Sexual dimorphism in Ramapithecinae

(Hominidae/paleoanthropology/sexual selection)

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ABSTRACT   The Ramapithecinae are an extinct, mainly Miocene group of hominoids comprising the genera *Sivapithecus* and *Gigantopithecus*. *Ouranopithecus* and *Ramapithecus* are other included genera, here regarded as invalid. Cladistically, ramapithecines are hominid, although, in most aspects of their anatomy, they remain very primitive or ape-like. Miocene ramapithecines show reduced sexual dimorphism in canine size. In this respect they resemble Pliocene/Recent hominids, not extant great apes (which have highly dimorphic canines). Reduced dimorphism in canine size is an important shared derived feature indicating the hominid status of ramapithecines. Among living anthropoids, a significant association has been observed between a monogamous social structure and low canine dimorphism. This supports the inference that ramapithecines may have been monogamous.

It is widely recognized that the amount of dental sexual dimorphism observed among living primates has to do with the degree of competition between the sexes and possible predator defense strategies (1–5). Therefore, knowledge of the amount of sexual dimorphism in fossil Hominoidea is a critical source of information for inferring the earliest stages of ape and human social behavior. Here, I provide an assessment of sexual dimorphism of the Miocene Ramapithecinae and discuss the implications for ape and human evolution.

METHOD OF ASSESSING SEXUAL DIMORPHISM

Sexual dimorphism is the best explanation for marked size differences in the teeth within an ostensibly homogeneous fossil sample when the sample consists of one species, the members of which lived in the same geographical area at the same time. Otherwise, size variability within such a sample could be due to its actually containing several (*i*) closely related species, (*ii*) geographical variants, or (*iii*) separate groups of individuals of one species from different time horizons if the species has undergone marked size fluctuation. The second and third sources of variation are relatively easy to control, but unappreciated interspecific differences are more difficult to detect. Consider, for example, sympatric species of Pliocene hominids. Recent work by Gingerich and others (6–8) suggests a method for distinguishing size difference due to species-mixing from that due to sex. It is now established that dental variability in living species is always lowest in the region of P_4–M_2. Although variability in this region is slightly higher among sexually dimorphic species, it never reaches the point where histograms of P_4–M_2 dimensions in single species form two distinct size peaks corresponding to the sexes. In contrast, among sexually dimorphic species, variability in canine and P_3 dimensions often reaches the point where histograms of these dimensions are distinctly bimodal. Histograms of sexual dimensions of balanced-sex dental samples of *Gorilla gorilla*, a dimorphic species, illustrate this point (Fig. 1).

Consideration of dental dimensions of canines and cheek teeth of extant Hominoidea emphasizes the need for a two-step analysis of variation, whereby species and sexual differences are considered separately in fossil taxa. By using the coefficient of variation (CV) as a convenient size-free measure of variability, as shown in Fig. 1, the CVs of mesial–distal dimensions of *Gorilla* teeth are shown to be low in the P_4–M_2 region and much higher in the canines and P_3. This observation may be generalized for mesial–distal and buccal–lingual dimensions of the same teeth in other hominoids (Table 1). To take advantage of this situation, the first step in an assessment of fossils, once a morphologically homogeneous sample is obtained, is to consider P_4–M_2 variation. If CVs of these dimensions in the sample exceed the maximum for living hominids, as shown in Table 1, we should assume that the sample probably includes more than one species. Conversely, if these values are at or below this threshold, there is probably only one species present, and we can go on to consider dental sexual dimorphism inferred from CVs of canine and P_3 dimensions.

A ratio of the means of male and female dental dimensions is often a convenient measure of sexual dimorphism in a living species. However, this ratio is difficult or impossible to estimate accurately in a fossil species because sex cannot be determined reliably. For example, large males and small females are easily recognized, but small males and large females overlap in all dental dimensions and are not otherwise distinguishable dentally. An alternative approach using the sample CV avoids this pitfall. Among living hominoids, the ratio of the dimensions of male canines to the same dimensions of females is highly correlated with the combined-sex CV of the same dimension (Fig. 2). Therefore CVs of canine dimensions provide an indication of dimorphism and obviate the need for sexing any individual in the sample. The presence of high CVs in canine or P_3 dimensions in a hominoid species points unequivocally to a high degree of sexual dimorphism in that feature. *Gorilla*, with CVs of 17–21 in upper and lower canine dimensions, is the most dentally dimorphic extant hominoid. Species of *Hylobates* have CVs between 4.7 and 8.6 in the same dimensions, comparable to populations of *Homo sapiens* and indicative of virtually no sexual dimorphism. [The data for statements about *Homo sapiens* are based on the American Indian sample from Dickson mound (12).]

