

Sexual Dimorphism in *Dryopithecus africanus*

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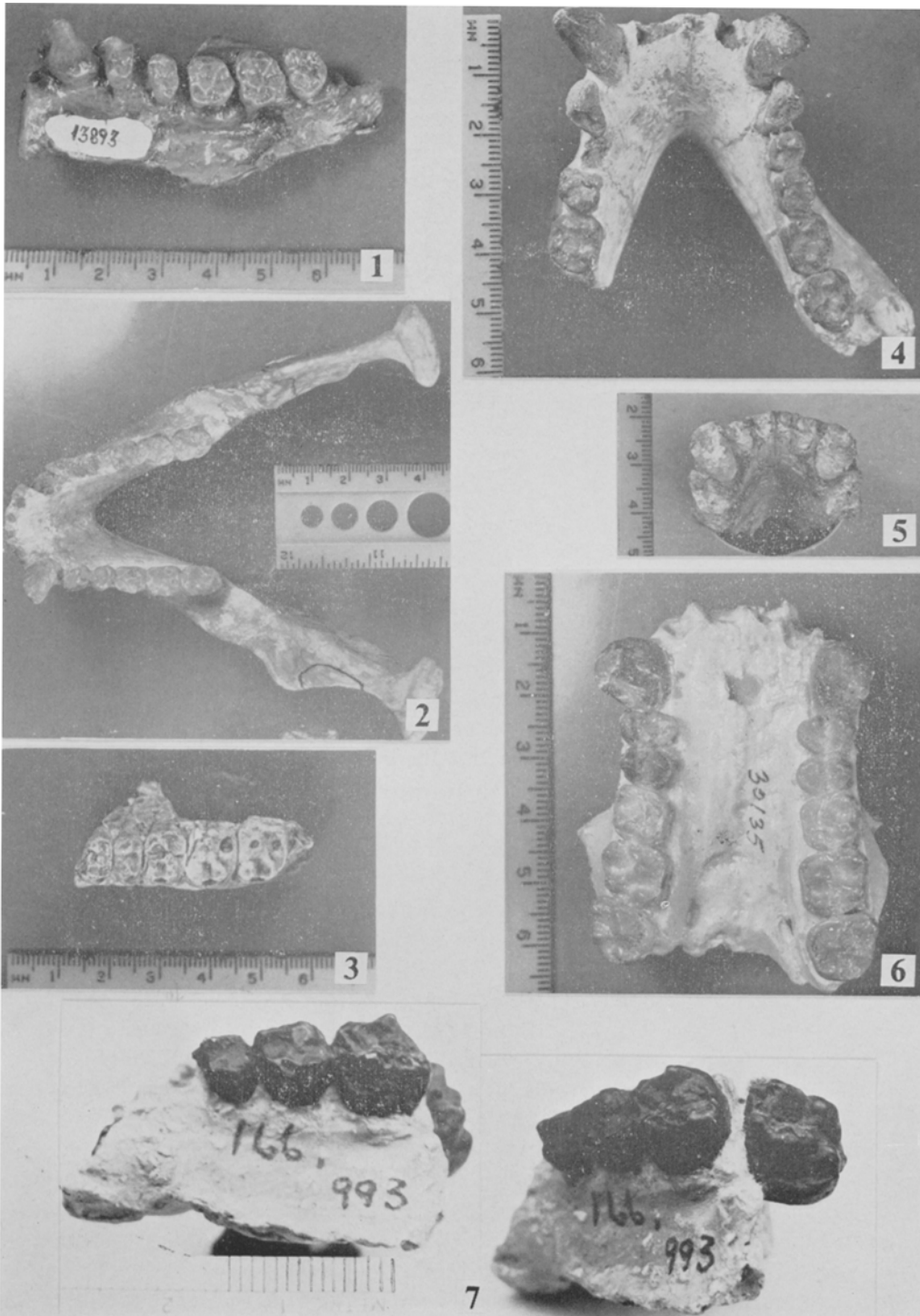
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ABSTRACT. Among the numerous specimens presently classified within *Dryopithecus africanus* only one can be identified as a male of this species. Poor sampling is not the reason for the unequal numbers of male and female specimens. Rather, the males have been classified elsewhere, specifically within *Dryopithecus nyanzae* and "*Kenyapithecus africanus*." The specimens to be transferred from these two taxa are proved to be males of *D. africanus*. The newly transferred males are compared with the females to show the cranial dimorphism of the species.

INTRODUCTION

Dryopithecus africanus was first described by HOPWOOD (1933), later by LE GROS CLARK and LEAKEY (1951), and by SIMONS and PILBEAM (1965). Since its original description, nearly one hundred specimens have been found and described. Despite this accumulation of specimens, no attempt has been made to define the sexual dimorphism within the species. I believe this is because most of the specimens now classified as *D. africanus* are probably females. In fact, at present, there is only one specimen classified within *D. africanus*, maxillary fragment BMNH 14084 (Fig. 1), that I think represents an adult male. Where are the males? The absence of male individuals is probably not due to sampling error, but rather to errors in classification. In my view, most of the males of *D. africanus* have been placed in either *D. nyanzae* or "*Kenyapithecus africanus*." Being males, these specimens represent larger individuals than the individuals already classified within *D. africanus*. I believe that their larger size (especially in the mandible) has been the major cause of their improper classification.

