A Comparison of Sexual Dimorphism and Range of Variation in *Papio cynocephalus* and *Gorilla gorilla* Dentition

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ABSTRACT. The dentitions of 48 baboons (*Papio cynocephalus*) and 242 gorillas (*Gorilla gorilla*) are compared metrically and the baboons are found to have a greater range of variation, and greater sexual dimorphism than the gorillas. This is explained in terms of the different ecologies of these species: life on the African savannah, with its sharp seasonal changes in available food, seems to have given selective advantage to broader niches than life in the rain forest. Further, the historic continuity of the savannah has provided fewer chances for allopatric speciation than the rain forest. These contrasts between forest and savannah speciation should provide insights into hominid evolution. In trying to judge whether australopithecines, probable savannah residents, can be lumped into one or several species, based upon dental variability, a comparison with baboons should be more informative than the now frequently used contrast with gorillas.

INTRODUCTION

The issue of sexual dimorphism and range of size variation in early man have been much discussed in recent years. The range of variation in australopithecine tooth size was at one time thought to fit neatly into the range of gorillas, and the greatest differences between large and small australopithecines seemed to be no greater than those between male and female gorillas. The comparison with gorillas was considered relevant since the latter are, like australopithecines, terrestrial hominoidea (BRACE, 1973). Recent australopithecine finds in East Africa have demonstrated more variation than can easily be accommodated by the gorilla model.

This difficulty may be due to the fact that more than one species is being considered, or to inadequacies in the model. A more informative comparison might be between variability in fossil savannah hominids and that in a modern savannah primate. One would expect a greater species range of variation on the African savannah, with its cline of somewhat different yet continuous environments, than one would expect in the gorilla's forest. This is not to imply that the tropical forest is a uniform environment, but the seasonal stability of the forest ecosystem means that relatively narrow niches are highly adaptive. The historic continuity of the savannah, plus its annual rain cycle, have decreased both opportunities for allopatric speciation and the adaptability of high specialization to the savannah.

Turning to sexual dimorphism, current theory accounts for this phenomenon in primates as at least partly a response to predation. Therefore, one would imagine that selection for sexual dimorphism would be greater on savannah primates, who must face more predators than their relatives in the forest.

It is postulated that greater size variability and sexual dimorphism should be found in a species of savannah primate than in a species of forest primate. The former, then, might prove a more appropriate model for the possible limits of variability in fossil sava-nah species. To test this hypothesis, the diversity, as reflected in dentition, of two primate species, *Papio cynocephalus* and *Gorilla gorilla,* was compared. Dentition was chosen to facilitate later comparison with fossil material.

Gorillas were selected because of their previous use as a standard against which to compare australopithecine variability, and because they show greater variation and more sexual dimorphism than either chimpanzees or orangutangs (P. MAHLER, Pers. Comm.). They seem to be among the most variable of forest species. Baboons were selected to represent the savannah primate because of frequent comparison of their niche with early hominids. The species *Gorilla gorilla* is taken here to include both mountain and lowland gorillas, following COOLIDGE (1929). Into *Papio cynocephalus* are lumped hamadryas and savannah baboons, after BUETTNER-JANUSCH (1966). Although the classification of baboons is debated, recent work by MAPLES (1972) indicates that the old species "cynocephalus" and "doguera" are subspecies, and NAGEL (1973) has found a hybrid zone between "hamadryas" and "anubis."

METHOD

The dentitions of 48 baboons were measured at the American Museum of Natural History, the Cleveland Museum of Natural History, and at New York University's Biological Anthropology laboratory. This number represents all female specimens and almost all male specimens available with at least second permanent molars erupted. Several *P. cyn. hamadryas* males were excluded, since the male sample already included a higher percentage of this subspecies than did the female sample. The baboon subspecies containing the largest and smallest size animals are represented, *P. cyn. cyn. kindae* and *P. cyn. hamadryas,* as well as *P. cyn. ursinus, P. cyn. furax,* and *P. cyn. papio.*

Buccal lingual and mesial distal measurements were obtained for all permanent teeth, areas were calculated, and right and left teeth were averaged. Measurements were taken in accordance with WOLPOFF (1971), with length representing the distance between the contact points of.the teeth as they appear "in normal tooth position or at the midpoint of the line of contact if interstitial wear occurred" (WOLPOFF, 1971). Breadth was the greatest diameter perpendicular to this distance. Vernier calipers were used, and diameters were recorded to the nearest 0.1 mm. An error analysis, made by repeating 56 measurements, indicates that the probable error in tooth area due to reproducibility is 2.13%. Means, standard deviations, and coefficients of variation were computed for males, females and the entire sample taken as a unit. These figures were contrasted with comparable ones taken by Dr. PAUL MAHLER (1973) on a sample of 242 gorillas.

