Some Aspects of the Evolution of Early Hominid Sexual Dimorphism[1]

by Milford H. Wolpoff

INTRODUCTION

The evolution of sexual dimorphism has only recently come to be of concern in broad reconstructions of human evolution (Brace 1973). The extent of the existing fossil record and the large available body of knowledge regarding the behavior of living nonhuman primates suggest that an understanding of this phenomenon is of critical importance, both for its own sake and as a possible explanation for the marked individual variability that seems to characterize almost every known fossil hominid site with more than one individual (Wolpoff 1976).

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The present paper, submitted in final form 2 II 76, was sent for comment to 50 scholars. The responses are printed below and are followed by a reply by the author.

Understanding the evolution of sexual dimorphism must begin with a determination of the amount of dimorphism at various stages of human evolution. The purpose of this work is to establish the degree of sexual dimorphism in the earliest clearly recognized hominids, the australopithecines, to place this determination in an evolutionary context with respect to the general trends in the pongid and hominid lineages, and to offer a selective explanation for these trends.

The question of sexual dimorphism is of considerable potential importance in any attempt to reconstruct the ecology, behavior, or phylogeny of the australopithecines. Establishing dimorphism depends on determining sex. Sexes were ascribed individually to many of the specimens in initial descriptions (Broom and Robinson 1952; Broom, Robinson, and Schepers 1950; Broom and Schepers 1946; Dart 1949a, b, 1962; Leakey 1972). Many specimens, however, remain unsexed, and moreover the sex designations for some specimens have changed as the result of new discoveries. My intentions are to establish a single uniform procedure for determining sex, ascertain its accuracy, determine whether any other criteria can be used, and then place the observed sexual dimorphism of the australopithecines in an evolutionary context.

All of the australopithecines will be discussed here. They will be treated separately in four groups and together as a single temporal sample. The four groups are South African graciles, South African robusts, East African "Homo," and East African robusts. These correspond to commonly recognized taxa. Their treatment as separate sets is in no way meant to prejudice the taxonomic level of distinction (e.g., subspecific, specific, generic, etc.), nor is it meant to imply that distinctions between them are at the same level. Designations of particular specimens follow common literature usage. The use of "australopithecine" as a convenient title for the combined temporal sample is not meant to imply the taxonomic unity of the sample at any particular level, although I would place all of these specimens in the genus *Australopithecus* (Wolpoff and Lovejoy 1975).

DETERMINING SEX

Once sex has been established, sexual dimorphism can be observed and quantified in many characteristics of both cranial and postcranial skeletons. Conversely, if sex is unknown, these characteristics may be useful in determining it. In *Homo*, the most accurate sexing criteria are in the pelvis (Krogman 1962). Of these, features of the os pubis are reported to yield unusual accuracy (Phenice 1969). My observations on

material of known sex from the Hamann-Todd collection confirm this. Unfortunately, only one published australopithecine skeleton may be sexed from the os pubis. In STS 14r, the ventral arc is very well defined, the neck of the pubic symphysis is narrow, the subpubic angle is broad, and the inferior surface of the ramus is concave. In all features STS 14r is female. Unfortunately, no cranial or dental material is associated with this skeleton, and in fact there is no associated cranial or dental material with any of the sexable australopithecine innominates which have been published. Consequently, it is necessary to turn to another means of determining sex for most of the hominid sample.

Because dental remains of the australopithecines outnumber all other remains combined, it is useful to attempt determination of sex from the dentition alone. This approach was first attempted by Robinson (1956) in his treatment of the then-known South African australopithecine teeth. He noted distinct bimodal distributions for the breadth of the maxillary canines and the mandibular first molars from Swartkrans and attributed these to sexual dimorphism.

In the nonhuman higher primates, sexual dimorphism is generally greatest in the canine (Freedman 1957, Lauer 1975, Schuman and Brace 1954, Orlosky, Swindler, and McCoy-Beck 1974). In taxa such as *Alouatta* (Zingeser 1967), canine dimorphism is exceeded by that of the lower first premolar, but because P_3 is part of the canine growth field and is functionally integrated with C^1 in the nonhuman primates this seems not to contradict the general observation.

In most modern human studies, the canine shows the greatest sexual dimorphism (Gonda 1959). Several studies indicate that dimorphism is greater in breadth than it is in length (Mijsberg 1931; Garn, Lewis, and Kerewsky 1964, 1966a, b). This may be the result of greater environmental influence on the population distribution of length because of interproximal wear (Wolpoff 1971b). Other evidence, based on brother-sister pairs, demonstrates genetic control for tooth-size sexual dimorphism (Garn et al. 1967). Variation indicates that there is a canine field of sexual dimorphism and some degree of relationship between dimorphism in tooth size and dimorphism in body size (Garn, Lewis, and Kerewsky 1966b, Garn et al. 1967). Taken together, these studies suggest that the greatest differences in the dentition due to sexual dimorphism can be expected in the breadth of the canine, that these differences have a significant amount of genetic control or heritability

(Alvesalo and Tigerstedt 1974), and that they bear some relation to sexual dimorphism in other characteristics of the body.

Not all studies of *Homo* population tooth breadth show the greatest sexual dimorphism in the canine. Indeed, one of Garn's studies of "Ohio whites" leaves the lower canine with the least dimorphism of any mandibular tooth. When considered on the species level, however, there is no ambiguity in determining the best dental correlate for sexual dimorphism in *H. sapiens*. Table 1 indicates sexual dimorphism in tooth breadth for eight human groups. The average sexual dimorphism values calculated for the eight human populations clearly show that the canine is the most dimorphic tooth for the species as a whole.

Indeed, a recent attempt to develop discriminant functions for sexing based on tooth dimensions (Ditch and Rose 1972) uses canine breadth in all six functions reported. Neither canine length nor length or breadth of any other tooth is used in all six functions. Apparently, canine breadth is also the most important single measurement in discrimination.

In sum, it appears that canine breadth is the best single dental indicator of sex for a wide range of primates. Consequently, one would expect it to be the best dental indicator for australopithecines and the best vehicle for studying sexual dimorphism.

Canine breadth is measured as the maximum labial-lingual diameter perpendicular to the medial-distal axis of the tooth. The corresponding measurement for the nonhuman primates is entirely homologous and analogous. There are several coincidental advantages in using this measurement. Maximum breadth is inevitably in the cervical region, in spite of the wide range of morphological variation in human canines (Taylor 1969). Thus, the breadth measurement is unaffected by even the most extreme occlusal wear. In addition, breadth of the root below the cervical region closely corresponds to crown breadth. Consequently, one would expect a close relationship between canine breadth and canine socket breadth. This expectation was tested for the australopithecine sample by measuring canine sockets as well as canines whenever possible. Calculation revealed that the correlation of socket to tooth breadth was 0.96, and the regression slope was not significantly different from 1.00. Therefore, it is possible to use socket breadth to estimate tooth breadth with a high degree of accuracy. Following this procedure greatly expanded the available sample.

TABLE 1

BREADTH SEXUAL DIMORPHISM FOR INDIVIDUAL TEETH IN EIGHT HUMAN GROUPS

TOOTH	ALEUTS	AUSTRALIAN ABORIGINES	JAPANESE	JAVANESE	LAPPS	LIBBEN AMERINDS	"OHIO WHITES"	TRISTANITES	AVERAGE
I^1	–	6.0	0.0	7.2	4.9	3.4	4.6	–	4.4
I^2	–	5.8	3.1	6.3	2.8	5.6	7.4	–	5.2
C^1	3.9	5.2	6.3	9.0	6.6	6.7	6.1	5.7	6.2
P^3	1.4	2.8	2.2	4.3	3.1	4.9	5.9	1.8	3.3
P^4	1.1	2.4	2.2	5.4	3.0	4.3	6.5	1.3	3.3
M^1	1.2	3.4	3.6	5.4	4.7	3.9	5.8	3.1	3.9
M^2	0.7	3.3	6.4	7.3	6.8	6.5	6.5	3.0	5.1
M^3	0.6	1.3	8.0	4.7	5.5	6.2	–	5.5	4.5
I_1	–	6.7	3.5	7.3	4.4	1.8	3.6	–	4.6
I_2	–	5.7	1.6	5.0	4.7	1.6	3.6	–	3.7
C_1	4.6	4.5	5.5	9.7	8.6	10.0	2.3	6.2	6.4
P_3	3.2	1.6	1.3	6.5	3.6	4.6	6.0	1.4	3.5
P_4	3.2	2.3	3.7	3.7	3.2	4.1	5.8	0.5	3.3
M_1	3.4	3.6	0.9	2.8	3.5	4.0	4.1	1.3	3.0
M_2	2.8	2.7	2.9	2.9	4.7	4.5	11.0	2.0	4.2
M_3	2.6	2.2	4.2	2.0	3.5	4.4	–	4.3	2.6

SOURCES: Aleuts, Moorrees (1957); Australian Aborigines, Barrett et al. (1964); Japanese, Miyabara (1916); Javanese, Mijsberg (1931); Lapps, Selmer-Olsen (1949); "Ohio whites," Garn, Lewis, and Kerewsky (1966a); Tristanites, Thomsen (1955). The Libben Amerind teeth come from a collection at Kent State University and were measured by me.
NOTE: Dimorphism is expressed by the index (100 times the ratio) of male mean to female mean minus 100.

The individual canine-breadth dimensions for all the measurable australopithecine specimens are given in table 2. All measurements are my own except for STS 71, where the area of the socket had been ground and polished so that it was impossible to identify the original socket borders; in this case I used the published socket measurement (Broom, Robinson, and Schepers 1950). STS 3 is considered a maxillary canine, as it was originally described (Broom, Robinson, and Schepers 1950), contra later statements by Robinson (1956). The tooth is significantly larger than any other South African canine. The breadth measurement on the STS 5 socket was carefully checked by additional cleaning of the internal area. TM 1528 is considered maxillary, rather than mandibular as reported by Robinson (1956), because of the clear convexity and the lingual tubercle development in the cervical portion of the lingual face. SE 1937 was originally published as a mandibular canine (Robinson 1962); I believe it is maxillary because of the well-developed lingual tubercle. It closely matches the TM 1512 canine in both morphology and wear. The socket-breadth measurement for MLD 9 is a minimum estimate. SK 94 was originally described as a mandibular canine (Robinson 1956) and later changed to maxillary by Robinson in the Transvaal Museum catalog. I believe the tooth is mandibular, because there is no lingual tubercle development, the distal buccal groove is only weakly developed, and the wear angulation better matches that of known mandibular specimens.

Table 3 gives breadth measurements for all *H. erectus* canines. Neandertal canine breadths are given in table 4. "Neandertal" is used here in the loose sense of all early *H. sapiens* preceding the appearance of anatomically modern populations.

