Folia primatol. *29:* 86–94 (1978)

Skeletal Differences between Pygmy *(Pan paniscus)* and Common Chimpanzees *(Pan troglodytes)*[1]

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Key Words. Pan paniscus · *Pan troglodytes* · Chimpanzees · Hominoid evolution · Skeletal analysis

Abstract. Skeletal dimensions of pygmy *(Pan paniscus)* and common *(Pan troglodytes)* chimpanzees were compared. Significant differences were found in the clavicles, scapulae, pelvises, and in the humerus/femur and femur head/length ratios. No significant differences were observed in long bone lengths or talar breadths. There is extensive overlap in body weights, so that the observed differences cannot be accounted for by body size alone. We conclude that pygmy and common chimpanzees are morphologically distinct. Implications for hominoid evolution are discussed.

Introduction

Pygmy chimpanzees *(Pan paniscus)*, the least known of the hominoids with the smallest geographical distribution, may be the most similar of living primates to the common ancestor of man and African apes. They were described and given species status about 50 years ago [SCHWARZ, 1929; COOLIDGE, 1933]. Descriptions emphasize their small size, pedomorphic body build, narrow shoulders, unusual hair patterns, rounded cranium and minimally prognathic face. Their vocalizations, gestures and copulation postures, and temperament have been noted as different from other chimpanzees [COOLIDGE, 1933; HILL, 1969].

A series of recent studies contribute to the general knowledge of this rare species and to clarification of its relationship with common chimpanzees

[1] A preliminary version was presented at the annual meetings, American Association of Physical Anthropologists, St. Louis, Mo. April 1976.

(Pan troglodytes), gorillas *(Pan gorilla)* and man. Biochemically, all chimpanzees show closer affinities to one another than to either humans or gorillas, even though *P. paniscus* and *P. troglodytes* are separable immunologically, electrophoretically [GOODMAN *et al.*, 1970; CRONIN, 1975, 1977] and karyotypically [KHUDR *et al.*, 1973]. *P. paniscus* has significantly smaller deciduous and permanent teeth than *P. troglodytes* [JOHANSON, 1974]. Cranial capacity on the average is smaller for *P. paniscus* though overlapping much with *P. troglodytes* [FENART and DEBLOCK, 1973; CRAMER, 1977], and perfect discrimination between the two species is possible on mandibular length alone [CRAMER, 1977]. Sexual dimorphism exists only in canine teeth and body weight, not in overall dentition, cranial capacity and facial features, long bone lengths or robusticity [CRAMER and ZIHLMAN, 1976]. Field studies so far have revealed little about their ecology and behavior [NISHIDA, 1972; MACKINNON, 1976; BADRIAN and BADRIAN, 1977; KANO, in press]. Their distribution is apparently limited to the enclave formed by the Zaire (Congo) and Lualaba rivers [NAPIER and NAPIER, 1967; VANDEBROEK, 1969] compared to the extensive distribution of common chimpanzees from West Africa into East Africa along the eastern shores of Lake Tanganyika [see maps in HILL, 1969; CRAMER, 1977]. Since the arrival of several pygmy chimpanzees at Yerkes Primate Research Center, intensive studies are underway on communication, sexual and social behavior [SAVAGE *et al.*, 1976, in press].

Morphological studies have been carried out on cranial, facial and dental characters, and the little done on the entire skeleton has been on a few available specimens, not always adult or of both sexes [COOLIDGE, 1933; SCHULTZ, 1940, 1969; MILLER, 1952]. This is due in part to the bias of collections in favor of skins and skulls, skeletons being less numerous, and to less interest in the postcrania for taxonomic purposes. This study, carried out on 21 adult pygmy chimpanzee skeletons, presents morphological information and focuses on the extent to which species differences already demonstrated for the dentition, craniofacial features, blood proteins and chromosomes are mirrored in the skeleton. Are pygmy chimpanzees simply a scaled down version of common chimpanzees [e.g. GOULD, 1975]? Similarities to and differences from common chimpanzees are examined, and the implications for hominoid evolution are discussed.