RESULTS

The baboon sample consistantly showed more sexual dimorphism and a greater range of variation than did the gorillas. Consider the contrast between summed posterior areas for maximum and minimum individuals. In the mandibular measurements (P_4-M_3), the largest and smallest baboon differed by 194%, while the gorillas differed by 103%. For the maxilla (P^3-M^3), the figures were 202% and 94%, respectively. This is all the more striking a comparison, if one considers the small size of the baboon sample, 48, as opposed to that of the gorillas, 242. Further, the baboon contrast is not contingent upon any of the current species classification arguments, since the sample's largest and smallest individuals were *P. cyn. doguera* and *P. cyn. cyn. kindae*. These are subspecies MAPLES (1972) saw hybridize in the wild.

As another test of variability, coefficients of variation ((standard deviation/mean)×

Table 1. Coefficients of variation for tooth areas of *P. cynocephalus* and *G. gorilla*.*

	Males		Females		Males and females	
Tooth	N	CV	N	CV	N	CV
Baboons						
Maxilla						
I^1	28	23.4	18	22.4	38	24.8
I^2	25	15.1	18	22.8	37	19.5
C	29	22.1	17	19.1	34	51.9
P^3	29	19.8	17	24.7	37	24.9
P^4	30	19.2	18	21.4	38	22.2
M^1	29	17.0	18	19.5	38	20.2
M^2	25	13.9	18	18.3	38	18.3
M^3	25	14.0	14	21.0	31	20.8
Mandible						
I_1	30	16.6	18	24.0	38	20.5
I_2	29	22.6	18	22.9	37	23.3
C	26	19.0	17	26.5	35	51.9
P_3	28	34.5	18	33.7	37	49.0
P_4	27	14.1	18	20.7	37	19.5
M_1	30	15.4	17	19.6	37	18.2
M_2	29	13.0	18	19.0	38	18.5
M_3	25	16.3	14	20.9	31	21.1
Gorillas						
Maxilla						
I^1	30	15.5+	20	17.0	40	18.5
I^2	30	17.2	20	18.1	40	19.4
C	30	21.1	20	15.4	40	39.2
P^3	30	14.2	20	14.2	40	16.5
P^4	30	12.5	20	14.0	40	14.6
M^1	30	12.4	20	13.1	40	13.6
M^2	30	12.8	20	14.7	40	15.3
M^3	30	12.7	20	16.3	40	17.8
Mandible						
I_1	30	17.1	20	15.5	40	17.8
I_2	30	16.4	20	14.8	40	19.0
C	30	17.2	20	13.4	40	40.0
P_3	30	13.4	20	13.0	40	25.0
P_4	30	14.4	20	13.0	40	18.2
M_1	30	12.1	20	10.5	40	16.0
M_2	30	13.9	20	11.0	40	19.0
M_3	30	15.0	20	13.1	40	21.2

*CV=(standard deviation/mean (mm))×100. +CV=mean CV of six samples of size N.

100) were calculated for males, females, and the sample as a whole (Table 1). Coefficients of variation were used, since comparing standard deviations for very different means did not seem legitimate. This index adjusts for such size differences, but is still somewhat dependent upon sample size. To alleviate this problem, the large gorilla sample was broken into a series of small units. For comparison with the 30 baboon male, the average coefficient of variation for six samples of 30 male gorillas was calculated; a similar procedure was followed for the female comparison. For statistics including both males and females, six samples of 40 were used, with 20 males and 20 females in each sample. For the comparable calculation with baboons, 18 females and 20 males were considered; 10 males were eliminated from the original sample of 30 to balance the sex ratio. The majority of these 10 animals were *P. cyn. hamadryas* and *P. cyn. doguera,* and were preferentially eliminated since the female sample contained fewer representatives of these subspecies than did the original male sample.

Table 1 shows that the baboons consistantly show a wider range of variation than the gorillas. The average coefficient of variation for male baboon tooth areas is 18.46, for females, 22.98, and for the combined sample, 26.55. The same figures in gorillas are 14.87, 12.29, and 20.68, respectively. The contrast in variability between the separated sexes demonstrates that this difference is not simply due to greater sexual dimorphism in baboons.

To compare sexual dimorphism in these two species, the percent increase in mean male tooth area over female tooth area was computed. Mean tooth areas are given in Table 2, and the percent differences in Table 3. From these figures, baboons show, on the average, 20% more sexual dimorphism than gorillas (canines and lower third premolars are excluded).