CANINE-BREADTH FREQUENCY DISTRIBUTIONS IN LIVING PRIMATES

As a basis for interpreting fossil hominid distributions, it is important to determine the canine-breadth frequency distributions for living primates of known sex. Data for *Pan gorilla* specimens of known sex are given in table 5 (see also figure 1). In both mandibular and maxillary canines, there is virtually no overlap between male and female distributions. The combined distributions are very clearly bimodal, and the separate modes represent sex to a high degree of accuracy. To determine accuracy, the combined distributions were split at the class of minimum frequency between the modes (13.0–13.9 mm for the maxillary canine, 12.0–12.9 mm for the mandibular), and the specimens within this class were split evenly between the larger and smaller mode. The means for each side of the divided distribution were then calculated and compared with the actual male and female means. For the maxillary canines, the male mean was overestimated by 0.2 mm using this procedure, but the female estimate was exact. For the

TABLE 2

CANINE BREADTH (MM) IN AUSTRALOPITHECINES

SOUTH AFRICAN		EAST AFRICAN	
Gracile	Robust	"Homo"	Robust
Maxillary			
STS 3........12.1	TM 1517[a]...... 9.4	OH 15........11.9	ER 816........ 9.5
STS 5[a]........ 8.9	SK 4.........10.6	OH 39......... 9.3	OH 5..........10.0
STS 17[a].......10.2	SK 12[a].......12.0	ER 803........ 9.0	OH 30......... 9.1
STS 48....... 9.5	SK 13[a]........ 8.0	ER 1470[a]......11.5	Chesowanja..... 8.5
STS 52....... 9.9	SK 27.........10.4	ER 1590.......12.7	
STS 53[a]....... 8.5	SK 38.........10.0		
STS 71[a].......10.0	SK 46[a]........10.0		
TM 1511[a].....11.0	SK 47[a]........ 8.6		
TM 1512...... 9.2	SK 48......... 9.2		
TM 1514[a]....10.2	SK 52[a].......10.1		
TM 1527...... 8.8	SK 55......... 9.4		
TM 1528...... 9.0	SK 65.........10.2		
SE 1937....... 9.0	SK 79[a]........ 8.9		
MLD 6[a]...... 8.3	SK 80[a]........ 9.4		
MLD 9[a]...... 9.0	SK 83.........10.5		
MLD 11/30...10.1	SK 85/93...... 9.4		
	SK 86......... 8.9		
	SK 95......... 8.4		
	SK 845.......11.4		
	SK 884........ 8.8		
	SK 1590....... 8.7		
Mandibular			
STS 7........11.0	TM 1517....... 8.8	OH 7.......... 9.8	ER 729........10.1
STS 36.......10.5	SK 23......... 8.0	OH 13......... 7.4	ER 802........ 9.1
STS 50....... 9.8	SK 29......... 8.5	OH 16.........10.1	ER 810[a].......10.0
STS 51....... 9.2	SK 34......... 8.8	OH 37[a]........ 9.4	ER 818[a].......10.9
STS 52.......10.2	SK 74[a]........ 9.2	ER 730[a]....... 8.2	OH 30......... 7.7
MLD 18...... 8.9	SK 87......... 9.4	ER 992........ 9.2	Omo L7.......10.0
MLD 27[a]..... 9.0	SK 94......... 8.5	ER 1482[a]...... 8.8	Omo L74...... 9.1
MLD 40...... 9.1	SK 858........ 8.0	ER 1483[a]......11.4	Omo L58[a].....10.5
	SK 876........10.8	ER 1501[a]...... 9.4	Natron........ 8.4
	SK 1596.......10.1		

NOTE: Breadth measurements could not be taken for STS 2, SK 92, and SK 96. MLD 13 does not seem to be hominid; the preserved root height is 32 mm and the dimensions at the distal break show little evidence of significant tapering. Of two additional canines listed by Robinson (1956), one, SK 84, shares its identifying number with a metacarpal; it is SK 845. The other, SK 820, does not appear in the Transvaal Museum catalog; it is unerupted and not completely formed.

[a] Breadth of canine socket is used as estimate.

TABLE 3

Canine Breadth (mm) in *Homo erectus*

Maxillary		Mandibular	
OH 11[a]	10.6	OH 22[a]	9.4
Sangiran 4	11.9	Sangiran 1[a]	9.6
Sangiran 17	8.4	Sangiran 7	11.0
Peking		Sangiran 8[a]	8.3
C1	9.9	Sangiran 9	8.9
D2	9.8	Lantian	9.2
F4	10.4	Peking	
H4	8.2	AN 16	9.0
L1	10.6	B1	8.2
L2	9.8	B5	9.5
O1[a]	9.5	C2	10.4
Ternifine	10.0	G1	10.1
Rabat	10.0	H1	8.7
Thomas Quarry	9.9	H4	8.2
		I1	8.7
		K1	9.3
		Ternifine 1[a]	10.0
		Ternifine 2[a]	11.0
		Ternifine 3	10.7
		Mauer	8.5
		Rabat	9.5
		Casablanca	9.0

SOURCES: Sangiran 17, Sartono (1971); Thomas Quarry, Ennouchi (1972); Ternifine, Arambourg (1963). I measured the Olduvai specimens. The sources for all the remaining specimens are listed in Wolpoff (1971a).
[a] Breadth of socket is used as estimate. The measurement for Sangiran 1 was taken from the Wenner-Gren cast; accuracy appears great, because measurements of the cheek teeth on this cast come within 1% of the published measurements for the specimen.

mandibular canines, both male and female means were overestimated, by 0.2 and 0.1 mm respectively.

Data for *P. troglodytes* of known sex are presented in table 6 (see also figure 2). The mandibular combined sample is bimodal both in the table and in the figure, which has twice as many classes. The maxillary sample is less strongly bimodal; the figure shows the separate modes, but the table does not. For both maxillary and mandibular canines, the modes are separated by a gap of lesser, but not particularly low, frequency. If the mandibular distribution is split at the class of minimum frequency between the modes, following the procedure just described, the estimated means are surprisingly accurate. The known male mean is overestimated by 0.4 mm; the female mean estimate is exact. When this procedure is followed for the maxillary distribution, both male and female means are overestimated by 0.1 mm. This accuracy is particularly interesting in light of the extensive overlap between male and female distributions in both jaws. Analysis of both African pongid distributions suggests that when bimodality is present, division of the modes accurately estimates male and female *means*, even though the distributions may overlap.

Data for *H. sapiens* are presented in table 7 (see also figure 3). The Libben Amerinds were chosen to exemplify *Homo* because they represent a preindustrial biological population with a large number of associated pelves and crania. In all cases, sex designation was based on the pelvis, and whenever possible characteristics of the os pubis (Phenice 1969) were used. Each individual was sexed independently by C. O. Lovejoy and by me, and the few specimens for which agreement could not be reached on the basis of the pelvis were disregarded. In all cases these were individuals without a pubis. All canines were measured by me, and no socket measurements were used. Male and female distributions are clearly different. The modal frequencies for each are close enough together, however, that the combined distribution is unimodal. Individual sexes could not be ascertained on the basis of the combined distributions alone. Comparison with the few other studies that present

male and female distributions separately (Miyabara 1916, Selmer-Olsen 1949) indicates that the unimodal combined distribution based on distinct male and female distributions is the usual condition for *H. sapiens* populations. (It is interesting that gibbons, with a sex ratio within the range of *Homo* population means [see table 10], distribute exactly the same way.)

As samples of the three living taxa most closely related to the australopithecines, the distributions just discussed are of particular relevance in interpreting the australopithecine canine-breadth frequency distribution. They do not present

TABLE 4

Canine Breadth (mm) in Neandertals

Maxillary		Mandibular	
Krapina		Krapina	
46/47	10.6	E	9.8
E	9.6	H	9.1
86.1.1	10.0	I	11.5
86.1.2	9.9	D	8.7
86.1.3	9.6	86.2.2	8.4
86.2.1	10.3	86.2.3	9.9
91.1	11.4	91.11	9.8
91.2	10.6	91.12	9.4
91.3	9.6	91.16	10.1
91.4	9.4	Amud 1	8.5
91.5	11.2	Arcy-sur-Cure 2	9.5
91.6	10.3	Circeo 3	8.9
91.7	10.1	Ehringsdorf child	8.5
91.8	10.2	Ehringsdorf adult	8.8
91.9	10.8	Hortus 2	7.5
91.10	10.0	Hortus 6	7.5
91.13	9.9	Jersey	10.0
91.14	10.1	Lazaret	9.4
91.15	8.8	La Ferrassie	9.9
Africanthropus	9.0	La Quina	9.0
Amud 1	9.5	Le Moustier	9.5
Arcy-sur-Cure 3	9.9	Monsempron b	9.0
Broken Hill	10.9	Ochoz	9.8
Croze del Dua	8.6	Petralona 4	9.0
Jebel Irhoud 2	10.0	Régourdou	10.0
Kůlna	9.6	Shanidar 2	9.6
La Ferrassie	11.2	Skhūl 2	8.4
La Quina 5	10.0	Skhūl 4	8.0
Le Moustier	10.0	Skhūl 5	8.5
Monsempron h	9.5	Skhūl 10	7.0
Omo 1	8.1	Spy 1	8.3
Petralona 1	9.1	Spy 2	8.8
Petralona 2	10.0	Subalyuk	9.9
Petralona 3	10.0	Tabūn 1	8.3
Qafzeh 6	10.0	Tabūn 2	9.0
Qafzeh 7	10.0	Šipka	7.0
Qafzeh 8	10.2		
Saccopastore 2	9.2		
Shanidar 1	10.7		
Shanidar 2	8.5		
Shanidar 4	10.0		
Skhūl 1	8.0		
Skhūl 4	8.5		
Skhūl 5	9.5		
Skhūl 6	9.6		
Spy 1	9.0		
Spy 2	10.0		
Tabūn 1	8.8		
Tabūn B	9.0		
Tangier	10.7		

SOURCES: All the Krapina canines were measured by C. L. Brace, and these measurements are used here with his permission. The Amud canines were published by Suzuki and Takai (1970), Hortus and Lazaret by De Lumley and Piveteau (1969), Omo by Day (Leakey, Butzer, and Day 1969), Kůlna by Jelínek (1967), Petralona by Kannelis and Savas (1964), and Qafzeh by Vallois and Vandermeersch (1972). I measured the canines of Skhūl 5, Skūhl 6, Tabūn B, and Tangier. The remaining measurements are from sources listed in Twiesselmann (1973) and Wolpoff (1971a).

TABLE 5

FREQUENCY DISTRIBUTION OF CANINE BREADTHS (MM) IN
ABSOLUTE NUMBERS OF A *Pan gorilla* SAMPLE

CANINE BREADTH	MAXILLARY			MANDIBULAR		
	Female	Male	Both	Female	Male	Both
8.0–8.9.........	–	–	–	1	–	1
9.0–9.9.........	1	–	1	14	–	14
10.0–10.9........	15	–	15	27	–	27
11.0–11.9........	21	–	21	7	–	7
12.0–12.9........	11	–	11	1	3	4
13.0–13.9........	2	1	3	–	13	13
14.0–14.9........	–	8	8	–	17	17
15.0–15.9........	–	12	12	–	12	12
16.0–16.9........	–	15	15	–	3	3
17.0–17.9........	–	8	8	–	1	1
18.0–18.9........	–	4	4	–	1	1
19.0–19.9........	–	1	1	–	–	–
20.0–20.9	–	1	1	–	–	–
Total........			100			100

SOURCE: Data set measured by me and by P. Mahler (see Mahler 1973) at the American Museum and the Cleveland Museum of Natural History. No mountain gorillas were included in the sample.
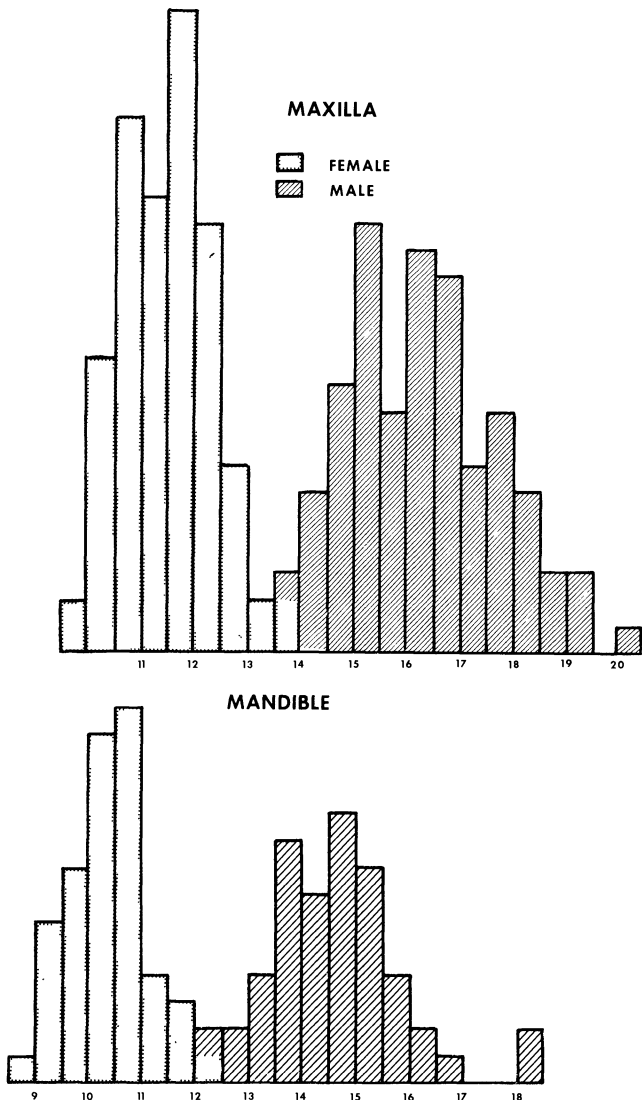