DIMORPHISM IN RAMAPITHECINES

Ramapithecine specimens are for the most part quite fragmentary, isolated in occurrence, and unsuitable for an analysis of sexual dimorphism, with the possible exception of two samples. The first is the material collected in the 1970's by de Bonis, Melentis, and coworkers from Rain Ravine in Greek Macedonia (13–16). The second, larger, sample includes Indian and Pakistani material collected by many workers over the past 100
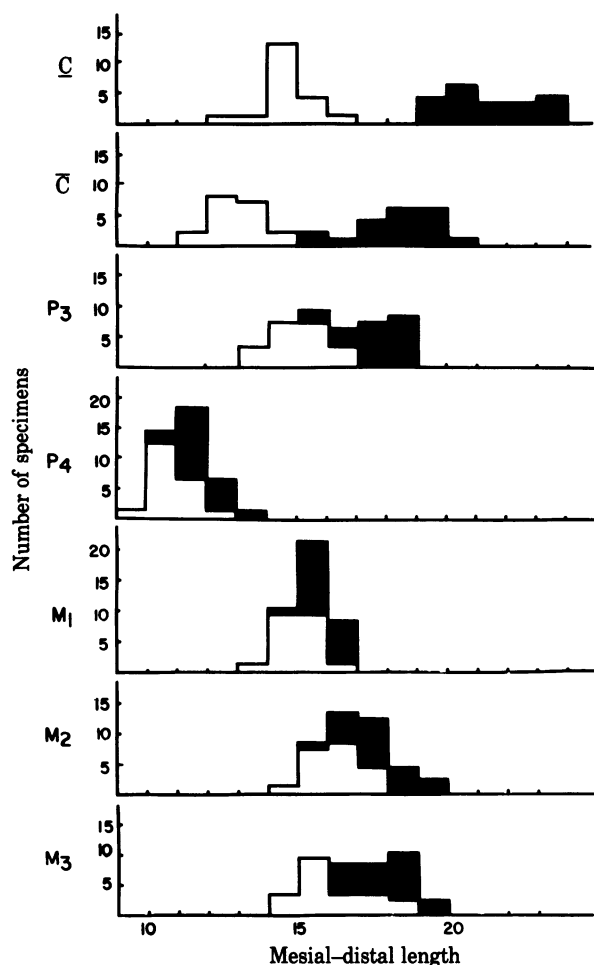
FIG. 1. *Gorilla gorilla.* Histograms of mesial–distal length of C̲, C̄–M₃ in balanced-sex samples of 40 animals. Male specimens are represented by the black areas of the histograms; females are represented by the clear areas. Data is from Pilbeam (9). CVs: $\underline{C}$, 20.0; $\bar{C}$, 17.9; P_3, 10.0; P_4, 6.8; M_1, 4.9; M_2, 6.5; M_3, 7.9.

Table 1. Variability in selected canine and cheek-tooth dimensions as expressed by the CV

Tooth	Dimension	Hominoidea* CV		
		Mean	Maximum	Minimum
$\underline{C}$	L	14.6	20.5 (*G. gorilla*)	5.4 (*H. agilis*)
	B	15.2	19.9 (*G. gorilla*)	8.6 (*H. agilis*)
$\bar{C}$	L	11.5	17.9 (*G. gorilla*)	4.7 (*H. hoolock*)
	B	13.8	19.1 (*G. gorilla*)	6.8 (*H. agilis*)
P_3	L	7.4	10.4 (*P. pygmaeus*)	4.5 (*H. hoolock*)
	B	9.1	10.9 (*P. troglodytes*)	6.9 (*H. agilis*)
P_4	L	5.6	7.3 (*P. troglodytes*)	3.5 (*H. agilis*)
	B	6.5	8.4 (*G. gorilla*)	2.6 (*H. agilis*)
M_1	L	5.3	6.1 (*H. agilis*)[†]	3.8 (*P. pygmaeus*)
	B	5.2	6.4 (*G. gorilla*)[‡]	3.7 (*H. agilis*)
M_2	L	4.9	6.5 (*G. gorilla*)	3.6 (*H. hoolock*)
	B	5.4	7.3 (*P. troglodytes*)	3.2 (*H. agilis*)
M_3	L	6.2	8.7 (*P. troglodytes*)	4.2 (*H. hoolock*)
	B	6.9	9.5 (*P. troglodytes*)	4.9 (*H. hoolock*)

