb, and hindlimb values ($p<.05$).

Comparisons of both *P. t. schweinfurthii* samples and *P. t. troglodytes* size-adjusted values for the radius, femur, forelimb, and hindlimb show significant differences ($p<.05$). In *P. t. troglodytes–P. t. verus* comparisons for size-adjusted values for femur and tibia lengths, there are significant differences ($p<.05$). Finally, in *P. t. schweinfurthii–P. t. verus* comparisons, size-adjusted values for the tibia ($p<.001$), forelimb and hindlimb ($p<.05$) also are different. These data suggest further work is needed to delineate *P. troglodytes* subspecies variation in body weight and linear dimensions [see also GROVES (1986); JUNGERS & SUSMAN (1984); SHEA & GROVES (1987)].

Comparisons of the Gombe skeletal series with free-ranging *Pan paniscus* also show significant differences in long bone lengths (Table 6a). Size-adjusted values using each of the three methods are significantly different between the Gombe series and *Pan paniscus* (humerus and tibia, $p<.01$; femur, $p<.05$) with the exception of radial length. When the Gombe series is combined with other *P. t. schweinfurthii*, there are statistical differences in the size-adjusted values for the humerus ($p<.001$) and femur ($p<.05$) from *P. paniscus*.

P. paniscus compared to *P. troglodytes* (other than the Gombe sample) show statistical differences in the humerus, radius, and forelimb values ($p<.05$). The common chimpanzees have relatively longer humeri and pygmy chimpanzees have relatively longer femora, but there are no significant differences between these taxa in humeral or femoral lengths in the combined sex sample (ZIHLMAN & CRAMER, 1978). Our current data, which use larger samples for both *Pan* species, reveal significant differences in means for absolute values of humeral length ($p<0.05$) but not for femoral length.

Compared to *P. t. schweinfurthii* and *P. t. troglodytes* but not to *P. t. verus*, *P. paniscus* shows significant differences in lengths of humerus, radius, and the corresponding forelimb ($p<.05$). All comparisons between *P. paniscus* and *P. t. troglodytes* in size-adjusted values display significant differences [humerus, $p<.001$; radius and tibia, $p<.05$; femur, $p<.01$ (methods 1, 2), $p<.05$ (method 3)]. Those values for the humerus, forelimb, and hindlimb between *P. paniscus* and *P. t. schweinfurthii* also are significantly different (humerus, $p<.001$; forelimb and hindlimb, $p<.05$). In contrast, when comparing *P. paniscus* and *P. t. verus* the tibia, forelimb, and hindlimb are significantly different in size-adjusted values ($p<.001$). The

small-bodied representatives of Gombe *P. t. schweinfurthii* parallel the differences between all groups of *P. troglodytes* and *P. paniscus.*

Limb Proportions

Humero-femoral and intermembral indices in Gombe chimpanzees are similar to other *P. troglodytes.* In contrast, brachial and crural indices are similar in all chimpanzees, including both *P. troglodytes* and *P. paniscus* (Table 8).

Common chimpanzees have higher humero-femoral and intermembral indices compared to pygmy chimpanzees. The humero-femoral index in this Gombe series is 102; it is 101 in other *P. troglodytes*, but only 97 in *P. paniscus.* The intermembral index is the same in Gombe and other common chimpanzees (106) whereas that of *P. paniscus* is 102 (see also Morbeck, 1972; Table 8). The absolutely longer femur of pygmy chimpanzees (Table 6a) influences these indices, as noted previously by Zihlman and Cramer (1978).

Shoulder and Pelvic Complexes

Linear Dimensions

Average values for Gombe chimpanzee clavicular length and iliac breadth are intermediate between those of larger *P. troglodytes* and smaller *P. paniscus* (Table 9).

Clavicular length of Gombe chimpanzees is significantly different from other *P. troglodytes.* In contrast, there is no statistically significant difference in the clavicle between the Gombe individuals and *P. paniscus.* Mean clavicular length is shorter in *P. paniscus* compared to other *P. troglodytes* (105 versus 125) with some overlap in ranges (Table 9) [see also Zihlman & Cramer (1978); Jungers & Susman (1984); McHenry (1984)]. Comparative data availa-

Table 8. Means, ranges, and sample sizes for chimpanzee limb proportions for combined sex samples.

	Gombe *Pan troglodytes*	Other *Pan troglodytes*	*Pan paniscus*
Humero-femoral index	102 (7)	101 (50)	97 (17)***[1)]
	99–105	94–106	94–104
Intermembral index	106 (7)	106 (50)	102 (17)***
	104–108	98–112	98–106
Brachial index	91 (9)	93 (50)	92 (22)
	87–94	84–101	86–99
Crural index	83 (7)	84 (50)	84 (17)
	82–85	80–89	78–95

1) Difference in mean values for Gombe *P. t. schweinfurthii* series and comparative sample. ***$p<.001$.