FIG. 1. Frequency distribution of maxillary and mandibular canine breadths (in mm) for a *Pan gorilla* sample (see table 5).
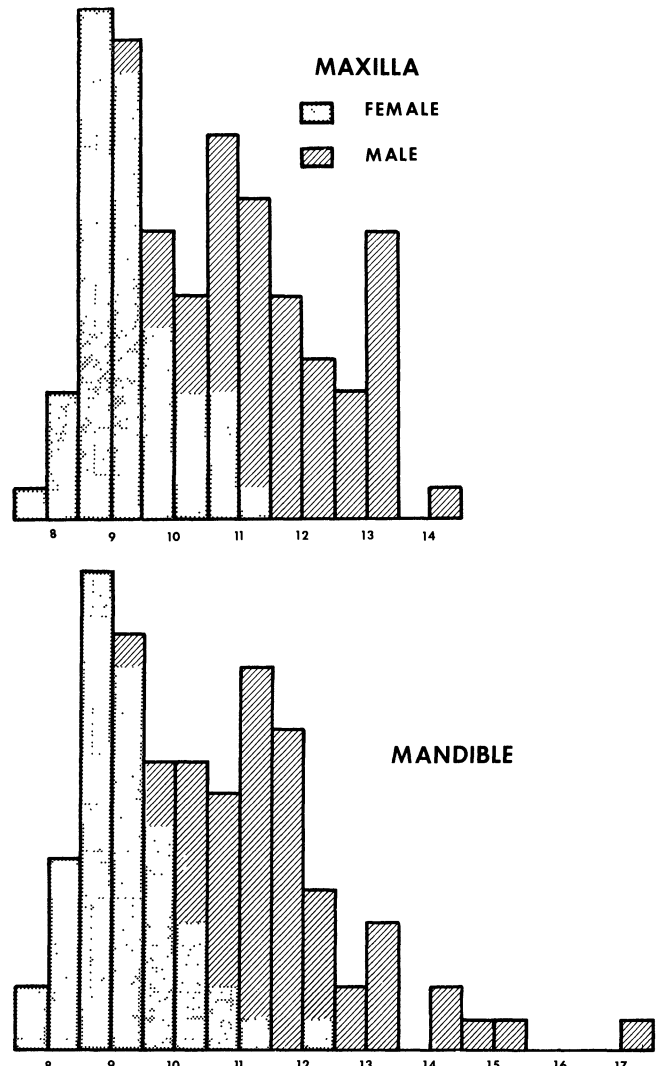

FIG. 2. Frequency distribution of maxillary and mandibular canine breadths (in mm) for a *P. troglodytes* sample (see table 6).

TABLE 6

FREQUENCY DISTRIBUTION OF CANINE BREADTHS (MM) IN ABSOLUTE NUMBERS OF A *P. troglodytes* SAMPLE

CANINE BREADTH	MAXILLARY			MANDIBULAR		
	Female	Male	Both	Female	Male	Both
7.0–7.9.........	1	–	1	2	–	2
8.0–8.9.........	20	–	20	21	–	21
9.0–9.9.........	20	4	24	19	3	22
10.0–10.9.......	8	11	19	6	11	17
11.0–11.9.......	1	16	17	2	21	23
12.0–12.9.......	–	9	9	0	6	6
13.0–13.9.......	–	9	9	–	4	4
14.0–14.9.......	–	1	1	–	3	3
15.0–15.9.......	–	–	–	–	1	1
16.0–16.9.......	–	–	–	–	–	–
17.0–17.9.......	–	–	–	–	1	1
Total........			100			100

SOURCE: Data set measured by me and by P. Mahler (see Mahler 1973) at the American Museum and the Cleveland Museum of Natural History and Liberian chimpanzee specimens from the Museum of Comparative Zoology measured by C. L. Brace (Schuman and Brace 1954). No pygmy chimpanzees were included in the sample.

TABLE 7

FREQUENCY DISTRIBUTION OF CANINE BREADTHS (MM) IN ABSOLUTE NUMBERS FOR A *Homo sapiens* SAMPLE

CANINE BREADTH	MAXILLARY			MANDIBULAR		
	Female	Male	Both	Female	Male	Both
6.0–6.4...........	–	–	–	–	–	–
6.5–6.9...........	–	–	–	2	–	–
7.0–7.4...........	1	–	1	8	2	2
7.5–7.9...........	10	1	11	10	6	10
8.0–8.4...........	13	6	19	3	12	16
8.5–8.9...........	8	19	27	–	6	15
9.0–9.4...........	1	12	13	–	5	5
9.5–9.9...........	–	4	4	–	1	5
10.0–10.4.........	–	1	1	–	–	1
10.5–10.9.........	–	–	–	–	–	–
Total.........			76			54

SOURCE: Libben Amerind data set measured by me at Kent State University.
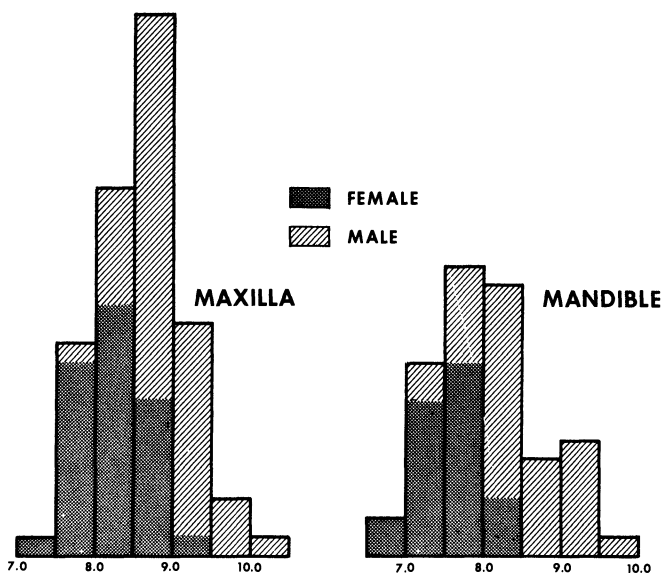

FIG. 3. Frequency distribution of maxillary and mandibular canine breadths (in mm) for a *H. sapiens* sample (see table 7).

three separate and distinct models of sexual dimorphism. Rather, they fall on a continuum, with *P. gorilla* at one end and *H. sapiens* at the other. Neither extreme is unique among the higher primates. The amount of sexual dimorphism in baboons exceeds that in gorillas (Lauer 1975), while the gibbon dimorphism closely approximates that of living humans. By itself, the variation of sexual dimorphism in the living hominoid species allows no prediction as to that in the fossil hominids. Therefore, it is necessary to turn to their actual frequency distributions.

HOMINID CANINE-BREADTH FREQUENCY DISTRIBUTIONS

Table 8 gives the frequency distributions of maxillary and mandibular canine breadths for the three fossil hominid groups examined and for living people. In both jaws, the fairly large Neandertal sample is clearly unimodal and is different from *H. sapiens* only in average breadth (fig. 4). The *H. erectus* sample, although considerably smaller in number, also appears unimodal (fig. 5). In both maxilla and mandible, however, *the australopithecine sample is bimodal* (fig. 6). In both jaws the modes are distinct and separate, with only a few specimens between them. The two distributions are almost completely independent of each other: only a few individuals have both a

mandibular and a maxillary canine. Table 9 breaks down the australopithecine distribution in terms of four subsamples. The South African gracile and robust samples are separately bimodal for the maxillary canine. The modes are in the same range, and the section point is the same. The East African sample is too small to show modality of any sort. The sample for mandibular canine breadth is 27% smaller than the maxil-
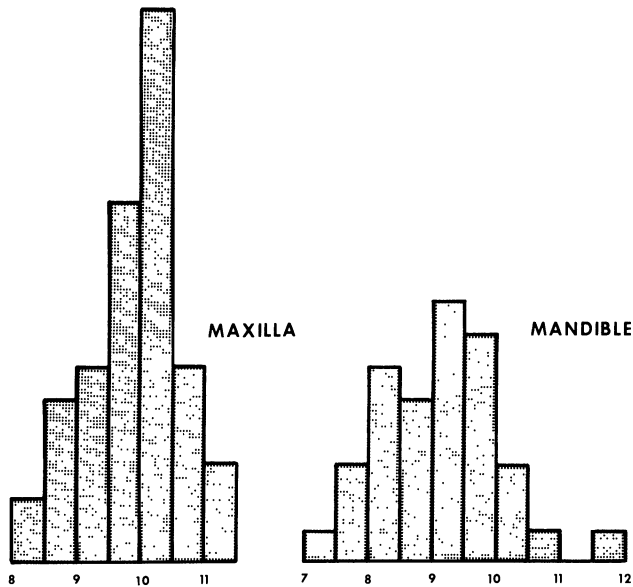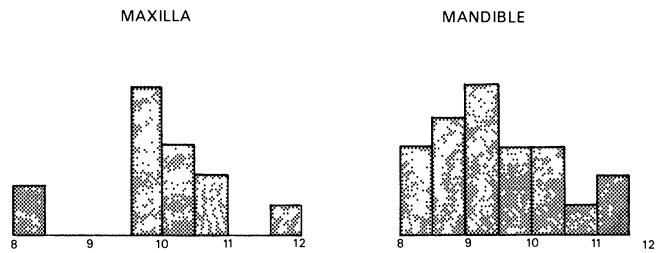

FIG. 5. Frequency distribution of maxillary and mandibular canine breadths (in mm) for a *H. erectus* sample (see table 8).

FIG. 4. Frequency distribution of maxillary and mandibular canine breadths (in mm) for a Neandertal sample (see table 8).
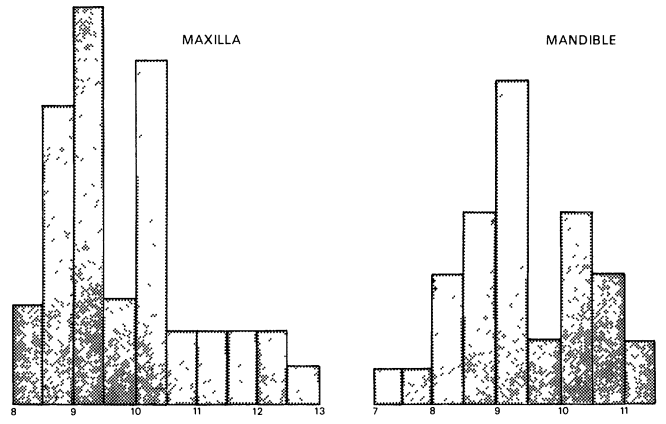

FIG. 6. Frequency distribution of maxillary and mandibular canine breadths (in mm) for an australopithecine sample (see table 8).