L and B signify mesial–distal length and buccal–lingual breadth, respectively, except for C and P_3, where they signify the greatest dimension in the occlusal plane and the dimension at right angles to it. $\underline{C}$ and $\bar{C}$ signify upper and lower canines, respectively.

* Includes data for *Gorilla gorilla, Pan troglodytes, Pongo pygmaeus, Hylobates agilis,* and *Hylobates hoolock* from Mahler (10) and unpublished data. All samples were adjusted to a balanced sex composition. Data for *Pongo* came from a subset of 40 animals from Borneo measured by Mahler (10). Mahler's summary CVs are higher for some teeth because he includes Hoojier's (11) 1948 measurements of *Pongo.* The latter's measurements average as much as 25% larger, although they come from the same geographic areas. The measurement technique apparently accounts for the difference.

† Also *G. gorilla.*

‡ Also *P. troglodytes.*

years. Each sample presents special problems for interpretation.

The Rain Ravine sample available for analysis consists of 12 specimens with two or more teeth comprising a minimum of 7 individuals which come from a single restricted horizon, faunally dated as being of Vallesien Provincial age—about 10–11 million years old. De Bonis *et al.* (13–16) consider all this material to belong to a single gorilla-sized species called *Ouranopithecus macedoniensis.* This material might better be regarded as *Sivapithecus* (17) and, moreover, probably more than one species is represented.

The Rain Ravine specimens have been allocated to a single species because all are morphologically similar, and all have been recovered from a single locality. This evidence by itself is not definitive. There are numerous instances among extant anthropoids of several sympatric species that cannot be distinguished dentally except by size. For example, *Cercopithecus nictitans, C. pogonias, C. cephus,* and *C. neglectus* are sympatric in northeastern Gabon (18). It would not be surprising if specimens of all four of these taxa were to occur in the same burial assemblage. A more critical test of whether one or several species are present is to see whether CVs of P_4–M_2 dental dimensions of the Rain Ravine sample are within the expected range for extant hominoids (Table 2). In all cases, the samples are quite small. However, of six P_4–M_2 CVs in Table 2, four exhibit CVs exceeding the range observed for extant hominoids and two are within the observed range. Pending the recovery

of more specimens, the Rain Ravine material is best interpreted as containing two ramapithecine species. Given the presence of two species at Rain Ravine, and the small number of canines and P_3s from the site, it is not possible to observe the amount of sexual dimorphism in this sample of ramapithecines.

A second, much larger sample of ramapithecines has been
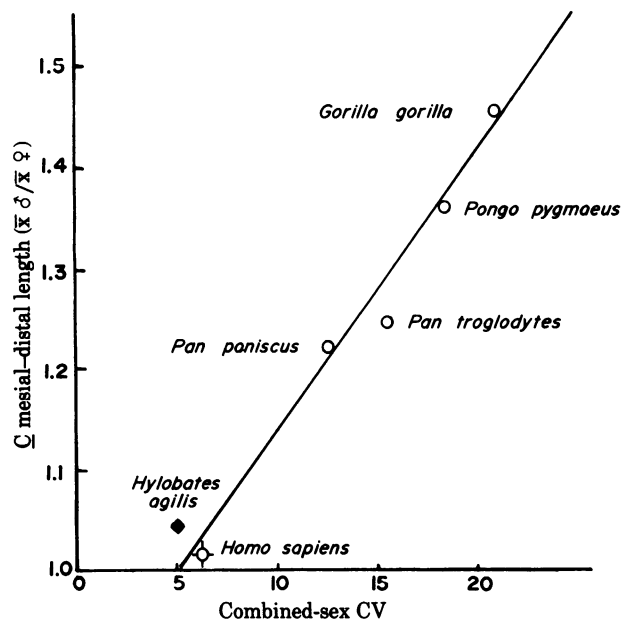

FIG. 2. Bivariate plot of the CV of upper canine mesial–distal length in balanced-sex samples versus the ratio of male to female upper canine mesial–distal length for the same samples. The correlation (*r*) between these factors is 0.99.