Table 9. Means, ranges, and sample sizes for chimpanzee shoulder and pelvic lengths (mm) for combined sex samples.

	Gombe *Pan troglodytes*	Other *Pan troglodytes*	*Pan paniscus*
Clavicle length	109.4 (9)	124.7 (34)***[1)]	104.9 (20)
	95.5–127.0	106.0–147.0	84.5–113.0
Innominate length	254.9 (8)	272.6 (17)**	256.7 (17)
	244.0–269.0	245.0–308.0	223.0–274.0
Iliac breadth	104.0 (8)	118.7 (18)***	99.2 (21)*
	99.0–107.3	100.5–147.5	79.0–118.0

1) Difference in mean values for Gombe *P. t. schweinfurthii* series and comparative sample. *$p<.05$; **$p<.01$; ***$p<.001$.

Table 10. Means, ranges, and sample sizes for chimpanzee shoulder and hip joint surface areas (mm^2) for combined sex samples.

	Gombe *Pan troglodytes*	Other *Pan troglodytes*[1]	*Pan paniscus*[2]
Glenoid fossa	439.5 (9)	484.5 (10)	417.5 (5)
	314.9–552.2	391.3–650.6	342.9–491.0
Humerus head	1790.8 (9)	1999.0 (10)	1736.0 (5)
	1429.4–2210.9	1703.4–2528.7	1578.7–2002.0
Acetabulum	1041.1 (9)	1091.5 (9)	960.0 (5)
	843.0–1201.4	787.0–1315.0	643.9–1185.1
Femur head	1841.3 (7)	2195.9 (10)*[3]	2050.3 (5)
	1465.9–2100.0	1771.5–2670.7	1687.8–2268.7

1) Data are from captive common chimpanzees; 2) *P. paniscus* surface areas are measured in three captive and two free-ranging individuals; 3) difference in mean values for Gombe *P. t. schweinfurthii* series and comparative sample. $*p<.05$.

ble for our *P. troglodytes* captive sample also are significantly different in scapular morphological length from Gombe. However, no significant difference occurs when compared to our limited *P. paniscus* sample.

Iliac breadth is intermediate between the two *Pan* species. Statistical differences appear when Gombe is compared to *P. troglodytes*. Innominate length, as with other link values, approximates that of pygmy chimpanzees and is considerably shorter than in other *P. troglodytes* (Table 9).

Joint Surface Areas

Joint surface areas of Gombe chimpanzees are compared to those of captive and free-ranging *P. troglodytes* and *P. paniscus*. Average long bone lengths are similar in captive and free-ranging *P. troglodytes* with no statistically significant differences between these combined sex samples. Therefore, captive *P. troglodytes* justifiably are used for analyses of joint surface areas.

Mean values for shoulder and hip joint surface areas (i.e., glenoid fossa, humeral head, and acetabulum) are intermediate in size between common and pygmy chimpanzees (Table 10). However, in Gombe individuals, the femoral head surface area is absolutely smaller than in both species of *Pan*. Linear dimensions are significantly different between Gombe and common chimps, but joint surfaces generally are not.

Ratios of joint surface areas within joints (glenoid fossa to humeral head area) and between joints (glenoid fossa to acetabulum and humeral head to femoral head) show no significant differences between Gombe chimpanzees and *P. troglodytes* or *P. paniscus*. Only in the acetabular-femoral head area ratios do significant differences occur between the Gombe sample and *P. paniscus* ($p<.05$).

SUMMARY AND CONCLUSIONS

In summary, compared with other *P. troglodytes*, Gombe chimpanzees are lower in body weight, but similar in cranial capacity and tooth size. In linear dimensions, the forelimb and hindlimb segment lengths are shorter in Gombe, but *limb proportions* are the same.

Compared to *P. paniscus*, Gombe chimpanzees have lower body weight, higher cranial capacity, larger tooth size, broader trunk, shorter forelimb and hindlimb lengths, and

different limb proportions. Joint surface areas, except for the femoral head in Gombe chimpanzees, are intermediate between *P. troglodytes* and *P. paniscus.*

The methodology here uses volume, linear and surface area dimensions. This combination demonstrates that body size is more than a matter of weight or linear dimensions (GRAND, 1977). Here, we use joints with limb bone lengths and thereby increase information from the skeleton.