The specimens that should be transferred to *D. africanus* as males of that species are as follows: 1, CMH 1 (Fig. 2), the 1942 mandible, and its associated maxilla 155,712 (Fig. 3) which are presently classified as *D. nyanzae*; mandible R 394 (Fig. 4), originally placed within "*Kenyapithecus africanus*" (LEAKEY, 1968), but later shown to be an African dryopithecine (PILBEAM, 1968); SGR 276 (Fig. 5), the symphyseal portion of a mandible, placed by LEAKEY (1967) in "*Kenyapithecus africanus*"; and maxilla KNM-SO 700 (Fig. 6), already recognized as having close affiliations with *D. africanus* (ANDREWS, 1970). An additional specimen, the left side of a maxilla of an immature individual, specimen 166,993 (Fig. 7), should also be transferred from *D. nyanzae* to *D. africanus*. The reasons for this will be discussed later. Tooth measurements for these proposed males can be found in Table 11 at the end of this paper.



MATERIAL

I have seen casts of the great majority of specimens mentioned in this paper at the Yale Peabody Museum. I have used descriptions (LE GROS CLARK & LEAKEY, 1951) of those specimens not available to me. Measurements for most of the miocene material comes from PILBEAM (1969). Specimen KMN-SO 700 was measured by ANDREWS (1970), and I have used his measurements in this work. Specimen R 394 was measured by the author from a cast.

Samples of modern African pongids, mentioned later in this paper, were also measured by the author. These samples come from the Hamann-Todd Collection, housed in the Cleveland Museum of Natural History.

DISCUSSION

The specimens I wish to transfer are all dryopithecines (proconsuls), and are similar to each other metrically and morphologically. There are two possible alternatives in classifying them. The first and less likely alternative is that they represent females of *D. nyanzae*. The argument for this is that their smaller dentitions are indicative of presumably smaller females of *D. nyanzae*. In addition, the large size of the above mentioned mandibles places them metrically closer in size to *D. nyanzae* than to *D. africanus*. The second alternative, the one I will try to prove, is that these specimens are males of *D. africanus*.

EXPLANATION OF FIGURES

Fig. 1. Specimen 14084 (YPM 13893), originally described by HOPWOOD (1933), is the only adult male specimen presently classified within *D. africanus*. Note the relatively large canine.

Fig. 2. Specimen 1, CMH 1, the 1942 mandible, was originally placed by MACINNES (1943) in *D. africanus*. It was removed from this taxon by LE GROS CLARK and LEAKEY (1951) and placed into *D. nyanzae* as a female of this species because of its small dentition. However, note the long projecting canine, indicating that it is a male.

Fig. 3. Specimen 155,712 was placed with its associated mandible (1, CMH 1) in *D. nyanzae*. A metric analysis of its dentition indicates that it belongs in *D. africanus*.

Fig. 4. Specimen R 394 was classified by LEAKEY (1968) in *Kenyapithecus africanus*. Its long projecting canine (which indicates that it is a male), sectorial lower third premolar (with wear on its mesiobuccal surface from the shearing action of a long maxillary canine), and external cingula indicate that it is an African Dryopithecine. Its dentition falls metrically closer to *D. africanus* specimens.

Fig. 5. Specimen SGR 276 was also placed by LEAKEY (1967) in *Kenyapithecus africanus*. It is very similar to the symphyseal portions of R 394 and 1, CMH 1, both metrically and morphologically. Its canines were large, and the third premolars were elongate.

Fig. 6. Specimen KMN-SO 700 (YPM 30135), described by ANDREWS (1970), is undoubtedly an African dryopithecine. Note the large canines. Metrically, this specimen's dentition falls within the range of variation for *D. africanus* specimens.

Fig. 7. Specimen 166,993 was placed by LE GROS CLARK and LEAKEY (1951) in *D. nyanzae*. A metric analysis of the two permanent molars indicates that it should be transferred to *D. africanus*. It may be a male of this species.

A decision whether to place these specimens in *D. africanus* or *D. nyanzae* cannot be made on the basis of dental morphology. Differences in dental morphology between the two taxa have been noted (LE GROS CLARK & LEAKEY, 1951). However, the differences cited involve only the more variable traits such as development of the cingulum, hypocone size, degrees of expression for minor cuspules, and the relative heights of the cusps on the third maxillary premolar. Differences in the morphologies of the mandibular dentitions were not noted. In addition, the differences cited do not involve all the specimens. Thus, these morphological features do not really separate the two species. However, metric differences do separate *D. africanus* and *D. nyanzae*. By *D. nyanzae*, I am referring to all specimens classified in that taxon (PILBEAM, 1969) except specimens 1,CMH 1, 155,712, and 166,993.

Table 1 lists summed posterior areas for the maxillary and mandibular dentitions of *D. africanus* and *D. nyanzae*. Summed posterior areas is merely an approximation of the area of mastication. Areas (mesiodistal length \times buccolingual breadth) for each posterior tooth on one side of the dental arch are calculated, and then the individual areas are summed. Summed posterior areas are calculated separately for maxillary and mandibular dentitions. Also in Table 1 are average summed posterior areas. These were calculated by taking the average dimensions for each posterior tooth (of all specimens in each taxon except the proposed males) to determine average tooth areas. The average tooth areas were summed separately for maxillary and mandibular tooth rows.

Table 1. Summed posterior areas for *D. africanus* and *D. nyanzae*.

<i>D. africanus</i>			
Maxilla		Mandible	
Specimen	S.P.A.	Specimen	S.P.A.
1948,50	357.5	35,CMH 102	330.0(est.)
14084*	371.7	51,1499	340.0(est.)
KNM-SO 700*	355.0	1948,50	361.2
155,712*	438.0	R 394*	386.0
average ⁺	367.2	1,CMH 1*	381.9
		average ⁺	322.5
<i>D. nyanzae</i>			
Maxilla		Mandible	
Specimen	S.P.A.	Specimen	S.P.A.
16647	583.4	562,1145	499.9
5,CMH 3	553.0	4, CMH 4	547.3
average ⁺	602.0	average ⁺	496.9

*Proposed male. ⁺This average does not include proposed males.