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Table 2. CV of mandibular teeth for the hominoids of Rain Ravine

Tooth	Dimension	N	CV
$\overline{C}$	L	7	14.2
	B	7	15.5
P_3	L	8	15.8
	B	7	9.5
P_4	L	7	9.2*
	B	7	12.4*
M_1	L	5	6.8*
	B	3	9.2*
M_2	L	7	6.1
	B	7	6.5
M_3	L	7	8.5
	B	7	8.1

L and B are the same as defined in Table 1. N, sample size. Measurements were by the author.
* Sample CV exceeds the known range for extant hominoids.

Table 3. Sample sizes (N) and CV of lower-cheek teeth of Siwalik ramapithecines

Tooth	Dimension	Total sample		S. indicus		S. sivalensis	
		N	CV	N	CV	N	CV
P_4	L	19	7.2	7	5.5	7	5.5
	B	19	12.3	7	5.9	7	9.2
M_1	L	15	7.7	8	4.8	7	3.0
	B	11	10.9	6	6.3	5	3.3
M_2	L	23	11.1	11	7.9	12	5.7
	B	23	12.3	11	6.0	12	5.7
M_3	L	35	10.1	8	7.2	9	7.6
	B	31	10.6	8	4.7	9	9.8

"Total sample" includes those specimens assignable to species and additional specimens too fragmentary to be assigned. S. sivalensis sample includes specimens previously assigned to *Ramapithecus*.

collected in the Siwalik series of India and Pakistan. Pilbeam *et al.* concluded that all but a few of the Pakistani hominoids come from a relatively narrow time range of perhaps a million years (between 7.5 and 8.5 million years ago); the bulk of the Indian material appears to be about the same faunal age (19, 20). The greatest distance between the Siwalik localities is no more than about 500 km, so no great geographic variation is likely to have existed (single subspecies of extant anthropoids range over 3 to 4 times that distance in Africa today). In any event, there is no compelling evidence that any of the observed variation in the Siwalik ramapithecine sample is due to geographic variation or evolutionary change during a several-million-year interval.

Recent reviews indicate that there are four species of Siwalik ramapithecines (17). The largest, *Gigantopithecus giganteus* (Pilgrim) 1915, is known only from the type molar and a lower jaw described by Simons and Chopra (21). Another taxon, *Sivapithecus* n. sp., is known only from a few extremely small specimens, some of which were hitherto attributed to *Ramapithecus* and some to *Dryopithecus laietanus* (17) (unpublished data). The remaining Siwalik sample is clearly too variable to belong to a single species (Table 3). CVs of seven of eight dimensions of the total sample exceed the observed range for single species of extant hominoids (compare Tables 1 and 3). These specimens are best considered as representing two species— *Sivapithecus indicus* Pilgrim 1910 and *Sivapithecus sivalensis* (Lydekker) 1879. *Ramapithecus punjabicus* (Pilgrim) 1910 is the same animal as S. *sivalensis* and should properly be called by

the same species name (17). CVs of dental dimensions of these two species fall within the range of variation of living hominoids in all but 1 of 16 dimensions in Table 3.

A few dentitions of S. *sivalensis* and S. *indicus* preserve the canines. Where samples are large enough, they show consistently low CVs for occlusal length and breadth, indicating a low sexual dimorphism in canine size. Five upper canines of S. *indicus* have CVs for occlusal length and breadth of 4.8 ± 1.5 and 9.3 ± 2.9 (numbers which follow ± indicate the standard error of CV). Six lower canines of S. *sivalensis* have CVs for occlusal length and breadth of 8.4 ± 2.4 and 13.6 ± 3.9. All these values are below those for extant large-bodied apes (Table 4). Except for the value for lower canine breadth in S. *sivalensis*, they fall within the range of values for species like *Hylobates* and *Homo* with low canine sexual dimorphism (Table 4).