TABLE 8

FREQUENCY DISTRIBUTION OF CANINE BREADTHS (MM) IN
ABSOLUTE NUMBERS FOR VARIOUS HOMINID SAMPLES

CANINE BREADTH	AUSTRALOPITHECINE	H. ERECTUS	NEANDERTAL	H. SAPIENS
Maxillary				
6.0–6.4	–	–	–	–
6.5–6.9	–	–	–	1
7.0–7.4	–	–	–	3
7.5–7.9	–	–	–	33
8.0–8.4	3	2	2	84
8.5–8.9	9	0	5	81
9.0–9.4	12	0	6	49
9.5–9.9	3	5	11	27
10.0–10.4	10	3	17	5
10.5–10.9	2	2	6	5
11.0–11.4	2	0	3	–
11.5–11.9	2	1	–	–
12.0–12.4	2	–	–	–
12.5–12.9	1	–	–	–
Total	46	13	50	288
Mandibular				
6.0–6.4	–	–	–	2
6.5–6.9	–	–	–	18
7.0–7.4	1	–	1	66
7.5–7.9	1	–	3	88
8.0–8.4	4	3	6	87
8.5–8.9	6	4	5	53
9.0–9.4	10	5	8	24
9.5–9.9	2	3	7	10
10.0–10.4	6	3	3	1
10.5–10.9	4	1	1	–
11.0–11.4	2	2	0	–
11.5–11.9	–	–	1	–
12.0–12.4	–	–	–	–
12.5–12.9	–	–	–	–
Total	36	21	35	349

SOURCES: For fossil specimens, tables 2–4; for *H. sapiens*, table 7 and the worldwide distribution reported in Wolpoff (1971*a*).

lary sample, and the individual distributions in the South African sample are not as well defined. The South African robusts are apparently bimodal, with the smaller mode more frequent than the larger. The East African robusts are also likely bimodal, and the section point for both robust samples is the same. In contrast, there is no apparent modality in either the South African gracile subsample or the "Homo" subsample from East Africa. In sum, the phenomenon is far more obvious in the maxilla than in the mandible and is more visible in the larger mandibular samples. That this is very likely the result of small sample size can be seen in the fact that the combined mandibular distribution is apparently bimodal.

The *appearance* of bimodality is not necessarily a proof of it, since it is possible to sample a bimodal-appearing distribution from a normal population. There is no direct test for demonstrating bimodality, but it is possible to determine whether or not a distribution is normal. For this determination, a normal distribution with the same mean, variance, and sample size as the observed distribution was prepared and a chi-square test was used to compare observed and constructed distributions. The combined australopithecine distribution for maxillary canine breadth is significantly different from normal at the 5% level, and so is the maxillary breadth distribution for the South African sites alone. For mandibular canine breadth, the level of significance is much less, approximately .40%. I believe that the difference is due to the smaller size of the mandibular sample, although of course this cannot be proved. The fact remains that the mandibular and maxillary samples are virtually independent, except for three specimens. If the probability of drawing the observed maxillary distribution from a normal sample is 5% and the probability of drawing the observed mandibular distribution from a normal distribution is 40%, the probability of sampling both observed distributions from two underlying normal populations is only 2%. Given the small sizes of the samples and the fact that they represent numerous biological populations widely separated in space and time, it is most likely that the actual australopithecine distribu-

tions are in fact not normal, but rather as the sampling distributions appear: bimodal.

Either the australopithecine bimodal distributions are spurious and due to chance or they have an underlying biological cause. I believe it is unlikely that they are due to chance for a number of reasons: (1) Whatever the odds are against sampling a bimodal distribution out of a unimodal underlying distribution, the odds are multiplicative against getting two independent bimodal distributions. In this case, as I have said, there is only a 2% probability that the observed mandibular and maxillary distributions were sampled from an underlying normal distribution. (2) If the bimodality in the combined samples were spurious, the individual subsamples would be rather unlikely to be approximately the same. Yet, this appears to be the case when the sample sizes are large enough, as in the comparison of the South African gracile and robust maxillary breadth distributions (table 9). (3) Comparison with the Neandertal sample, of about the same size and collected under similar conditions, resulting in a sample representing wide spans of both space and time, shows significant difference between the distributions. A chi-square test shows that neither the mandibular nor the maxillary distributions for the Neandertals are significantly different from normal, even at the 50% level. When compared with the australopithecines, however, the Neandertal distributions are significantly different at the 1% level. (4) If the separate modes are taken to indicate sex, and if mean values are calculated for each mode, the "male-female" ratios for maxillary and mandibular canine breadth are almost identical. Because the samples are independent, this would be very unlikely if the bimodal distributions were attributable to chance. (5) There is no evidence that the bimodality is site-specific. The graciles are not all females and the robusts all males (a contention incorrectly attributed to the author and his colleagues [Holloway 1970, Pilbeam 1972, Greene 1973, Robinson and Steudel 1973]). The bimodality is neither sample-specific nor site-specific. Thus it does not result from combined distributions of different but overlapping

TABLE 9

FREQUENCY DISTRIBUTION OF CANINE BREADTHS (MM) IN ABSOLUTE
NUMBERS FOR AUSTRALOPITHECINE SAMPLES

CANINE BREADTH	SOUTH AFRICAN		EAST AFRICAN		TOTAL
	Gracile	Robust	"Homo"	Robust	
Maxillary					
7.0–7.4.....	–	–	–	–	–
7.5–7.9.....	–	–	–	–	–
8.0–8.4.....	1	2	–	–	3
8.5–8.9.....	3	5	–	1	9
9.0–9.4.....	4	5	2	1	12
9.5–9.9.....	2	0	0	1	3
10.0–10.4....	4	5	0	1	10
10.5–10.9....	0	2	0	–	2
11.0–11.4....	1	1	0	–	2
11.5–11.9....	0	0	2	–	2
12.0–12.4....	1	1	0	–	2
12.5–12.9....	–	–	1	–	1
Mandibular					
7.0–7.4.....	–	–	1	–	1
7.5–7.9.....	–	–	0	1	1
8.0–8.4.....	–	2	1	1	4
8.5–8.9.....	1	4	1	0	6
9.0–9.4.....	3	2	3	2	10
9.5–9.9.....	1	0	1	0	2
10.0–10.4....	1	1	1	3	6
10.5–10.9....	1	1	0	2	4
11.0–11.4....	1	–	1	–	2
11.5–11.9....	–	–	–	–	–
12.0–12.4....	–	–	–	–	–
12.5–12.9....	–	–	–	–	–

samples of taxa. In sum, the likelihood of all these factors' occurring together is extremely small unless there is a biological reason for the distribution. Rather than suggest that these data result from a combination of unlikely coincidences, it seems far more reasonable to posit the single simple explanation that the australopithecines are like most other higher primates. *Consequently, I believe the australopithecine bimodal distributions are due to sexual dimorphism.* I suggest this as the most likely explanation of the data and consider it a working hypothesis. It is of some interest to explore its implications and ramifications.

QUANTIFICATION OF SEXUAL DIMORPHISM IN PRIMATES

Table 10 indicates some statistics and indexes that can be used to quantify the nature and degree of sexual dimorphism in a number of primates. Bimodality in the australopithecine frequency distributions is much more distinctive than it is in those for chimpanzees. The separate modes in chimpanzee maxillary canine breadth are close together, compared with the variation in the sample. For mandibular canine breadth they are somewhat farther apart, and the distribution is slightly more bimodal. Even in this case, however, the least frequent class is not much smaller than the modes. For gorillas the least frequent class is much smaller than the surrounding classes, and the australopithecine distribution lies midway

between the two in this feature. No other hominid group is bimodal. The statistic that best shows this relation is the difference between male and female means weighted by the standard deviation of the combined sample. This ratio is higher for the australopithecines than it is for chimpanzees even though the male-female index of means is greater in the latter. In other words, while sexual dimorphism is greater in the chimpanzee, variation within each sex is also greater, obscuring bimodality in the combined sample. Variation is usually inversely related to stabilizing selection, and one might infer that the australopithecines were under more intense selection for sexual non-overlap than are chimpanzees. The other measures show that the average degree of sexual dimorphism is greater in chimpanzees, suggesting that the extent of sexual dimorphism under selection in the australopithecines is less. These two inferences are not contradictory, but rather suggest that the pattern of sexual dimorphism in the australopithecines is not the same as that in chimpanzees.

In these respects the australopithecines are more like gorillas. There are, however, two important differences. First, both relative and absolute measures of variation are less in the australopithecines for either sex and for the combined sample. Second, the australopithecine canine breadths are reduced to Mid-Pleistocene hominid size. Maxillary average breadths in *H. erectus* and Neandertals are 10.2 mm and 9.8 mm, and the

TABLE 10

QUANTIFICATION OF SEXUAL DIMORPHISM IN CANINE BREADTH FOR VARIOUS PRIMATE SAMPLES

	MEAN			STANDARD DEVIATION			SAMPLE SIZE		100M/F	M−F/SD$_B$	100(M−F)/B	t
	Male	Female	Both	Male	Female	Both	Male	Female				
Maxillary												
Gorillas	16.31	11.40	13.85	1.4	0.9	2.7	100	100	143	1.81	35.4	29.44
Chimpanzees	11.61	9.19	10.40	1.2	0.8	1.6	50	50	126	1.50	23.1	11.77
AUSTRALO-PITHECINES	*10.79*	*9.05*	*9.77*	*0.9*	*0.4*	*1.1*	*20*	*26*	*119*	*1.63*	*17.8*	*19.2*
Libben Amerinds	8.87	8.19	8.53	0.5	0.4	0.5	43	33	107	1.26	8.0	6.59
Australian Aborigines	9.12	8.67	8.90	0.6	0.4		41	36	105		5.6	4.07
Aleuts	8.47	8.15	8.31	0.4	0.4	0.5	65	44	104	0.62	3.9	4.15
Japanese	8.40	7.90	8.15	0.5	0.3	0.4	142	52	106	1.19	6.1	7.18
Javanese	8.50	7.80	8.15	0.6	0.7		136	43	109		8.6	6.61
Lapps	8.18	7.67	7.93	0.6	0.5	0.6	197	167	107	0.81	6.4	8.95
Tristanites	9.38	8.87	9.13	0.5	0.5	0.7	211	190	106	0.75	5.6	9.44
Gibbons	5.29	4.92	5.11	0.3	0.4	0.4	18	18	108	0.93	7.2	3.16
Mandibular												
Gorillas	14.54	10.31	12.43	1.2	0.7	2.4	50	50	141	1.80	34.0	26.26
Chimpanzees	11.72	9.19	10.46	1.5	0.9	1.8	50	50	128	1.43	24.2	10.23
AUSTRALO-PITHECINES	*10.40*	*8.81*	*9.32*	*0.5*	*0.7*	*1.0*	*13*	*23*	*118*	*1.63*	*17.2*	*7.22*
Libben Amerinds	8.34	7.52	7.93	0.6	0.4	0.6	32	23	110	1.28	10.3	5.96
Australian Aborigines	8.39	8.03	8.21	0.5	0.4		41	36	105		4.4	3.61
Aleuts	7.93	7.58	7.76	0.6	0.5	0.6	74	57	105	0.61	4.5	3.55
Japanese	7.70	7.30	7.50	0.4	0.3	0.4	146	48	106	0.95	5.3	7.07
Javanese	7.90	7.20	7.55	0.5	0.5		139	42	110		9.3	8.54
Lapps	7.55	6.95	7.25	0.4	0.4	0.7	211	190	107	0.91	8.3	14.24
Tristanites	8.97	8.45	8.71	0.7	0.7	0.7	54	43	106	0.75	6.0	3.88
Gibbons	5.12	4.65	4.89	0.5	0.3	0.5	19	19	110	0.96	9.6	3.34

SOURCES: Gibbon (*Hylobates moloch*) measurements come from a data set measured by L. Greenfield at the American Museum and are used here with his permission. All other data come from sources given in tables 1, 2, 5–7.

NOTE: Statistics expressing sexual dimorphism are the index of male to female means, the ratio of the difference between male and female means to the standard deviation of the combined sample, the index of this difference to the mean of the combined sample, and the results of calculation of Student's t between the means. Values of t are all significant at the 0.1% level.

Individual sexes are known for all specimens except the australopithecines. Here the least frequent class between the modes was divided in half, with the larger individuals being considered males and the smaller females. For both maxillary and mandibular canines, the section point is at 9.7 mm. This procedure seems an accurate estimator of the difference between the mean values, although it may be a less accurate estimator of individual sex. Its use appears justified on the basis of the foregoing analyses of gorilla and chimpanzee data, where it was found that when separate modes appear, the male and female mean estimates based on a division between the modes are surprisingly close to the actual male and female mean values, even though there may be extensive overlap of the distributions. This is apparently true because, when overlap occurs, it is symmetric.

corresponding mandibular breadths are 9.3 mm and 9.0 mm.