Table 1 clearly shows the proposed males are metrically closer to *D. africanus* specimens than they are to *D. nyanzae* specimens. In addition, they are generally larger than the *D. africanus* specimens, and this is to be expected if they represent males of this species. Similar conclusions can be reached when one compares the average summed posterior areas (which were calculated to include those specimens with incomplete posterior dentitions), with the summed posterior areas for the proposed males.

Table 2. Ranges of occlusal surface areas⁺ for mandibular and maxillary molars of *D. africanus* and *D. nyanzae*.

<i>D. africanus</i>					
Maxilla			Mandible		
	Range	n		Range	n
M ¹	56.0–89.1	10	M ₁	48.0–70.2	11
M ²	72.2–105.8	7	M ₂	75.3–92.7	5
M ³	86.9–95.5	4	M ₃	66.5–111.9	9

<i>D. nyanzae</i> *					
Maxilla			Mandible		
	Range	n		Range	n
M ¹	69.9–115.2	6	M ₁	65.5–87.0	11
M ²	96.0–169.9	7	M ₂	91.8–149.5	9
M ³	110.2–159.3	4	M ₃	109.0–173.6	8

⁺Area = mesiodistal length (mm) × buccolingual breadth (mm). *Includes proposed males.

To support my position, I have set up ranges of occlusal surface areas (mesiodistal length × buccolingual breadth) for molars of *D. africanus* and *D. nyanzae*. In Table 2, I have included the proposed males within *D. nyanzae*. The resulting ranges for the two taxa overlap (with the exception of M³). In Table 3, the proposed males were included in *D. africanus*. There is now discontinuous metric variation between the two taxa (except M₁, where there is a small overlap). The dentitions of the proposed males fall metrically into the upper portions of the *D. africanus* ranges (and extend them), and outside the *D. nyanzae* ranges. Clearly, inclusion of the proposed males in *D. africanus* creates a valid metric distinction between *D. africanus* and *D. nyanzae*.

I believe two criteria can be used to prove the sex of the proposed males. They are relative canine size (expressed in a canine to first molar index), and canine morphology.

A canine to first molar index usually indicates sex among modern African pongids. The index is equal to 100 × the area of the canine (maximum length × breadth) divided by the area of the first molar (mesiodistal length × buccolingual breadth). Samples of dentitions of *Pan troglodytes* and *Pan gorilla* in the Hamann-Todd

Table 3. Ranges of occlusal surface areas⁺ for mandibular and maxillary molars of *D. africanus* and *D. nyanzae*.

<i>D. africanus</i> *									
Maxilla					Mandible				
	Range	n	\bar{x}	CV		Range	n	\bar{x}	CV
M ¹	56.0–90.7	13	74.0	15.3	M ₁	48.0–71.9	13	61.8	11.0
M ²	72.2–116.4	10	96.0	15.4	M ₂	75.3–92.7	7	83.6	—
M ³	86.9–128.0	6	100.2	—	M ₃	66.5–111.9	11	93.3	16.2

<i>D. nyanzae</i>									
Maxilla					Mandible				
	Range	n	\bar{x}	CV		Range	n	\bar{x}	CV
M ¹	100.5–115.2	3	108.8	—	M ₁	70.3–87.0	9	79.0	6.9
M ²	135.2–169.9	4	159.6	—	M ₂	107.0–149.5	7	126.3	—
M ³	156.4–159.3	2	157.8	—	M ₃	128.8–173.6	6	156.8	—

⁺Area = mesiodistal length (mm) × buccolingual breadth (mm). *Includes proposed males.

Collection were measured, and maxillary and mandibular indices were calculated (Table 4). For the maxilla, males (n=89) of both species do not have indices below 110.0, while females (n=93) do not have indices above 115.0. Where the ranges overlap, one may use canine morphology to separate males and females. Males with low indices have long projecting canines (and very large first molars), while females with high indices have small canines (when compared to male individuals) and very small first molars. Thus overlap in the ranges is not due to overlap in canine size, but rather to the variation in first molar size. The combination of metric and morphological information permits one to separate all males from females.

Certainly, one could separate all these individuals on the basis of canine morphology. However, with fossil specimens, the canine is often broken, and only the basal portion of it remains. In these situations, one cannot use canine morphology to determine sex, but one may calculate the relative canine size index (measurements are taken at the base of the canine). A bimodal distribution exists, for the relative canine size index, among the modern African pongids. I suspected these closely related miocene pongids would show a similar distribution for the index, even though the precise numerical boundaries for each sex would be different (from those of the modern African pongids). Fortunately, many specimens of *D. africanus* (including the proposed males) have at least the basal portions of their canines, and I have used these specimens to establish a model for sex determination in *D. africanus* (Table 5).

The model proposed here for *D. africanus* is similar to the model proposed for the modern African pongids. For the maxilla, the proposed males (with long projecting canines) have indices above 132.0, while the females (those specimens already classified within *D. africanus* with small non-projecting canines) have indices below 110.0. The index clearly separates the males from the females. Figure 8 (a, b, & c) compares a female specimen (1948,50) with two males (14084, and KNM-SO 700) to show the sexual difference in the length of the canine in relation to the occlusal plane of the posterior dentition.