Gombe chimpanzees are not smaller than other chimpanzees in all dimensions. Taking all linear measurements, the upper and lower limbs of the Gombe skeletons are shorter than those in *P. troglodytes* and *P. paniscus.* However, linear dimensions of the shoulder and pelvis, i.e., clavicular length and iliac breadth, are intermediate between the two *Pan* species. The exception is innominate length which, like the long bone lengths, is shorter in Gombe individuals compared to both *P. troglodytes* and *P. paniscus.*

Using joint surface information, a somewhat different but complementary pattern appears. Three of the four measurements for Gombe chimpanzees are intermediate between the two *Pan* species: glenoid fossa, humeral head, and acetabulum. The femoral head, however, follows the pattern of long bone and innominate lengths and is smaller in Gombe than in the other *Pan* groups.

During the process of growth of Gombe chimpanzees which produces overall small adults, the long bones apparently exhibit greater plasticity. By contrast, joint surface area sizes and trunk breadth, reflected in clavicular length and iliac breadth, perhaps come closer to achieving species potential size.

Cranial capacity and tooth size in Gombe chimpanzees are equivalent to other *P. troglodytes.* These features apparently do not scale to the general indicators of body size as measured by weight and bone lengths. Furthermore, brain and tooth size develop early and achieve adult dimensions well before the musculo-skeletal system and body weight. These data suggest that the growth curves for the cranium, dentition, and trunk are equivalent for all *P. troglodytes* but there is more potential variation in duration and/or rate of growth in bone lengths.

Because body size and proportions are a result of different growth trajectories, the spectrum of variation must be multi-dimensional. Subspecific variation and especially variation in local breeding populations of *P. troglodytes* can pose a problem when chimpanzees are compared to other hominoids. Although different skeletal populations are studied [e.g., Powell Cotton collection, *P. t. troglodytes* (SHEA, 1982); Tervuren, *P. t. schweinfurthii* (CRAMER, 1977), or, more often, mixed subspecies], in many studies all *P. troglodytes* are treated as one group. Our findings indicate that even with small subspecies samples we see variation among *P. troglodytes* in some linear dimensions and proportions (also see JUNGERS & SUSMAN, 1984). Therefore, subspecies should be taken into account in comparisons.

Our results have direct bearing on the debate about the taxonomic status of *P. paniscus* as a separate species. On the basis of body proportions, several researchers have argued for distinct species status of *P. paniscus* (COOLIDGE, 1933; HILL, 1969); others have disagreed (HORN, 1979; GROVES, 1982). For example, because there is so much overlap in linear measurements and body weight in the two species, GROVES (1981, 1986) maintains that the taxonomic status of *P. paniscus* will not be solved "as long as the question of the differences between the other vicariant forms of chimpanzee is ignored" (1986). Our work addresses GROVES's concerns by presenting a test case from the Gombe population which represents a small

P. troglodytes. It shows that the two species of *Pan* have distinct morphological patterns.

We can quantify body size and the mosaic nature of morphological variation in the Gombe skeletal population, but we cannot resolve why Gombe individuals are small-bodied. Environmental and genetic factors have affected the phenotype of an adult chimpanzee, as reflected in body weight and skeletal dimensions.

An ecological explanation which emphasizes Gombe as a drier and more seasonal environment than for most other chimpanzee populations implies limited resources. With increasing geographical isolation of this population as a result of natural barriers and human activity, a higher population density and a shifting demographic pattern, increased individual, and group competition may exist for resources. The duration and timing of phases of growth and development take place as individuals interact within a social group and in the context of the physical environment. Body size adjustments to the ecological setting may occur.

A genetic explanation emphasizes that Gombe chimpanzees are part of the most eastern distribution of the genus *Pan*. Not only are they on the eastern edge, but their range is limited to the West by Lake Tanganyika and to the East by mountains so their travel is limited. Such a geographically marginal population implies decreased genetic variability. It is possible that genetic drift may contribute to small body size in this local population. This fits with our data that show *P. t. schweinfurthii* as the most variable of the *P. troglodytes* subspecies. There may be more to being small-bodied than living in a "deficient" environment.

This issue of body size and proportions is more complex than can be expressed in length of bones or joint surface areas. The Gombe skeletal series analyzed in this paper represents a local breeding population that can be placed within the wider spectrum of variation within the subspecies *P. troglodytes schweinfurthii*, within the species *P. troglodytes*, and within the genus *Pan*. Individual and therefore ranges of population variation are products of growth and development of individuals in a particular population in a dynamic social and physical environment. Any approach to explaining variation in body size therefore must be multifaceted. But, as shown here using Gombe chimpanzees as an example, the bottom line is: A small *P. troglodytes* is still a *P. troglodytes*.

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