While in distinctness of the modes australopithecines are similar to gorillas, the extent of the differences between the modes falls about midway between chimpanzees and the human groups. In both male-female mean index and male-female mean difference weighted to the combined average, the australopithecines lie completely outside the ranges for human groups or any reasonable extension of these ranges. It is unlikely that this difference is due to larger average canine size than in *Homo*, because the Mid-Pleistocene hominid ·canines are also large, while the distributions are clearly unimodal. Thus, the pattern of sexual dimorphism in the australopithecines is distinct from that in *Homo* only in the average difference between means for the sexes. Combined sample means, as mentioned, are nearly the same for australopithecines and Mid-Pleistocene hominids, and combined sample standard deviations are also almost identical. Variation and size, in other words, follow the Mid-Pleistocene *Homo* pattern, while the male and female distributions do not.

In sum, the australopithecines have a more distinct pattern of mode separation than the chimpanzee, and one might expect less overlap in male and female distributions. The actual difference between the modes is less than that in chimpanzees, but significantly greater than that in *Homo*. The variation of the combined sample and the average breadth follow the Mid-Pleistocene *Homo* pattern.

SEXING INDIVIDUAL AUSTRALOPITHECINE SPECIMENS

The presence of clear bimodality in australopithecine canine breadths allows some estimation of individual specimen sexes. Discriminant function analysis has shown that this is possible in a unimodal distribution (Ditch and Rose 1972), and the accuracy should be much greater under bimodal conditions. It is unlikely, however, that every individual in the "male" australopithecine mode is actually female. Even the gorilla distribution shows some overlap. Consequently, I have calculated estimated error functions for gorilla, chimpanzee, and a *H. sapiens* population (Libben); these are given in table 11. In the three samples, there is almost no overlap of males below the female mean and females above the male mean. The percentage of males within each quartile of the range between the means forms the basis of the error function, expressing the probability that an individual designated male within that quartile is actually male. Designations of male above ·the male mean or female below the female mean are nearly, if not completely, certain.

Generally speaking, the function is steepest in gorilla and shallowest in *H. sapiens*, although more chimpanzee male maxillary canines extend into the female range than is the case with *H. sapiens*, while for the mandibular canines the opposite is true.

Which error function is most applicable to the australopithecines? The answer is probably none, as the australopithecine pattern of sexual dimorphism is not exactly like any of the samples. As a conservative means of estimating the australopithecine error step-function, I have averaged the three functions. I believe this estimate is conservative because of the clear separation of australopithecine modes. If there were extensive overlap of males into the female range and vice versa, the class between the modes would be far more frequent than it is, as in the chimpanzee situation. The estimated australopithecine error function and the ranges for the four quartiles between the means are given in table 12. Using tables 2 and 12, the sex of any australopithecine individual can be determined and the probability of error estimated.

It is of some interest to compare the sexes determined here with previously published statements. Table 13 gives this information for 30 specimens. There is disagreement in 9 instances. For none of these is the estimated probability of correct sexing 1.00. Some of the disagreements require explanation. Broom's (1939) sexing of TM 1517 as male was done with some hesitation, because the Kromdraai skull was the only adult of its species. Between 1946 and 1950 there was a change in the sexing of some Sterkfontein crania. Before the large canine STS 3 was discovered, TM 1511 was considered male; with the discovery of STS 3, Broom changed his mind and in the end classified every Sterkfontein cranium as female. A comparison of tables 2 and 9 shows that the South African gracile maxillary sample, much larger now than it was then, is bimodal. Three of the crania Broom classified as female, TM 1511, STS 17, and STS 71, fall in the male mode. Because TM 1511 is the second largest canine, if it is considered female, the gracile maxillary sample consists of one male and fifteen females. My feeling is that Broom's initial determination was correct, and his subsequent sexing of STS 17 and STS 71 should be considered with this in mind.

SK 46 and SK 48 come out as different sexes, although neither determination is absolutely certain. This seems unusual in view of the similarities between the crania. They were both sexed initially as female in view of comparisons with the much larger SK 12. That they might be different sexes is suggested by the extremely large parietal dimensions of SK 46 (Wolpoff 1974). The cranium actually approaches ER 1470 in size, and provides (albeit inconclusive) evidence that Broom's early suggestion of large cranial capacities at Swartkrans may yet

TABLE 11

CALCULATED SEXING-ERROR STEP-FUNCTIONS FOR
THREE PRIMATE GROUPS

	PERCENTAGE OF MALES BETWEEN FEMALE AND MALE MEANS IN CANINE BREADTH			
	First Quartile	Second Quartile	Third Quartile	Fourth Quartile
Maxillary				
Gorilla.......	0	1	99	100
Chimpanzee..	33	38	71	92
H. sapiens.....	17	33	75	77
Mandibular				
Gorilla.......	0	0	100	100
Chimpanzee..	15	50	79	93
H. sapiens.....	32	43	67	83

NOTE: Percentage of males below the female mean can be taken as 0 and percentage of males above the male mean as 100. In the Libben Amerind sample, only 2 out of 44 male canines fall below the female mean, and 1 out of 33 female canines exceeds the male mean. Similar figures apply to the mandibular sample.

TABLE 12

ESTIMATED SEXING-ERROR STEP-FUNCTION
FOR AUSTRALOPITHECINES

	PROBABILITY OF MALES BETWEEN FEMALE AND MALE MEANS BY QUARTILE
Maxillary	
First quartile (8.9–9.3 mm)..........	.16
Second quartile (9.3–9.7 mm).......	.23
Third quartile (9.7–10.1 mm).......	.82
Fourth quartile (10.1–10.5 mm)......	.90
Mandibular	
First quartile (8.7–9.1 mm)..........	.15
Second quartile (9.1–9.5 mm).......	.31
Third quartile (9.5–9.9 mm)........	.82
Fourth quartile (9.9–10.3 mm).......	.92

NOTE: Probability of males below the female mean is taken to be 0 and probability of males above the male mean 1.0.

prove to be correct. Unfortunately, little direct comparison between the cranial vaults of SK 46 and 48 is possible because of the extremely crushed nature of the latter. I believe it possible that they are both the same sex, and I take this result to indicate the presence of some overlap between male and female distributions. Whatever the sex, there is clearly extensive variation within both male and female distributions. If SK 46 is male, the corresponding dimensions of male specimens such as SK 12 and SK 845 are considerably larger. If, on the other hand, it is female, corresponding dental dimensions of other females such as SK 21 and SK 47 or cranial dimensions of SK 80/847 are considerably smaller.

STS 5 (Mrs. Ples) was initially described as female, and this work suggests the same conclusion. There has been some recent discussion as to whether STS 5 may actually be male in view of the fact that its cranial capacity is the highest for any South African gracile adult. Unfortunately, cranial capacity estimates for the other specimens are based on reconstruction of at least one missing endocranial dimension from the average of that dimension in the specimens exhibiting it (Holloway 1970). This procedure tends to reduce observed variation in the sample and to make subsequent comparisons less certain. There are only two canine-breadth dimensions smaller than the STS 5 value in the South African gracile sample, and on this basis I find it highly likely that the specimen is female.

STS 52, the complete Sterkfontein maxilla and associated mandible, comes out as male. The maxillary canine is more strongly male than the mandibular canine, which is in the most questionable interval. In fact, the probability of correct sexing for this specimen is among the lowest for any male (.82), and it has been reported as female. This is one case in which I do not trust the calculated designation. The maxillary dentition is rather small compared with specimens such as TM 1514 and STS 1, and the mandibular dentition is very small compared with "known" males such as STS 7 and STS 36. I believe that the overall size of the specimen as well as certain aspects of the morphology (e.g., the sharp lower nasal border) suggest that it is a female rather than a male.

Interestingly, the other two specimens with both mandibular and maxillary canines (TM 1517 and OH 30) both sex as females, and in both cases the mandibular tooth is more strongly female (i.e., has a smaller error estimate) than the maxillary. Because the measures of dimorphism are slightly greater in the mandible than in the maxilla, these data support the inference that sexual dimorphism is more pronounced in the mandible.

Prior sexes have not been suggested for most of the East African sample. OH 7 is classified as a male, but it falls in the intermediate class and has the smallest male canine. The sexing of this specimen is probably the least certain for the sample. Other East African specimens attributed to the "Homo" sample can be sexed with greater certainty. The ER 1470 and ER 1590 palates (Day et al. 1975), with canine socket breadth and canine breadth of 11.5 mm and 12.7 mm, are strongly male, as are the mandibular canine for OH 16 and the socket for ER 1483. The sexable small "Homo" mandibles (i.e., ER 730, ER 992, ER 1501, OH 13, and OH 37) are all strongly female, as is the "V"-shaped ER 1482 (Leakey and Wood 1974). In the robust sample from East Africa, the female mandibles (Natron, OH 30, Omo L74) are all quite large, although the apparent males (ER 729, ER 810, ER 818, Omo L7) are markedly larger. The only sexable male maxilla of the group is OH 5. This specimen is much larger than the female palates OH 30 and Chesowanja.

SEXUAL DIMORPHISM IN OTHER FEATURES

Assuming a reasonable degree of accuracy for the canine-breadth sexing procedure, it is possible to ascertain the degree

TABLE 13

COMPARISON OF SEXES DETERMINED HERE WITH PREVIOUSLY PUBLISHED SEXES

SPECIMEN	SEX DETERMINED IN THIS WORK	PROBABILITY OF CORRECT SEXING	SEX GIVEN IN LITERATURE	REFERENCE
TM 1511	M	1.00	M	Broom and Schepers (1946:47)
TM 1512	F	.84	F	"
TM 1514	M	.90	M	"
TM 1527	F	1.00	F	Broom and Schepers (1946:57)
STS 3	M	1.00	M	Broom, Robinson, and Schepers (1950:39)
STS 5	F	1.00	F	Broom, Robinson, and Schepers (1950:15)
STS 7	M	1.00	M	Broom, Robinson, and Schepers (1950:34)
STS 17	M	.90	F	Broom, Robinson, and Schepers (1950:24)
STS 36	M	1.00	M	Dart (1962:276)
STS 50	M	.82	M	Broom and Schepers (1946:53)
STS 51	F	.69	F	Broom and Schepers (1946:57)
STS 52	?M	.82	F	Dart (1962:277)
STS 71	M	.82	F	Broom, Robinson, and Schepers (1950:39)
MLD 6	F	1.00	F	Dart (1949a:189)
MLD 9	F	.84	F	Dart (1949b:335)
MLD 18	F	.85	F	Dart (1962:269)
MLD 22	F	.85	M	"
MLD 40	F	.85	M	"
SK 12	M	1.00	M	Broom and Robinson (1952:6)
SK 13	F	1.00	F	Broom and Robinson (1952:pl. 5)
SK 23	F	1.00	F	Broom and Robinson (1952:18)
SK 27	M	1.00	M	Broom and Robinson (1952:26)
SK 34	F	.85	M	Broom and Robinson (1952:16)
SK 46	M	.82	F	Broom and Robinson (1952:14)
SK 47	F	1.00	F	Broom and Robinson (1952:29)
SK 48	F	.77	F	Broom and Robinson (1952:10)
SK 55	F	.77	M	Broom and Robinson (1952:35)
SK 74	F	.69	F	Broom and Robinson (1952:23)
SK 85/93	F	.77	F	Broom and Robinson (1952:35)
TM 1517	F	.77	M	Broom (1939:328)

of sexual dimorphism in other features. For instance, in a similar analysis Robinson (1956) suggested that the distribution of M_1 breadth at Swartkrans was also bimodal and possibly indicative of sexual dimorphism in the posterior dentition. With the larger samples from all of the South African sites now available, I have determined that no distribution except the canine shows any evidence of bimodality. This does not mean, however, that the other teeth are not dimorphic. Dimorphism in the other teeth can be determined by comparing female and male averages, based on canine sexing. Table 14 presents the ratio of female to male mean values of various tooth dimensions for the australopithecine sample and for individual subsamples. For incisors, only breadths are considered, because there are virtually no unworn incisors and the immediate effect of wear is to reduce the mesiodistal length of these teeth. No comparisons involving a sample size of less than four are reported. Any sample smaller than ten should probably be considered suspect, but if such samples were also eliminated there would be virtually nothing left to compare. With samples this small, the *pattern* becomes more important than each individual tooth comparison.