I have listed in Table 5 an index of 145.0 ± 10 for maxilla 155,712 even though it lacks a canine. As mentioned earlier, this specimen is associated with mandible 1,CMH 1, which does have an intact canine (which is long and projects well above the occlusal plane). I calculated an index of 143.4 for this mandible. I think it is reasonable to use this mandibular index to approximate an index value for the maxilla. I will base by approximation on two models.

Table 4. Ranges of canine to first molar indices for *Pan troglodytes* and *Pan gorilla*.

<i>Pan troglodytes</i>				
	Male		Female	
	C/M1 × 100	n	C/M1 × 100	n
max.	113.5–209.7	37	77.9–108.4	40
mand.	112.0–183.5	33	78.7–115.1	41
<i>Pan gorilla</i>				
	Male		Female	
	C/M1 × 100	n	C/M1 × 100	n
max.	110.8–185.9	52	66.1–113.9	53
mand.	92.0–172.2	52	55.0–92.1	51

The first model applies to modern African pongids. I examined the relationship between maxillary and mandibular indices. In a sample of *Pan gorilla* (n=105), it was observed that an individuals mandibular index was always less than its maxillary

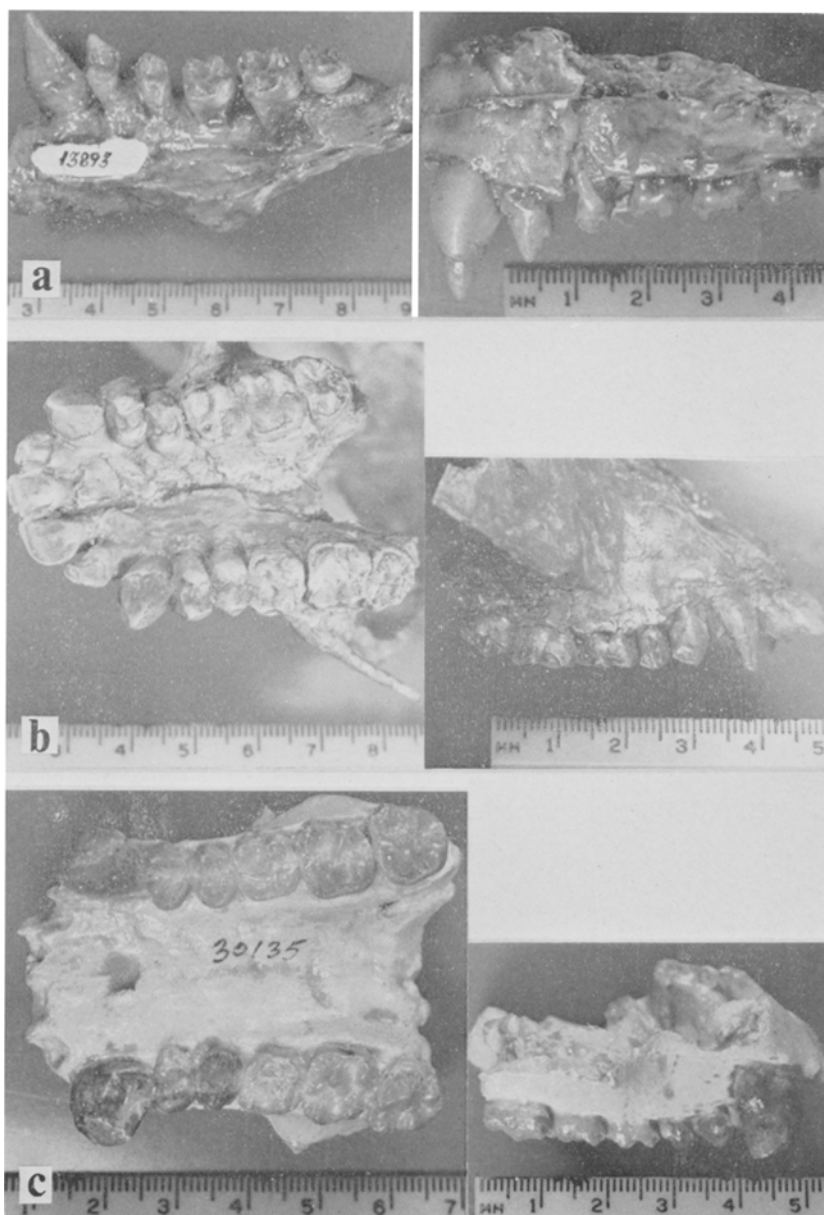


Fig. 8. (a) Specimen 14084 (male), occlusal and buccal views. (b) Specimen 1948,50 (female), occlusal and buccal views. (c) Specimen KNM-SO 700 (male), occlusal and buccal views. Note the differences (between males and female) in the projection of the canine and its size relative to first molars.