A number of ramapithecine upper canines from Siwalik collections are isolated specimens which cannot be assigned to a species. However, given the rarity of occurrence of *Gigantopithecus giganteus* and *Sivapithecus* n. sp., the bulk of these probably belong either to S. *indicus* or S. *sivalensis*. (As will be noted below, if this sample actually does include some specimens of these other taxa, the argument that follows is further strengthened.) Taking these together with those that definitely can be assigned to a species, there are 21 upper canines in all.

CVs of length and breadth for this mixed-species sample of ramapithecine upper canines are surprisingly low: 10.9 ± 1.7 for occlusal length and 14.4 ± 2.2 for occlusal breadth. This group of canines from two species actually exhibits lower vari-

Table 4. CV in Pliocene–Recent hominid and modern great ape canine occlusal dimensions

	CV*			
	Upper canine		Lower canine	
	L	B	L	B
Australopithecus afarensis[t]	7.5 ± 1.7 (10)	10.1 ± 2.3 (10)	16.8 ± 5.3 (5)	11.3 ± 2.7 (9)
Australopithecus robustus[‡]	7.8 ± 1.5 (13)	8.6 ± 1.8 (12)	7.1 ± 1.8 (8)	9.0 ± 2.3 (8)
Australopithecus africanus[‡]	4.3 ± 1.4 (5)	5.0 ± 1.8 (4)	7.0 ± 2.0 (6)	9.6 ± 2.8 (6)
Homo sapiens[§]	5.6 ± 0.4 (113)	6.7 ± 0.6 (113)	6.1 ± 0.4 (123)	7.7 ± 0.6 (124)
Modern great ape range[¶]	15.2 – 20.5	14.6 – 19.9	13.3 – 17.9	16.7 – 18.6

* Mean ± SEM; sample size is in parentheses.
[t] Data from Johanson and White (22).
[‡] Data from Robinson (23) for Swartkrans and Sterkfontein sites, respectively.
[§] Data on Dickson mound from Wolpoff (12).
[¶] See Table 1 for data sources.

ability than any single species of extant large-bodied ape (Table 4). This finding of low CVs in canine dimensions strongly supports the indications for individual species that Siwalik ramapithecines have low canine dimorphism.

The inescapable conclusion that can be drawn from the available sample is that the canines of Siwalik ramapithecines have low sexual dimorphism, comparable to that of *Homo* and *Hylobates*. The evidence for a high degree of dimorphism in Macedonian hominoids is weak. By analogy with the variability in living hominoids and Siwalik ramapithecines, it is likely that two species are being sampled by de Bonis and coworkers at Rain Ravine.

DISCUSSION

Studies of extant anthropoids suggest that the amount of sexual dimorphism in canines is related to social organization (1–5). In species with high dimorphism, the condition typically found among extant Anthropoidea, there is usually considerable overt male–male competition for oestrous females or female selection of males during courtship, or both. In marked contrast to this is the pattern seen among relatively monomorphic anthropoids. These species are always monogamous and tend to share equally the role of protecting the family group from same-sex intruders, so there is little selection for dimorphism between the sexes. By this analogy, ramapithecines were likely monogamous.

The inferred low degree of canine dimorphism in ramapithecines is a shared derived feature indicating their hominid status. Unlike living great apes, modern humans show very reduced sexual dimorphism in canine size. This was true of australopithecines as well. Samples of canines from Sterkfontein and Swartkrans sites in South Africa have low CVs of occlusal length and breadth measurements by the standards of extant great apes (Table 4). The same is true of *Australopithecus afarensis* (22). In this species the CVs of canine dimensions fall below the range for extant great apes except in lower canine length. (The sample of *A. afarensis* lower canines for which the length dimension is offered is just five, and the standard error of the CV is extremely large, so a high CV for this dimension should be discounted.) This information confirms that ramapithecines share a similar low degree of canine dimorphism with Pliocene hominids, unlike the more primitive dimorphic condition seen among extant great apes. Parenthetically, the extent of sexual dimorphism in body size in hominids does not mirror canine dimorphism as it does in living apes. Humans appear to be unique among living primates in having considerable body-size dimorphism but very little canine-size dimorphism. The same may have been true in australopithecines (22).

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