In both jaws the degree of sexual dimorphism is least in the anterior teeth and increases posteriorly. There is a reversal of the relative position of P3, however. This tooth is more dimorphic than P_4 and less dimorphic than P^4. The mandibular condition is likely the result of a recent ancestry of hominid forms with a very dimorphic sectoral P_3, while the maxillary condition verifies a general australopithecine trend first suggested by Robinson (1952): the incorporation of P^3 into the anterior tooth field. The degree of sexual dimorphism is maximum in the molars of both jaws and increases posteriorly. When the separate subsamples are considered, there is some apparent variation in the degree of dimorphism. The same *pattern* occurs, however, in subsamples widely divergent in both space and time, suggesting that the pattern itself is not spurious even though the exact figures will probably be changed with larger sample sizes. The comparison of South and East African mandibles is particularly interesting. The East African sample consistently shows a higher degree of dimorphism. The explanation for this is not immediately obvious. While it may be due to a "mixture" of different taxa, it may also reflect the sampling of a wider range of populations over a longer period of time. Even in this comparison, the patterns of variation are the same.

Table 15 compares the combined australopithecine sample with a series of living primates and with *Dryopithecus africanus*. The table shows that while the australopithecines show a primate-like degree of sexual dimorphism, the *pattern* is unlike that of any nonhuman primate group and the *extent* of dimor-

phism is close to or at the primate extreme. In both jaws, canine dimorphism is less than that in any of the apes, while posterior-tooth dimorphism is as great as in any and in some cases even greater. P3 dimorphism in both jaws is low compared with all the pongids except the chimpanzee. From P4 on back, however, the australopithecine dimorphism is rather great. P^4 and M^2 dimorphism exceeds that in all other primates (although the latter not by much), and in the mandible the dimorphism in the three molars exceeds that in the other primates. If the dimorphism in the four most posterior teeth is averaged, leaving out the effect of the canine functional field on P3, the australopithecines have the maximum mandibular dimorphism and in the maxilla are only exceeded by *D. africanus*. The australopithecine condition, however, is not greatly different from that of the orang, and given the general problems of sampling in the australopithecines it would probably be incorrect to conclude that these fossil hominids were *significantly* (in the statistical sense) more dimorphic than any living fossil hominoid in the posterior tooth row. Rather, the data suggest that the australopithecines are at the pongid extreme.

In contrast, canine dimorphism is less than in any of the living nonhuman primates and *D. africanus*, although it is much greater than the living-human maximum. In other words, it exceeds the pongid extreme at the other end of the range. Incisor dimorphism is much like that in pongids and specifically resembles that in gorillas. Unfortunately, not enough incisors are available to establish dimorphism in *D. africanus*. Interestingly, both the pattern and the degree of dimorphism so closely resemble those established for the late *H. erectus* sample from Choukoutien by Weidenreich (1937) that there probably is no significant difference. The australopithecine condition remains virtually the same, but for the loss of canine bimodality (fig. 5). In my view, the fact that *H. erectus* maintains the same marked dental dimorphism justifies the treatment of all Pliocene/Lower Pleistocene hominids together. The data suggest that, regardless of possible taxonomic distinctions, the same pattern persists.

There are only a few possible explanations for the high degree of sexual dimorphism in australopithecine posterior-tooth size. The most likely of these is that it indicates a similarly high degree of body-size dimorphism. There is insufficient data to examine this contention directly. The two preserved Swartkrans innominates, SK 50 (Broom and Robinson 1952, Robinson 1972) and SK 3155 (Day 1973, Robinson 1974), are in my opinion those of a male and a female. I base this judgment mainly on the shape of the greater sciatic notch. A sample size of one for each sex is virtually useless, and in addition the extreme distortion of SK 50 leaves only a few comparable

TABLE 14

RATIO OF FEMALE TO MALE MEAN FOR VARIOUS TOOTH DIMENSIONS IN AUSTRALOPITHECINES

	BREADTH		AREA					
	I1	I2	C	P3	P4	M1	M2	M3
Maxillary								
South African gracile....	–	–	–	97.5	–	89.6	86.5	–
South African robust....	–	–	79.7	91.5	84.8	84.1	86.6	79.0
South African combined.	–	91.6	79.1	93.8	84.8	86.1	86.7	83.8
Total[a]................	92.0	87.7	75.7	87.2	82.0	86.5	81.8	77.8
	(4F,5M)	(9F,10M)	(19F,13M)	(17F,16M)	(17F,14M)	(19F,18M)	(16F,14M)	(13F,10M)
Mandibular								
South African gracile....	–	–	–	81.2	–	82.4	–	–
South African robust....	–	–	–	89.8	89.5	85.2	82.0	82.5
South African combined.	–	–	–	86.4	93.4	87.7	84.9	81.7
East African combined...	–	88.2	81.3	–	76.9	71.9	66.7	64.4
Total[a]................	91.6	93.1	79.7	82.4	84.2	81.1	77.1	73.7
	(9F,5M)	(11F,5M)	(19F,7M)	(18F,12M)	(17F,15M)	(24F,13M)	(19F,14M)	(15F,10M)

NOTE: Sexing is on the basis of canine breadth.

[a] No subsample smaller than four is presented separately. The East African subsamples are consequently not listed, though some information on the combined East African sample can be considered. Numbers of individuals of each sex in the total sample are given in parentheses below the ratios.

measurements. Table 16 shows five possible dimensional comparisons and provides similar data for a set of Libben Amerind innominates. If the Swartkrans comparison is considered to represent average sexual dimorphism at the site, its degree appears little greater than that in the Libben Amerind sample for these measurements, with the exception of ischium length, which may be incorrect in the Swartkrans male because of crushing. With respect to body-size dimorphism, the measure best correlating with femur length in the Libben sample is acetabulum height ($r = .839$). The Swartkrans (?) dimorphism in acetabulum height is identical to the Libben. These data suggest that the Swartkrans innominates differ little more than Libben Amerind male and female average values, but the sample is ludicrously small and inappropriate for drawing firm conclusions.

Considerable ongoing research is concerned with the relation of tooth size and body size in the living hominoids. Preliminary

results suggest that correlations of posterior-tooth areas and femur length are very high and statistically significant in gorillas (Martin 1971) and much lower in living humans and chimpanzees (White 1974). A significant correlation between femur length and body weight in humans has yet to be established (Wolpoff and Brace 1975). Mahler (1973) published a limited amount of body-weight data for orangs with full dentitions. The correlation of summed posterior-tooth area with body weight for a sample of eight is .704, significantly different from zero at the 5% level. In sum, it appears that in hominoids with a high degree of sexual dimorphism there is a significant relation between posterior-tooth area and body size as measured by femur length or weight. In hominoids with a low degree of dimorphism, the level of relationship between posterior-tooth area and femur length is often lower, and the

TABLE 15

RATIO OF FEMALE TO MALE MEAN FOR VARIOUS TOOTH DIMENSIONS IN LIVING AND FOSSIL PRIMATES

	BABOON	LIVING-HUMAN MAXIMUM	*H. erectus*	AUSTRALO-PITHECINE	*Dryopithecus africanus*	ORANG	GORILLA	CHIMPANZEE
Maxillary								
Breadth								
I^1	–	93.6	–	92.0	–	91.7	90.7	96.3
I^2	–	93.0	–	87.7	–	82.7	89.0	95.0
Area								
C	38.8	87.9	–	75.7	66.1	54.4	48.6	66.0
P^3	79.8	91.5	–	87.2	83.4	82.7	87.4	93.8
P^4	84.2	92.2	–	82.0	83.0	83.2	89.2	93.8
M^1	83.4	92.0	–	86.5	87.1	83.3	90.0	97.4
M^2	83.1	89.6	–	81.8	87.8	81.8	87.7	95.1
M^3	80.8	91.4	–	77.8	82.3	78.0	84.3	94.6
P^4–M^3 average	82.9	91.3	–	82.0	85.1	81.6	87.6	95.2
Mandibular								
Breadth								
I$_1$	–	97.2	99.3	91.6	–	89.3	90.2	95.5
I$_2$	–	96.7	97.2	93.1	–	88.3	88.6	95.2
Area								
C	37.0	86.4	75.6	79.7	60.2	56.3	51.3	67.2
P$_3$	48.8	91.2	78.0	82.4	72.8	73.9	74.5	88.2
P$_4$	84.6	92.0	88.2	84.2	71.2	82.4	86.1	94.7
M$_1$	83.6	92.8	77.0	81.1	81.8	83.6	89.1	95.4
M$_2$	81.7	91.0	83.9	77.1	86.3	80.5	86.7	95.8
M$_3$	82.2	90.7	71.0	73.7	80.4	78.1	82.8	92.7
P$_4$–M$_3$ average	83.0	91.6	80.0	79.0	79.9	81.2	86.2	94.8

SOURCES: Baboon data are from Lauer (1975), pongid from Mahler (1973). *D. africanus* specimens were sexed and the data kindly provided by L. O. Greenfield; they include some specimens not available in Greenfield (1972). The living-human maximum is represented by data collected in the Murray Valley of Australia; this group has the greatest degree of sexual dimorphism of a very large series of Australian Aborigines recently measured by C. L. Brace and probably represents the living-human maximum or something close to it. The data are used here with Brace's permission. *H. erectus* (Choukoutien) measurements and designation of sex are from Weidenreich (1937); sample size in the maxilla, especially for males, was too small to use.

TABLE 16

MEASUREMENTS OF VARIOUS DIMENSIONS OF THE INNOMINATE AND RATIOS OF FEMALE TO MALE MEANS FOR THESE DIMENSIONS IN TWO AUSTRALOPITHECINE SPECIMENS AND IN A *H. sapiens* SAMPLE

	MEASUREMENT (MM)				RATIO OF FEMALE TO MALE MEAN	
	Australopithecines		*H. sapiens*			
	SK 50 (?M)	SK 3155 (?F)	Males (*n* = 17)	Females (*n* = 14)	Australo-pithecines	*H. sapiens*
Acetabulum height	43.5	38.5	53.9	47.7	88.5	88.4
Ischial length (to tuberosity midpoint)	60.0	40.0	77.0	70.4	66.7	91.5
Acetabulum center–top of ischial tuberosity	42.5	34.5	46.6	40.4	81.2	86.8
Acetabulum rim–closest point on ischial tuberosity	21.5	16.5	15.0	11.5	76.4	76.7
Minimum distance–greater sciatic notch to anterior notch (between anterior spines)	61.0	51.0	71.7	67.1	83.6	93.6

SOURCES: My own measurements, except for the acetabulum height for SK 50, which is taken from Robinson (1972).

relationship between this dental measure and body weight is unknown (Lauer 1975).

Since the australopithecines are at the pongid maximum for sexual dimorphism in the posterior dentition, I believe it likely that the former model applies—that is, that a very high degree of body-size dimorphism underlies the posterior-tooth dimorphism. The favorable dimorphism comparison with orangs and baboons indicates that australopithecine body-weight dimorphism may have approached, if not exceeded, 100%. This high degree of dimorphism characterizes specimens from individual sites as well as the combined sample. Yet, at the same time, the individual male and female ranges are considerable. Female mandibles, for instance, vary from the size of OH 13 to that of Natron. Together, these data suggest that a 100% level of dimorphism is a *populational* characteristic in a highly *polytypic* taxon. That is, the australopithecines appear to consist of numerous populations varying considerably in body size, with a level of sexual dimorphism approaching 100% *within* each population.