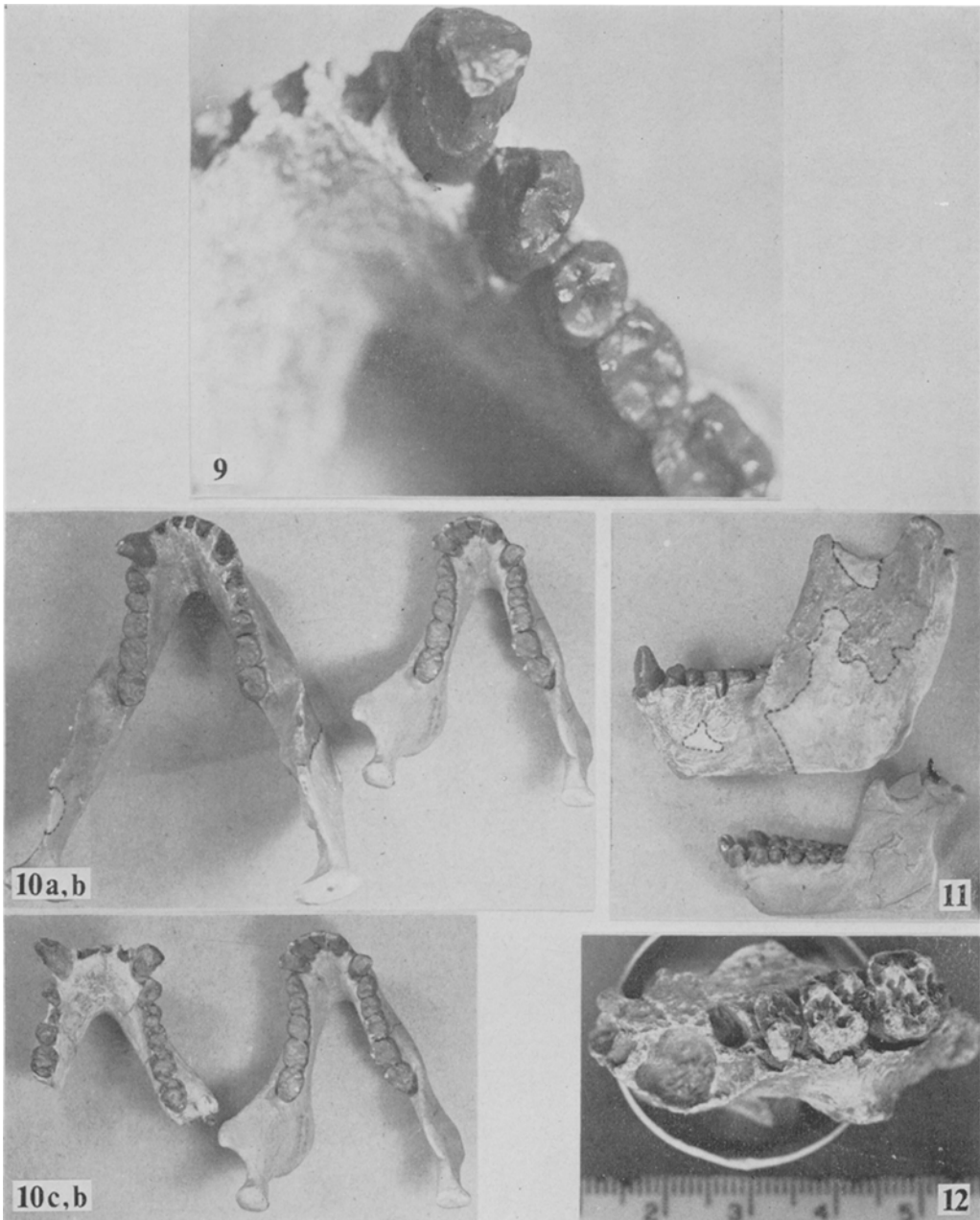


Fig. 9. Specimen R 394 has an elongate lower third premolar with the mesio Buccal surface worn flat from the shearing action of a large projecting maxillary canine.

Fig. 10. (a) Specimen 1, CMH 1 (male), occlusal view. (b) Specimen 1948, 50 (female), occlusal view. (c) Specimen R 394 (male), occlusal view. Note the differences in projection and relative canine size (relative to first molars) between males and female. Also note that the third molars are almost metrically identical.

(Continued)

Table 5. Canine to first molar indices for *D. africanus*.

Maxilla	
Specimen	C/M1 \times 100
34, CMH 101	104.5
1948,50	108.3
14084*	132.0
KMN-SO 700*	144.0
155,712*	145.0 \pm 10
Mandible	
Specimen	C/M1 \times 100
51,1499	86.3
35, CMH 102	85.0 (est.)
1948,50	95.4
R 394*	134.0
1, CMH 1*	143.4

*Proposed males of *D. africanus*.

index. However, this rule does not apply as strictly for *Pan troglodytes*. Approximately 40 percent of the individuals (n=73) had higher mandibular indices than their corresponding maxillary indices. An average difference of ten units in the index was noted for individuals with higher mandibular indices. Applying this model to specimen 155,712, I feel an index of 145.0 \pm 10 is reasonable, a value that indicates it is a male.

The other model is based upon the few *D. africanus* specimens for which I have calculated indices. Specimen 1948,50 (the only individual with mandibular and maxillary canines) has a higher maxillary index than mandibular index. The other specimens listed in Table 5 show that generally, maxillary indices are higher. I feel this evidence also supports the approximation reached.

For mandibles of individuals belonging to *Pan troglodytes* and *Pan troglodytes* it was found that males (n=85) had indices as low as 92.0, while females (n=92) had indices that ranged as high as 115.0, but never went above this value. Again, we have a bimodal distribution for the index.

By including the proposed males with specimens already classified within *D. africanus* we begin to see a bimodal distribution (without overlap) for the mandibular index. The supposition that each mode represents a sex is supported by the evidence of canine morphology. In Table 5, specimens with low mandibular indices have small non-projecting canines, and thus represent females. Specimens with high indices have long projecting canines and specimen R 394 shows wear, from a long maxillary canine, on the mesiobuccal plane of the third premolar (Fig. 9). Figure 10 (a, b, & c) is a comparison between a female (specimen 1948,50) and two males (specimens R 394, and 1,CMH 1), and it shows sexual differences in relative mandibular canine size and projection.

Fig. 11. Specimens 1948,50 (female) and 1,CMH 1 (male) are compared to show absolute differences in mandible size. However, note the general similarity in mandibular morphology and the relative size of the canine.