Materials and Methods

The sample of *P. paniscus* consists of 21 adult skeletons, 10 females and 11 males, 18 skeletons are housed at the Musée Royale de l'Afrique Centrale, Tervuren, Belgium.

and 3 are from the Museum of Comparative Zoology, Harvard University. The *P. troglodytes* sample (18 female, 12 male) includes 14 skeletons from the Anthropologische Institut, Zürich, 8 from Tervuren, 3 from the MCZ, Harvard, and 5 from the Smithsonian Institution, and represents several different populations.

Standard bone lengths [after SCHULTZ, 1937], breadths and diameters were taken on the major bones of the postcranium – 18 measurements in all: lengths on the humerus, radius, ulna, femur, tibia, fibula and clavicle; scapular length and breadth; innominate length, iliac and sacral breadths, and maximum breadth of the superior articular surface of the talus. Joint sizes were measured by diameters of the acetabulum, femoral and humeral heads, and bicondylar width of the femur and biepicondylar width of the humerus. Indices of humerus to femur length and femoral head diameter to femur length were also calculated.

The measurements were analyzed in two ways. First, data on males and females of each species were combined and the species differences determined by Student's t-test. On p, 0.01 (or 0.02 where indicated) was taken as significant. Second, the male-female data for *P. paniscus* (which do not show sexual dimorphism) were compared to the female *P. troglodytes* data (which are sexually dimorphic). The results are summarized in tables I and II.

Results

Comparison between the Two Species (table I)

In pygmy chimpanzees the clavicle is unusually short, with only 2 mm of overlap in 5 of a sample of 51 individuals. Overall, the scapula is smaller, longer and narrower than in common chimpanzees, noted by COOLIDGE [1933] and confirmed in this study. Differences in humerus and radius lengths are not significant, but ulna lengths are significantly different to less than the 0.02 level. Although humerus *lengths* are similar, the head diameters and biepicondylar widths are significantly *smaller* in *P. paniscus*.

The pelvis and lower limb are significantly different in innominate length, iliac and sacral breadth, which indicates overall a smaller, lighter pelvis for *P. paniscus*, also noted by COOLIDGE. Both acetabulum and femur head diameters are also significantly different between the two species. Femur, tibia and fibula lengths are not significantly different, and there is no difference at all in the means of the breadth of the superior articular surface of the talus.

Although the average lengths of the humerus and femur do not differ significantly, they vary in opposite directions, that is, pygmy chimpanzees have a shorter humerus and longer femur than common chimpanzees. The ratio between the humerus and femur lengths is significantly lower in pygmy than in common chimpanzees. The ratio of femoral head diameter to femur length is significantly different and illustrates that in *P. paniscus* the femur is longer relative to head diameter.

Table I. Comparison of skeletal measurements of *Pan paniscus* and *Pan troglodytes*, in mm

Measurement	*Pan paniscus*			*Pan troglodytes*			Significance of difference
	n	$\bar{X}$	σ	n	$\bar{X}$	σ	
Clavicle length	21	105.0	4.3	30	126.0	9.5	0.01
Scapula length	21	138.0	11.0	16	149.0	13.0	0.01
breadth	21	72.0	5.4	16	81.0	7.0	0.01
Humerus length	21	285.0[1]	12.0	30	292.0[1]	19.0	n.s.
head diameter	19	35.0	1.9	30	38.0	3.2	0.01
biepicondylar breadth	21	56.0	3.0	30	61.0	4.6	0.01
Radius length	21	262.0	14.0	30	270.0	17.0	n.s.
Ulna length	21	274.0	13.0	30	285.0	18.0	0.015
Innominate length	19	253.0	15.0	16	271.0	18.0	0.01
Iliac breadth	20	97.0	8.7	30	117.0	13.0	0.01
Sacrum breadth	17	63.0	4.8	29	68.0	5.4	0.01
Acetabulum diameter	20	36.0	2.0	30	38.0	2.4	0.01
Femur head diameter	16	30.5	1.6	30	32.0	2.3	0.01
bicondylar breadth	15	58.0	4.3	30	58.0	5.4	n.s.
length	15	293.0[2]	10.0	30	288.0[2]	16.0	n.s.
Tibia length	21	242.0	10.0	29	241.0	17.0	n.s.
Fibula length	20	218.0	7.8	30	224.0	15.0	n.s.
Talus breadth, superior surface	17	19.6	1.3	26	19.6	2.0	n.s.
Ratio humerus/femur length	15	98.0	2.0	30	101.0	3.0	0.01
head diameter/ femur length	15	10.4	0.4	30	11.2	0.6	0.01