It should be remembered that while an average body-weight dimorphism of 100% is clearly different from living human populational means, it is well within populational ranges. It is common to find males and females in a human population who differ in body weight by 100%, and such individuals regularly occur in small samples from living populations, such as classrooms. Indeed, finding males with three times the body weight of females is far from unheard of in human populations. The point is that the australopithecine condition represents a shift in *frequency* when compared with living humans.

Finally, while no posterior-tooth-size distributions are bimodal, the male and female ranges fall far short of completely overlapping. In the molars, few males are below the female mean value and few females above the male mean. In fact, for the mandible only in M_1 does such overlap occur: two females above the male mean and one male below the female mean (see table 14 for sample sizes). In the maxilla, the corresponding figures are two and four for M^1 and one and one for each of the other two molars. These distributions suggest that, at the extremes, molar size can be used for fairly accurate sexing, although sexes determined this way cannot be used in calculations of sexual dimorphism. Table 17 provides a list of tentative sexes for specimens with molar areas unambiguously above the male mean or below the female mean.

The other osteological structure preserved in sufficient numbers to allow a sexual-dimorphism determination in the australopithecines is the mandible. A total of 26 mandibles or mandibular corpus fragments can be sexed using the canine or canine socket breadth. Selected dimorphism values of these are compared with Libben Amerind values in table 18. The degree of dimorphism in the australopithecines is rather great. In corpus breadths the pattern follows that of the modern human group used for comparison: the greatest dimorphism is at the symphysis, and posterior dimorphism is less. The gradient, however, is steeper in the fossil hominids. In corpus heights, there is a rather different pattern. In the living group the dimorphism increases posteriorly, whereas in the australopithecines the trend is not really consistent. Thus, the greatest australopithecine height dimorphism is between the canine and the first molar. The difference in pattern may be due to greater dimorphism in the australopithecine canine root length.

In gorillas, with the greatest degree of corpus dimorphism of the three great-ape species, maximum dimorphism is at the anterior of the mandible (Frayer 1973); the female-male symphysis height ratio is .77. This ratio is virtually the same in the australopithecines. More posteriorly, however, the dimorphism decreases rapidly. Between the first and second molars the ratio for height is .86, closely approximating that in the human sample and significantly exceeding that in the australopithecines. In corpus breadth at M_2, gorilla females are actually slightly larger than males, although a Student's t

TABLE 17

Tentative Assignment of Sexes to Australopithecine Specimens on the Basis of Molar Size

FEMALES	MALES
MLD 19	MLD 2
MLD 22	STS 1
MLD 29	STS 10
STS 4	STS 18
STS 24	STS 21
STS 41	STS 28/37
STS 55b	STS 29
STS 56	STS 44
SE 1508	TM 1515
SK 45	TM 1518
SK 79	SK 36
SK 840	SK 828
SK 841b	SK 836
SK 885	SK 838a
SK 1587	SK 851
SK 1588	SK 871
SK 1591	SK 1592
TM 1536	SK 3976
OH 4	SK 3977
OH 6	SK 14129a
OH 21	OH 41
OH 24	ER 733
OH 27	ER 801
OH 44	ER 1171/1172
OH 45	ER 1176
ER 806	ER 1177
ER 807	ER 1509
ER 808	
ER 820	
ER 1462	
ER 1480a	
ER 1502	
ER 1506	
ER 1507	
ER 1508	

suggests that the difference is not significant. In sum, australopithecine corpus dimorphism matches or exceeds that of the living gorilla.

In the tooth row lengths, the australopithecine pattern is again similar to that of modern humans, but the extent of the sex difference is much greater. Virtually no dimorphism occurs in the anterior length measure; dimorphism is greater in the posterior segment (markedly so in the australopithecines).

In sum, the australopithecine pattern of dimorphism in the mandibular corpus is similar to that of living humans in breadths and alveolar lengths and somewhat different in corpus heights. The degree of dimorphism, however, is significantly greater: breadth and height measurements average .78, compared with .95 and .88 in the Libben Amerind sample. In other words, breadth dimorphism is nearly four times as great as in living humans and height dimorphism approximately twice as great. Furthermore, only at the symphysis does gorilla dimorphism match that of these fossil hominids. More posteriorly, the fossil hominid dimorphism is greater.

The mandibular measurements are not only markedly dimorphic, but in addition there is considerable non-overlap between male and female ranges. Of the measures discussed, the least overlap occurs in the corpus height at M_1/M_2, in spite of the fact that this variable does not have the maximum amount of dimorphism. Interestingly, this measurement *is* the most dimorphic in the corpus of the living groups. Table 19 presents a list of all australopithecine mandibles for which this measure is available, along with the sex when known. The four separate subsamples are distinguished, although the height distribution by sex seems to be the same in each. Below approximately 37 mm all the sexed specimens are female, and

above 41 mm all the sexed specimens are males. Between these values there are both sexed females and males, in approximately equal numbers. Given the large spans of non-overlap between the known distributions, I believe it is likely that the unsexed specimens with a corpus height at M_1/M_2 of less than 37 mm are probably females, and those with a height above 41 mm are probably males. This criterion suggests sexes for 11 additional specimens with a degree of certainty which I believe is higher than that of sexing based on molar size.

Sexing is possible for a few other corpus fragments not complete to the M_1/M_2 area, since all of the distributions of

corpus measurements presented in table 18 have some degree of non-overlap between specimens of known sex. MLD 22, SK 1587, ER 731, and ER 817 are probably females, and SK 81 is probably a male.

With sexes determined from canine breadth, molar size, and mandibular corpus dimensions (tables 2, 17, and 19) for 156 specimens, it is possible to deal with the female-male ratio in the australopithecines with a fair degree of accuracy. Ratios for the subsamples and the combined sample are given in

TABLE 18

MEAN MEASUREMENTS OF VARIOUS DIMENSIONS OF THE MANDIBULAR CORPUS IN AUSTRALOPITHECINES AND RATIOS OF FEMALE TO MALE MEANS FOR THESE DIMENSIONS IN AUSTRALOPITHECINES AND IN A *H. sapiens* SAMPLE

	MEAN MEASUREMENT (MM)		RATIO OF FEMALE TO MALE MEAN	
	Females	Males	Australopithecine	*H. sapiens*
Corpus breadth				
Symphysis......	21.7 (8)	29.1 (5)	74.6	94.1
P_4/M_1..........	21.3 (16)	27.5 (8)	77.3	–
M_1/M_2.........	23.1 (14)	27.8 (9)	83.0	95.8
Corpus height				
Symphysis......	38.3 (7)	48.5 (5)	78.9	92.1
C/P_3..........	36.5 (12)	49.0 (6)	74.4	87.2
P_3/P_4..........	36.5 (13)	47.0 (9)	77.6	–
P_4/M_1..........	35.9 (12)	44.3 (9)	81.0	–
M_1/M_2.........	34.3 (13)	43.1 (8)	79.6	86.1
Alveolar arch length				
I_1–C..........	19.3 (12)	19.9 (4)	96.9	99.6
P_3–M_3..........	62.6 (12)	73.6 (7)	85.1	95.5

NOTE: The number of sexable male mandibles is too small for accurate subsample comparisons. Only two South African gracile males and two robust males are measurable, and only one "Homo" male from East Africa. While there are five East African robust males, there are only two corresponding females. Number of individuals represented by each mean measurement is indicated in parentheses. Sexing of the *H. sapiens* sample (30 Libben Amerinds) is based on associated innominates.

TABLE 19

MANDIBULAR CORPUS HEIGHT AT M_1/M_2 (MM) FOR THE AUSTRALOPITHECINE SAMPLE

	SOUTH AFRICAN				EAST AFRICAN			
	Gracile		Robust		"Homo"		Robust	
Female range					OH 13 (F)	24.7		
					ER 1501 (F)	30.0	ER 1506	31
					OH 37 (F)	32.2	OMO 18	34.1
					ER 1482 (F)	32.2	ER 727	34.7
	MLD 18 (F)	33.1	SK 45 (F)[a]	33.0	ER 992 (F)	32.4	ER 728	36.0
	MLD 34	34.7	TM 1517 (F)	34.1	ER 730 (F)	34.0		
	MLD 40 (F)	35.5	SK 23 (F)	36.2				
Overlap	STS 7 (M)	37.0					ER 733 (M)[a]	38.3
	STS 36 (M)	37.0					ER 810 (F)	38.3
							ER 805	39.0
							Natron (F)	39.0
							ER 819	39.1
			SK 34 (F)	41.0			OMO L74 (F)	41.0
Male range					ER 1483 (M)	42.0	ER 725	42.7
							ER 1469	43.2
							OMO L58 (M)	43.5
			SK 12 (M)	44.0			ER 801 (M)[a]	43.7
							ER 1468	44.8
							ER 729 (M)	45.7
							ER 726	46.9
							ER 403	47.6
							OMO L7-125 (M)	48.3
							ER 404	49.0
							ER 818 (M)	51.0

[a] Sexing based on molar size.

TABLE 20

NUMBERS OF FEMALES AND MALES AND PROPORTION OF FEMALES IN THE AUSTRALOPITHECINE SAMPLES,
BASED ON SEXING BY CANINE BREADTH, MOLAR SIZE, AND MANDIBULAR CORPUS DIMENSIONS

| SAMPLE | FEMALES | | | | MALES | | | | PROPORTION FEMALE[a] |
	Canine Breadth	Molar Size	Mandibular Corpus	Total	Canine Breadth	Molar Size	Mandibular Corpus	Total	
South African									
Gracile........	13	9	2	24	10	10	0	20	.55
Robust........	19	9	1	29	11	10	1	22	.57
East African									
"Homo"......	9	7	1	17	5	1	0	6	.74
Robust........	5	10	4	19	7	6	6	19	.50
Total..........				89				67	.57

[a] Proportion is based on the sum of both jaws reduced by three specimens with both mandibular and maxillary canines (each of these is represented only once).

table 20. A binomial frequency test was used to test the calculated female ratios against the hypothesis of a .5, or 50%, female ratio for a sample of 156. The ratio for the combined distribution (.57) and the ratios for all of the subsamples except one were not significantly different from .5 at the 5% level. The single exception is the East African "Homo" sample, where the female ratio of .74 is significantly different from .5.

The "Homo" subsample is the smallest, and it is possible that sampling error alone accounts for the discrepancy. Another possible factor, however, is the fundamental difficulty in determining which specimens belong in this sample (Wolpoff and Brace 1975). There is little doubt that the dentitions of larger-brained specimens such as ER 1470 and ER 1590, if found without associated crania, would have been placed in the East African robust sample. Conversely, it is possible that some of the specimens in this robust sample would be placed in the "Homo" grouping if associated crania had been found. When the total East African sample is used, the female ratio is .59. This is close to the South African robust ratio (.57) and not significantly different from the hypothesized .5 female ratio. In sum, there is every reason to conclude that the sex ratio in the australopithecines was approximately 50–50.

A PHYLOGENETIC MODEL

The australopithecines appear to show pronounced canine dimorphism, with little overlap between male and female distributions. Given individual sexing by this criterion, equally pronounced although more overlapping dimorphism can be established for other teeth, as well as for dimensions of the mandibular corpus. Sexual dimorphism in these early hominids follows the general terrestrial primate pattern, but its specific nature is unique. Moreover, excepting canine bimodality, this pattern apparently persists through *H. erectus*.

The australopithecine pattern of dimorphism can be placed in an evolutionary context if the *D. africanus* sample (table 15) is used to represent the ancestral condition for both living pongids and hominids, Assuming that *D. africanus* actually is, or at least can represent, a common ancestor of pongids and hominids, substantive differences have accumulated between pongid and hominid lineages.