Fig. 12. Specimen 51,1499 (which has an associated mandible) has a fairly large canine socket. It has been treated as a female in this paper.

In summation, the proposed males have canines indicative of males, not females. Their maxillary and mandibular canines are long and project well beyond the occlusal planes. The one, uneroded mandibular third premolar of a proposed male (on specimen R 394) shows wear on its mesiobuccal surface, caused by the shearing action of a large maxillary canine. In addition, inclusion of the proposed males in *D. africanus* creates the expected bimodal distribution for relative canine size, with each mode indicating a sex.

I have shown thus far that metrically, the dentitions of the proposed males fall within and extend the old *D. africanus* ranges. This extension is not unexpected since these specimens represent males of this species. Also, the dentitions of the proposed males fall metrically below the new *D. nyanzae* ranges. In addition, the proposed males cannot represent females of *D. nyanzae* because they have canines indicative of males.

Another fact may be used to prove that the proposed males do not belong in *D. nyanzae*. If one was to consider specimens R 394 and 1, CMH 1 as females of *D. nyanzae* because of their very small dentitions one would also have to explain why the horizontal rami of these specimens are generally larger in breadth and height (taken at the fourth premolar and third molar) than other *D. nyanzae* mandibles with appreciably larger dentitions (Table 6). Certainly, one would not expect females of a pongid species, with very small dentitions, to have the largest mandibles.

There is yet another metric distinction between *D. africanus* and *D. nyanzae* specimens. It has been noted that first molars are markedly smaller than second molars in *D. nyanzae* (LE GROS CLARK & LEAKEY, 1951), while in *D. africanus*, first and second molars are relatively closer in size. A ratio of the mesiodistal length of the first molar to the mesiodistal length of the second molar has been used to express this relationship. A ratio is calculated for each specimen with first and second molars. I calculated ratios for *D. africanus* specimens, the proposed males, and *D. nyanzae* specimens. According to my thesis, values for the proposed males should be closer to *D. africanus* values than to *D. nyanzae* values. Maxillary ratios for the proposed males were 84.0, 88.5, and 87.0 (specimens 155,712, KNM-SO 700, and 14084 respectively) while *D. africanus* specimens produced a range of 87.0–97.4 (n=6). The remaining *D. nyanzae* specimens ranged between 72.3 and 77.4 (n=2). The man-

Table 6. Mandibular height and thickness at P₄ and M₃ for proposed males of *D. africanus* and *D. nyanzae* specimens.*

Proposed Males					
P ₄			M ₃		
specimen	height	thickness	height	thickness	
R 394	34.0	13.5	29.0?	17.0?	
1, CMH 1	33.2	15.7	33.5	20.0	
<i>D. nyanzae</i>					
P ₄			M ₃		
specimen	height	thickness	height	thickness	
562,1145	30.0	12.0	28.0	16.0	
6, CMH 5	27.5	15.5	23.4	15.9	

*All measurements in millimeters.

Table 7. Ratios of mesiodistal lengths (M_1/M_2) in *D. africanus* and *D. nyanzae*.

<i>D. africanus</i> *					
Maxilla			Mandible		
n	\bar{x}	range	n	\bar{x}	range
8	89.4	84.0–97.4	9	84.2	80.0–89.9
<i>D. nyanzae</i>					
Maxilla			Mandible		
n	\bar{x}	range	n	\bar{x}	range
2	74.9	72.3–77.4	3	76.5	75.4–77.1

*Includes proposed males.

dibular ratios for the proposed males were within the range for *D. africanus* specimens and outside the range for the remaining *D. nyanzae* specimens. *D. africanus* specimens had a range of 80.0–89.9 ($n=7$), the proposed males had values of 82.3 and 82.7 (specimens 1, CMH 1, and R394 respectively), and *D. nyanzae* specimens had a range of 75.4–77.1 ($n=3$). New ranges for both taxa (with the proposed males included in *D. africanus*) are listed in Table 7.

The old ranges between *D. africanus* and *D. nyanzae* overlapped because many of the proposed males (that belong in *D. africanus*) were classified within *D. nyanzae*. Thus the metric distinction (of first molar size relative to second molar size) noted by LE GROS CLARK and LEAKEY (1951), between these two taxa, was not a valid one (until now) because it did not separate *all* the specimens. Proper classification of the proposed males does make it (for the present) a valid metric distinction between *D. africanus* and *D. nyanzae*.

As I mentioned previously, specimen 166,993 (Fig. 7), the left maxilla of an immature individual, should also be transferred from *D. nyanzae* to *D. africanus*. The first and second permanent molars of this specimen can be seen and measured. Metrically, the first molar (area is 88.2 mm²) falls within the new *D. africanus* range, while the second molar (area is 116.4 mm²) falls at the upper extreme of the *D. africanus* range (the next largest second molar belongs to specimen 155,712 and has an area of 116.0 mm²). In addition, the ratio of the mesiodistal length of the first molar to the mesiodistal length of the second molar is 87.4, which is within the range of variation for *D. africanus* specimens (Table 7). For these two reasons, I would include this specimen in *D. africanus*. A determination of the sex of this specimen is not possible with any certainty. However its large molars, relative to molars of other *D. africanus* specimens, indicate that it may have been a male.