I felt that this figure might be high since the baboon sample, although having

Table 2. Mean tooth areas.*

	Baboons				Gorillas			
	Males		Females		Males		Females	
Tooth	N	x̄	N	x̄	N	x̄	N	x̄
Maxilla								
I^1	28	81.83	18	69.51	156	145.58	86	121.47
I^2	25	52.62	18	43.29	156	97.41	86	80.20
C	29	136.28	17	52.89	156	349.21	86	170.19
P^3	29	55.92	17	44.61	156	185.28	86	159.38
P^4	30	69.12	18	58.19	156	168.87	86	148.19
M^1	29	107.56	18	89.66	156	232.52	86	206.28
M^2	25	149.89	18	124.64	156	268.59	86	233.61
M^3	25	152.58	14	123.26	156	238.02	86	197.67
Mandible								
I_1	30	57.32	18	47.27	151	68.87	80	59.46
I_2	29	47.58	18	37.88	151	95.64	80	78.27
C	26	112.93	17	41.79	151	266.64	80	137.79
P_3	28	101.82	18	49.71	151	211.72	80	156.60
P_4	27	60.02	18	50.76	151	155.40	80	132.97
M_1	30	86.72	17	72.54	151	216.93	80	191.20
M_2	29	132.43	18	108.22	151	273.87	80	237.39
M_3	25	167.88	14	138.06	151	266.72	80	221.05

*Area = mesiodistal length (mm) × buccolingual breadth (mm).

Table 3. Percent difference between mean tooth areas of males and females.*

Tooth	Baboons % difference	Gorillas % difference
Maxilla		
I^1	17.7%	19.8%
I^2	21.5	21.5
C	157.7	101.3
P^3	25.3	16.2
P^4	18.8	14.0
M^1	19.95	13.8
M^2	20.2	15.0
M^3	23.8	20.8
P^3-M^3	20.6	16.0
Mandible		
I_1	21.3	13.5
I_2	25.6	21.3
C	170.2	93.6
P_3	104.8	35.0
P_4	18.25	17.0
M_1	19.5	13.5
M_2	22.4	15.2
M_3	21.6	20.9
P_4-M_3	20.8	16.65

*Percent diff. $= 100 \times \frac{\text{mean male tooth area (mm)} - \text{mean female tooth area}}{\text{mean female tooth area}}$.

proportionately equal representation of males and females of most subspecies, had 10 doguera males and only four females, and seven hamadryas males, as compared to two hamadryas females. Since these are large subspecies, I suspected that the inclusion of all these males might exaggerate the size difference between males and females. I then eliminated 13 of these large males and recalculated the mean differences. The results were not significantly different from those presented in Table 3. Generally, though, since amount of sexual dimorphism is probably a population characteristic, species comparisons may be somewhat misleading.

DISCUSSION AND CONCLUSIONS

Baboons live in a wider series of diverse but continuous environments than gorillas. Although gorillas do not simply live in one kind of forest, SCHALLER (1963) notes their presence in bamboo forest and in lowland and mountain rain forests, baboon habitats are even more varied. Papio lives in "all vegetational zones from tropical lowland evergreen forest to semi desert and mountains" (JOLLY, 1966). Their already omniverous diet changes according to habitat, with woodland and forest baboons getting most of their food from trees, and savannah and semi-desert baboons relying on roots, insects and whatever else they can find. The diversity of baboon adaptations seems to be reflected in a widely variable species dentition. Whatever the final species taxonomy may be, it is plain from the work of MAPLES and NAGEL that populations can adapt to very different environments, can look very different, and yet be part of the same species, and the above is facilitated on the savannah.

The picture with respect to sexual dimorphism is not as clear cut. Although baboons show more sexual dimorphism than gorillas, gorillas still show considerable dimorphism. One can perhaps account for the increase in baboons as a result of predation pressures, but this certainly does not explain all of sexual dimorphism. A more convincing explanation would have to carefully consider troop organization and local differences in habitat. Perhaps a close look at extra-troop males, their access to females, and their methods for joining troops would be informative. Except with regard to predation, the relationship of sexual dimorphism and savannah life is not clear.

This data has a number of implications for human evolution. The more variable savannah living baboons might provide a better model against which to compare the savannah living australopithecines than is provided by the gorilla. An example is informative. The mean coefficient of variation for gorill a tooth areas (excluding canines and lower third premolars) is 17.5, for baboons is 20.9, for South African australopithecines (including both gracile and robust forms), 14.8 and for East African australopithecines (robust and gracile form: the gracile forms are sometimes considered "*Homo*") is 21.8 (the australopithecine figures were computed from data given in WOLPOFF, 1974). Even the highly diverse East African material is only slightly more variable than that of the baboon species. Because of the small size of the australopithecine sample, it ranges from three to 24, these figures are very tentative, but they do suggest a pattern not unlike the baboons. High variability, whether the result of sexual dimorphism, local population differences, or both, is not unusual in a savannah species.

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