[1] SCHULTZ [1969]: 285 mm for *P. p.*; 295 mm for *P. t.*
[2] SCHULTZ [1969]: 291.5 mm for *P. p.*; 291 mm for *P. t.*

Comparison between Female P. troglodytes *and Both Sexes of* P. paniscus (table II)

Because male *P. troglodytes* are more robust than females, a comparison was made between female *P. troglodytes* and the *P. paniscus* group. No significant differences are found in scapular dimensions, humerus lengths, biepicondylar breadths, radius and ulna lengths; there are no significant differences in innominate length, acetabulum or femoral head diameter, fibula lengths and talus. However, the *significant* differences between the two species (table I) which hold also for the female *P. troglodytes* comparison are those in clavicle lengths, humeral head diameters, iliac breadths, sacral breadths (to 0.02), femur proportions and upper to lower limb proportions.

Additionally, femur and tibia lengths are significantly different from female *P. troglodytes*, but *not* from the pooled population of males and females. Interestingly, the tibia and femur lengths are significantly *longer* in pygmy chimpanzees. Thus, some of the similarities between female *P. troglodytes* and *paniscus* presumably reflect similarity in body size, whereas the differences reflect difference in body build and proportions between the two species.

Other Morphological Features

There is a misconception about body size of pygmy chimpanzees as compared to common chimpanzees [e.g. HILL, 1969, who states body weight is less than half of *P. troglodytes*]. Pygmy chimpanzees are not so 'pygmy'; body weights from 18 adults, including 13 wild-shot animals from the Tervuren sample and 5 captive animals, have an average of 35.5 kg, range 25–48 kg. Females averaged 31.5 kg and males 39.2 kg. The range in body weight of common chimpanzees is considerable. Reports by RAHM [1967] and NAPIER and NAPIER [1967] give weights of around 25 to over 50 kg, with an average of about 42 kg. Body weight of 15 adult Gombe Stream chimpanzees *(P. troglodytes)* averages 35 kg, male average, 39.5 kg, female, 30 kg [WRANGHAM, personal commun.]. Some adult male common chimpanzees weigh more than 60 kg in captivity [MCGINNIS, personal commun.]. There is much overlap between the two species, although common chimpanzees may achieve greater weights than pygmies.

Pygmy chimpanzees have significantly smaller dentition than common chimpanzees with no sexual dimorphism in anterior and postcanine teeth and with less sexual dimorphism in the canines [FENART and DEBLOCK, 1973; ALMQUIST, 1974; JOHANSON, 1974]. Cranial capacity in *P. paniscus* averages 350 cm^3 with no sexual dimorphism, and in *P. troglodytes*, 390 cm^3 (males 404 cm^3, females 375 cm^3) [CRAMER, 1977]. There is a great deal of overlap in cranial capacity of the two species, but the differences in the means are statistically significant.

Discussion

Pygmy chimpanzees are not merely a smaller version of common chimpanzees. Significant differences, even between female *P. troglodytes* and *P. paniscus*, in clavicle length, humerus head diameter, iliac and sacral breadths, indicate that pygmy chimpanzees are relatively lighter in their trunk and upper limbs. The tibia and femur in *P. paniscus* are relatively and

Table II. Comparison of skeletal measurements of *Pan paniscus* (both sexes) and *Pan troglodytes* (females only), in mm