I also mentioned earlier that specimen SGR 276 (Fig. 5) should be transferred to *D. africanus*. This specimen, the symphyseal portion of a mandible, has a striking resemblance to the symphyseal portions of specimens R 394 and 1, CMH 1. At the third premolar SGR 276 is about 33.5 mm deep and 14.0 mm? thick. These measurements are similar to the proportions for R 394 and 1, CMH 1. I calculated a value of .46 for the ratio of the symphyseal thickness to the symphyseal length. Ratio values for R 394 and 1, CMH 1 are .46 and .43 respectively. In addition, the symphyses of all three mandibles are similarly constructed. They have rounded chin contours and small superior transverse tori. The canines of these three specimens are similar in

size. The area of the canine (only the base of it remains) of SGR 276 is 96.0 mm² and the canines of R 394 and 1,CMH 1 are 91.0 mm² and 94.0 mm² respectively. These similarities favor placement of SGR 276 in *D. africanus*. I think we should also consider it as a male of this species because its canines are large, its third premolar was probably elongate (the crown of this tooth is missing), and its absolute size relative to the other mandibles of the proposed males and females of *D. africanus* (to be discussed later) indicates that it is a male.

SEXUAL DIMORPHISM IN *Dryopithecus africanus*

Thus far I have assumed that the specimens classified within *D. africanus* prior to this paper (except maxilla 14084) represent females of this species. Certainly, I have not assumed a sex for isolated teeth (except some of the canines). There are several criteria for determining whether a specimen represents a female. The most convincing is the presence of small, non-projecting canines. Small, non-elongate lower third premolars are also indicative of females. Mandibular specimens classified in *D. africanus*, with small canines and/or small lower third premolars, have small horizontal rami (thickness and height), when compared to the proposed males. The proposed males, with large projecting canines and elongate lower third premolars, have taller and thicker horizontal rami. I think it is reasonable to hypothesize that the absolute differences in mandible size reflects sexual differences within this species. Thus individuals with small rami are females and those with large rami are males. Table 8 lists measurements for the rami of the proposed males and females, and indicates which specimens have additional evidence (lower canines and/or lower third premolars) to support the assigned sex. Two of the mandibles listed (1948,50 and 1,CMH 1), one female, the other male, have ascending rami. Measurements taken on the left sides of both specimens are compared below. Despite absolute differences in size, the relative proportions of these two mandibles are very similar (Fig. 12). The ascending rami of both specimens project posteriorly at approximately 70 degree angles. I estimate their bicondylar breadths to be 75.0 mm and 110.0 mm (1948,50 and 1, CMH 1 respectively). Inferred from the bicondylar breadths, basal skull breadths for these two specimens (from the left mandibular fossa to the right mandibular fossa) would reflect a difference of similar magnitude. Including mandibular height and thickness, the male appears to be about 50 percent larger than the female. However, it cannot be overemphasized that I am dealing with two specimens and not many inferences concerning dimorphism in this species can be made at this time. One can say, for the mandibular features just mentioned, that males can be 50 percent larger than females, and probably, the average differences are less because 1948,50 is one of the smaller female specimens. In Table 8, for example, specimen 1,CMH 1 is only 30 to 35 percent larger than specimen 140,599 for mandibular height and thickness. With increasing samples, I feel we will undoubtedly find smaller males and larger females. In the meantime, it is interesting to note that in the samples presented here, there is no overlap in the variation in mandible size between the sexes. Therefore, absolute mandible size may be used as a criterion for sexing.

The mandibular symphyses of the males and females are built similarly. As mentioned earlier, the symphyseal ratio (symphyseal thickness divided by symphyseal

Table 8. Mandibular height and thickness at P₄ and M₃ for *D. africanus* specimens.⁺⁺

Specimen	P ₄		M ₃	
	Height	Thickness	Height	Thickness
58,CMH 129	—	—	19.6	15.0
262,235	22.0	10.0	—	—
8,CMH 8	23.3	10.5	21.7	11.6
573,1558 ⁺	19.5	11.0	—	—
140,599 ⁺	25.5	11.6	—	—
1948,50 ⁺	20.0	10.0	20.0?	10.0?
640,417 ⁺	22.0	11.0	—	—
91,D9	22.5	10.4	—	—
113,F 3104	—	—	17.5	12.0
380,1	27.0	12.0	22.0	14.4
381,2	15.0?	—	—	—
1,CMH 1 ⁺⁺	33.2	15.7	33.5	20.0
R 394 ⁺⁺	34.0	13.5	29.0?	17.0?
SGR 276 ⁺⁺	33.5?	14.0?	—	—

⁺⁺All measurements in millimeters. ⁺Additional evidence (either canine size and/or lower third premolar size) supports the assigned sex. ^{*}Proposed male, all unstarred specimens are females.

height) for three males of *D. africanus* ranged between .43 and .46. The male indices all fall within the female range which is .40–.49, with a sample size of six (P. ANDREWS, Pers. Comm.). Both males and females have rounded chin contours, and small superior transverse tori. There is only a difference in absolute size, between males and females, for this feature.

The mandibular dentitions of the females are also, as expected, smaller. Table 9 lists tooth area statistics for those specimens I have recognized as male or female. Isolated teeth (except most of the canines) have not been incorporated into the ranges for either sex. Incisors are known only for females, and therefore, measurements for these teeth have been left out of the table. Male and female ranges overlap entirely for first and second mandibular molars. Ranges for the other teeth will overlap when the samples become larger. In fact, many isolated teeth, excluded from the table, fall between the male and female ranges.

Because they are small (all are smaller than the canines of specimen 1948,50 which has the largest female canines), the following canines have been included in the female range; 134,465; 131,342; 147,645; 637,260; 90,D4; and 196,16. Measurements for these canines can be found in PILBEAM (1969).