Measurement	*Pan paniscus*			*Pan troglodytes*			Significance of difference
	n	$\bar{X}$	σ	n	$\bar{X}$	σ	
Clavicle length	21	105.0	4.3	18	122.0	8.0	0.01
Scapula length	21	138.0	11.0	8	140.0	8.8	n.s.
breadth	21	72.0	5.4	8	76.0	4.8	n.s.
Humerus length	21	285.0	12.0	18	286.0[1]	18.0	n.s.
head diameter	19	35.0	1.9	18	37.0	2.6	0.01
biepicondylar breadth	21	56.0	3.0	18	57.8	2.8	n.s.
Radius length	21	262.0	14.0	18	264.0	14.0	n.s.
Ulna length	21	274.0	13.0	18	278.0	16.0	n.s.
Innominate length	19	253.0	15.0	8	259.0	13.0	n.s.
Iliac breadth	20	97.0	8.7	18	116.0	12.0	0.01
Sacrum breadth	17	63.0	4.8	18	67.5	6.0	0.02
Acetabulum diameter	20	36.0	2.0	18	36.7	1.7	n.s.
Femur head diameter	16	30.5	1.6	18	30.9	1.6	n.s.
bicondylar breadth	15	58.0	4.3	18	56.0	4.4	n.s.
length	15	293.0	10.0	18	281.0[2]	13.0	0.01[3]
Tibia length	21	242.0	10.0	17	233.0	11.5	0.01[3]
Fibula length	20	218.0	7.8	18	218.0	12.0	n.s.
Talus breadth, superior surface	17	19.6	1.3	15	19.0	1.4	n.s.
Ratio humerus/femur length	15	98.0	2.0	18	102.0	4.0	0.01
head diameter/ femur length	15	10.4	0.4	18	11.0	0.5	0.01

[1] SCHULTZ [1969]: 289 mm, female *P. t.*
[2] SCHULTZ [1969]: 285 mm, female *P. t.*
[3] Note that *P. paniscus* is significantly *longer* than *P. troglodytes.*

significantly longer than those of female *P. troglodytes.* The measurements confirm the visual impression that pygmy chimpanzees are less robust animals than common chimpanzees, and with different proportions.

These conclusions support other data, particularly those of blood proteins and chromosomes, that *P. paniscus* is genetically distinct from *P. troglodytes.* There is still much to be done, however, on understanding the relationship between pygmy chimpanzees and populations of common chimpanzees. Immunologically and electrophoretically [CRONIN, 1977] the albumins and transferrins of *P. paniscus* show greater intraspecific diversity than do the

morphological data. It is possible that different populations of eastern and western common chimpanzees will show more or less morphological similarity to pygmy chimpanzees. As the Gombe chimpanzees show, body weights may be the same; we can only guess about the other comparisons.

Pygmy and common chimpanzees may provide a model for looking more critically at the two species of early hominids (e.g., *Australopithecus africanus,* sometimes called '*Homo*' and *Australopithecus robustus*) which coexisted for at least a million years. For example, the greater range of body weight in *P. troglodytes* may be comparable to that of the robust australopithecines, as compared with the more gracile *A. africanus;* small initial size differences between the two hominid species increased with time. A further 'lesson' from the chimpanzee comparison is that one cannot assume that *A. robustus* is simply a bigger version of *A. africanus.* The dentition does not support this conclusion either [STEUDEL and ROBINSON, 1976]. Nor can one assume that the proportions of a single bone, such as the femur, are similar even between two closely related species, so that 'normalization' of the australopithecine femur relative to *Homo sapiens,* has little validity [e.g. WALKER, 1973; LOVEJOY, 1975]. Parallels between the pairs of species may also be drawn in sexual dimorphism; sexual differences are not apparent from small samples of fragmentary postcranial fossils. Body weight differences are not necessarily revealed in the bones. *A. africanus* analogous to *P. paniscus* may have had less pronounced sexual dimorphism than *A. robustus.*

Finally, as COOLIDGE [1933, p. 56] noted, pygmy chimpanzees 'may approach more closely to the common ancestor of chimpanzees and man than does any living chimpanzee', and in fact they may provide the best model for a common ancestral form of chimpanzees, gorillas and man. Pygmy chimpanzees appear as the most generalized of the African apes and have many 'primitive' features, particularly the shorter humerus relative to femur. A creature somewhat like pygmy chimpanzees may very well have directly preceded the earliest hominids.

Acknowledgements

For access to chimpanzee materials, we thank T. VAN DEN AUDENAERDE, F. A. JENKINS, J. BIEGERT, R. THORINGTON and the late A. H. SCHULTZ. Chimpanzee body weights were made available by R. WRANGHAM (Gombe), P. MCGINNIS (Stanford) and the San Diego Zoo. K. WCISLO, J. M. LOWENSTEIN and T. GRAND provided helpful comments. We gratefully acknowledge grants from the Wenner-Gren Foundation for Anthropological Research and from the Faculty Research Committee, University of California, Santa Cruz (to A.Z.).

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