Mandible 35,CMH 102 (a female) was not listed in Table 8, because the inferior portions of the rami are missing. This individual probably had relatively small canines, by inference from the canine sockets. The measurements taken at these

Table 9. Ranges of mandibular tooth areas for *D. africanus* specimens.⁺

Tooth	Females			Males		
	n	\bar{x}	Range	n	\bar{x}	Range
C ₁	11	54.9	37.8–60.9	3	93.7	91.0– 96.0
P ₃	4	47.1	38.4–55.8	2	62.7	57.9– 67.6
P ₄	4	38.7	30.0–45.4	2	54.0	50.3– 57.7
M ₁	7	58.4	48.0–68.5	2	64.3	63.1– 65.5
M ₂	6	80.6	67.5–92.7	2	91.4	91.0– 91.8
M ₃	3	100.3	97.9–103.5	2	111.5	109.0–114.0

⁺All measurements in millimeters².

sockets are probably not appreciably smaller than what the actual canine measurements would have been. Even if the canines were 50 percent larger than what the sockets indicate, the relative canine size index would still be less than 100.0, a value not unexpected for females. In addition, the mandibular thickness at the fourth premolar falls within the range for females.

Specimen 51,1499 (DAVIS & NAPIER, 1963) is a difficult specimen to evaluate. The mandible (of this immature individual) has an unerupted third molar, and I feel that the canines (listed by PILBEAM, 1969 as permanent canines) may be deciduous. If they are permanent, there is no question that this specimen is a female. The relative canine size index is 86.3, which is an expected female value. The mandibular rami are small, but it is impossible to say how much larger they could have been (at maturity). Lastly, the third premolar is rather elongate (more male-like in morphology). For the present, I have treated this specimen as a female. I will discuss its associated maxilla later.

Dimorphism for most cranial features are impossible to quantify at present. The one complete female palate (specimen 1948,50) is badly crushed (Fig. 8b), and the only male palate (specimen KNM-SO 700) represents a subadult (the canines are not fully erupted). More cranial material is needed before any statements can be made.

Table 10 lists maxillary tooth area statistics for the specimens I have recognized as male or female. My decisions were based solely on canine size. Isolated teeth have not been incorporated in the table and comparative incisor measurements were not available. The female dentitions are, on the average, smaller than the male dentitions. However, the canine an exception, there is overlap in the range for all posterior teeth.

Table 10. Ranges of maxillary tooth areas for *D. africanus* specimens.*

Tooth	Females			Males		
	n	\bar{x}	Range	n	\bar{x}	Range
C ₁	8	67.1	50.4-85.3	2	102.4	99.2-105.6
P ₃	2	48.9	39.5-58.3	3	55.4	48.1- 59.9
P ₄	3	46.0	35.2-55.6	3	55.2	48.0- 63.8
M ¹	3	73.3	62.9-78.7	4	81.9	68.9- 90.7
M ²	2	95.3	89.4-101.2	4	108.7	96.0-116.4
M ³	1	98.1	89.1	3	108.0	86.9-128.0

*All measurements in millimeters².

Isolated canines, smaller than the canines of specimen 1948,50 (female), have been included in the female range for maxillary canines. The specimens included are as follows; 593,1988; 686,313; 131,342; 507,94; 557,1040; and 201,45.

Maxillary specimen 51,1499 (Fig. 12) was included as a female. This specimen has a fairly large canine socket. The relative canine size index (using the measurements from the socket) is just above 100.0, a female value. The actual canine could have been considerably larger than the socket indicates. An x-ray of the associated mandible is necessary (to see if there is an unerupted permanent canine) to determine this individual's sex with certainty.

Unfortunately, comparative postcranial evidence is lacking, and thus body size dimorphism cannot be estimated. However, I would not be surprised if the males were considerably larger than the females.

Table 11. Tooth measurements for the proposed males.*

Maxilla				
	155,712	KNM-SO 700	166,993	14084
C ¹ (L)	—	12.4	—	11.6
(B)	—	8.0	—	9.1
P ³ (L)	5.7	5.8	—	6.0
(B)	10.5	8.3	—	9.7
P ⁴ (L)	5.8	6.0	—	5.8
(B)	11.0	8.0	—	9.3
M ¹ (L)	8.4	8.5	9.0	8.0
(B)	10.8	8.1	9.8	10.0
M ² (L)	10.0	9.6	10.3	9.2
(B)	11.6	10.0	11.3	11.5
M ³ (L)	10.0	10.3	—	8.2
(B)	12.8	10.7	—	10.6
Mandible				
	1, CMH 1	R 394	SGR 276	
C ₁ (L)	10.8	11.1	12.1	
(B)	8.7	8.2	8.0	
P ₃ (L)	8.9	10.0	—	
(B)	6.5	6.7	—	
P ₄ (L)	7.4	6.5	—	
(B)	7.8	7.3	—	
M ₁ (L)	8.4	8.5	—	
(B)	7.8	8.0	—	
M ₂ (L)	10.2	9.7	—	
(B)	9.0	9.3	—	
M ₃ (L)	11.6	11.4	—	
(B)	9.4	9.9	—	

*All measurements in millimeters.

CONCLUSIONS

In this paper, a more precise metric distinction between *D. nyanzae* and *D. africanus* has been established. Models have been devised to provide guidelines for determining the sex of specimens within *D. africanus*. A subsequent description of the sexual dimorphism within this species has been attempted.

I think the immediate importance of this paper to the study of fossil primates should be made explicit. We must appreciate the sexual variation within modern primate species, and apply models, derived from this variation, to fossil primates. Often, we make interspecific comparisons between fossil primate species to determine phylogenies or differences in adaptation. To do this, we must control variables such as sex. Only then, can the inferences we make, between these species, be valid.

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