In the evolution of the pongids, the extent of posterior-tooth dimorphism has either remained approximately the same or slightly increased (orangs), slightly decreased (gorillas), or significantly decreased (chimpanzees). This is particularly apparent in the mandible, where posterior-tooth dimorphism in *D. africanus* and in orangs is virtually identical. In the maxilla, orang dimorphism is slightly greater and gorilla dimorphism slightly less than that of the ancestral form. Canine dimorphism, in contrast, *increases* significantly in the larger living pongids, whereas in chimpanzees it closely approximates

the ancestral condition. These trends, of course, are the result of the action of selection on past and living populations. The exact relation of the early Proconsuls to the living Asiatic pongids is unknown (Pilbeam 1969). In African pongid evolution, the two branches of the pongid lineage are both characterized by decreasing posterior-tooth dimorphism. This trend is carried much further in the living chimpanzees, which, however, retain the ancestral condition for canine dimorphism. The reduction of posterior-tooth dimorphism is least towards the rear of the posterior teeth and greatest in the P4-M1 region.

In the hominid lineage, the trends are almost exactly the opposite. Molar dimorphism significantly increases, while dimorphism in the canine and anterior premolar considerably decreases. P^4 increases in dimorphism while P_4 decreases (although not as much as in gorillas).

Obviously, there has been rather different selection operating on pongid and hominid lineages. One might argue that the increase in hominid posterior-tooth dimorphism is the result of a terrestrial savanna adaptation, drawing the common analogy with living baboons and relying on the known hominoid pattern of variation, in which the more terrestrial gorillas are more dimorphic than the less terrestrial chimpanzees. The fact that the large Asiatic arboreal hominoid, the orang, has the highest dimorphism of the living pongids suggests, however, that a broad ecological explanation may not be possible. Furthermore, there is the marked reduction in hominid canine dimorphism to be explained.

The key to many of these questions lies in an understanding of the *D. africanus* pattern. One might argue that body-size dimorphism, as indicated by posterior-tooth-size dimorphism, represents part of the initial arboreal hominoid adaptation. (Evidence for an arboreal adaptation in *D. africanus* comes mainly from ecological reconstructions of the relevant sites [Andrews and Van Couvering 1975], suggesting that they were primarily forested.) If so, the little-modified orang represents a retention of the ancestral condition, and the most variant of the modern pongids (i.e., the condition to be "explained") is the chimpanzee. Since orangs and, presumably, *D. africanus* are both arboreal, this would argue for an initial adaptive difference between the cercopithecoid and hominoid arboreal radiations and would partially reverse the usual argument that terrestrial primates are more dimorphic in body size than arboreal species. It would appear that, while this argument might apply to the cercopithecoids, a more complex relation applies to the hominoids: the most dimorphic species would appear to be both the most arboreal (orangs) and the most terrestrial (early hominids). In sum, it is evident that no single ecological or locomotive explanation can apply to the evolution of body-size sexual dimorphism in the hominoids. The situation is complex, and it is apparent that each case must be handled separately.

The increase in pongid canine dimorphism could possibly result from additional selection due to a greater importance of male canines in a more complex social organization. This,

however, would place the reduction of hominid canine dimorphism in glaring contrast, since increasing behavioral complexity is also a characteristic of the hominid lineage.

I believe that the contrasting trends of increasing body-size dimorphism and decreasing canine dimorphism in the hominids are linked together and functionally tied to the evolution of tool use and other aspects of cultural behavior rather than to any specific ecological or locomotor adaptation (except in the sense that tool use itself is functionally tied to such adaptations). The morphology and wear characteristic of australopithecine canines indicates that they were not used in the cutting and shearing functions of pongid canines. There is clear evidence for both a change in function and a change in morphology. While australopithecine canines, especially in the males, were high and pointed and sometimes show initial posterior wear facets, they rapidly wore to the level of the postcanine teeth. The known P_3 specimens are obviously nonsectoral, and many are rather highly molarized, as are the known dm_1 crowns.

All of the known functions of canines in the nonhuman primates could be influenced by selection due to cultural behavior. Of these, probably the most important are food preparation, maintenance of dominance, and defense. If there was a significant difference in the diets of male and female australopithecines, the existing dimorphism might result from the ineffectiveness of early hominid culture in supplanting the anterior dentition in food preparation. There is no evidence suggesting such a dietary difference, however, and in any event it seems to me that even the simplest stone tools would effectively replace the cutting function of the anterior dentition in a creature that shows flat canine and incisal wear soon after eruption. In other words, technology would tend to obviate any differential canine use in food preparation.

Dimorphism due to the differential use of canines in dominance displays is also influenced by cultural behavior. If tools and weapons were important enough to allow canine size reduction, selection for bipedal locomotion for carrying, and delayed maturation for effective transmission of cultural behavior, it is probable that they also replaced the canines in dominance displays. In fact, a rather important relation between the evolution of tool use and that of complex social organization can be seen in this replacement. Late eruption of the male canine in many of the higher primates acts to keep young males out of the adult dominance hierarchy until they have reached behavioral as well as physiological maturity. With the increasing importance of tool use, this physiological mechanism would have to be replaced by far more effective social control of behavior than exists in any of the living nonhuman primates. Direct evidence of complex social organization in the australopithecines can be found in both the early eruption of the canine and the demonstration of a delayed maturation period (Mann 1975). It is unlikely that selection for delayed maturation was purely in order to learn to make Oldowan tools: this "skill" can be taught to living apes in a very brief time.

Finally, there is the Darwinian argument that tools replace the canines as weapons of offense and defense early in hominid evolution. Such a replacement has two obvious advantages. First, while the canines become dull and blunted and are often broken as individuals grow older, the use of tools would not become less effective with increasing age. Second, even the simplest tool use (e.g., swinging clubs and throwing rocks) would have the important selective advantage of placing some distance between the hominid and the predator or prey. Both of these have an obvious effect on the ability of individuals to survive.

It is from the replacement, or at least supplementation, of the canines by tools that the relation of the contrasting hominid sexual dimorphism trends (*increasing* body-size dimorphism and *decreasing* canine dimorphism) can be seen. While it would be expected to lead to a reduction in the differences in selection

acting on male and female canines, at the same time it might well increase the difference in selection acting on body-size dimorphism. With the increasing use of tools, selection might be expected to shift from producing large projecting canines in the males to producing males with especially large and powerful bodies. Size and power would become particularly advantageous with the replacement of the canines by clubs and rocks. The effectiveness of these simple weapons would be increased in direct proportion to the size and strength of the user. Increased male body size and robustness would improve both the power of these weapons and the distance over which they are effective, and the application of force at a distance is likely one of the most important initial advantages of tool use over canine use.

In sum, I propose that while evolution of sexual dimorphism in the pongid lineage appears to be characterized by the development of more complex social organization and substantive role differences in the function of the canine premolar complex, evolution in the hominid lineage would seem to differ as the result of tool use and cultural behavior. The appearance of what must surely have been a significantly more complex social organization, with associated substantial role differences, did *not* lead to more canine dimorphism because of the assumption of certain canine functions by tools. At the same time, there was a commensurate increase in body-size dimorphism, precisely because of the reflection of these role differences in tool use. Tool use itself, rather than any specific ecological adaptation, seems to account for the reduction in canine dimorphism and the increase in body-size dimorphism that is suggested by the dimorphism in the posterior teeth and mandibles of early hominids.

SUMMARY

The canine is probably the single most useful tooth for determining sex in the higher primates because it shows the most dimorphism. Canine breadth is a more appropriate measure than length, since the former is not affected by interproximal wear and can be approximated by the breadth of an undistorted canine socket. Canine-breadth distributions have been examined for living primates and living humans of known sex. In gorillas the distributions (for both jaws) are bimodal, with little overlap between male and female modes, while in chimpanzees the distributions of males and females overlap to a far greater extent, although some evidence of bimodality is present. In both of the African pongids, the mode averages are very close to the actual breadth averages for the individual sexes. Living humans contrast in that the canine-breadth distributions are unimodal and not significantly different from normal, although it is rare for a female to fall above the male mean and for a male to fall below the female mean.

The canine-breadth distributions of three fossil hominid groups have been determined. In early *H. sapiens*, or Neandertals, and *H. erectus* the distributions are unimodal, but the australopithecines have bimodal canine-breadth distributions in both jaws. It is likely that the observed bimodality is due to sexual dimorphism.

Canine dimorphism in the australopithecines appears more distinct than in chimpanzees, although the average sex difference is less. Determining sex by canine breadth involves some ambiguity, but it is likely that the average characteristics of the modes closely approximate the actual female and male averages. The individual australopithecine sexes are generally the same as those established on the basis of other criteria.

Using the canine-breadth criterion, sexual dimorphism has been determined for the remaining teeth. Excepting P^3, posterior-tooth dimorphism in australopithecines exceeds that in the African pongids and closely approximates that in orangs

and baboons. It is suggested that the extensive posterior-tooth dimorphism is the result of significant body-size dimorphism, since the available evidence indicates a good relationship between tooth size and body size in the dimorphic higher primates. Australopithecine body-weight dimorphism is estimated at approximately 100%. Moreover, in molar size males rarely fall below the female average and females rarely fall above the male average. This allows additional teeth outside the range between male and female averages to be sexed with reasonable accuracy. Additional significant sex differences have been found in measures of the mandibular corpus, especially the height taken between the first and second molars. This criterion has also been used to determine sex when possible. In all, sex has been determined for 156 australopithecine specimens, and the female ratio is not significantly different from 50%.

On the assumption that D. *africanus* represents the ancestral condition for the hominoids, trends in the evolution of sexual dimorphism in hominid and pongid lineages have been examined. In the pongids, the trends in the three living great-ape species are for canine dimorphism to persist or significantly increase while posterior-tooth dimorphism persists or significantly decreases. No living pongid is like D. *africanus* in dimorphism. Thus, while chimpanzee canine dimorphism is unchanged, posterior-tooth dimorphism has the greatest reduction of the pongids. Similarly, while posterior-tooth dimorphism in the orangs is virtually unchanged from the ancestral condition, there is a significant increase in canine dimorphism. The trends in the hominid lineage are almost exactly the opposite: canine dimorphism decreases significantly while posterior-tooth dimorphism increases somewhat, approaching, but probably not significantly exceeding, the pongid maximum. It is suggested that the hominid dependence on tool use and cultural behavior, rather than any particular ecological or locomotor adaptation, is primarily responsible for the difference in evolutionary trends. Hominids likely resembled pongids in the evolution of complex social behavior and considerably different male and female roles. However, the supplementation and replacement of canines by tools in hominids seems to have reduced or reversed selection for canine dimorphism, while selection for body-size dimorphism was intensified. Large and powerful males might result from selection to maximize the application of force over distance through the use of simple tools and weapons.

A combination of data suggests that the australopithecines were both polytypic and significantly dimorphic. That female mandibles range in size from that of OH 13 to that of Natron indicates a range of body-size differences in the Plio/Pleistocene which would match that in sub-Saharan Africa today. An expectation of population height averages ranging from under 4.75 ft. to close to 6 ft. is not lessened by the known height range for australopithecine specimens, 3.5 ft. to over 6 ft. At the same time, it appears that within these polytypic populations, females averaged half the weight of males. In all, the australopithecines were unlike any living primate, combining the polytypism of living humans with the sexual dimorphism of baboons. Only the most variable of the higher primates can be used as an analog for australopithecine variation.

Comments

by EMILIANO AGUIRRE

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This is a remarkable, badly needed, and seriously carried out piece of scientific work on the early hominids. Its relevance for the taxonomy and phylogeny of the Plio-Pleistocene representatives of the Hominidae will be recognized, I am sure, in the near future. The identification of females in the "robust" groups and of males in the "gracile" ones is essential.

The basic grouping into four categories could be reexamined: the East African "Homo" group is certainly the poorest, but it is also likely to be a mixture of two taxa. The author's intention of avoiding taxonomic prejudices is clearly established and must be respected: consequently, I do not insist upon discussing whether there are in East Africa one or more species of *Australopithecus* and/or of *Homo*. Nevertheless, it is not clear whether the "Homo" group is based on large brain size; if it is, the position given to several specimens (e.g., OH 16) is not convincing. This group is questionable, and its unity must be considered problematic. I also miss some consideration of sexual dimorphism in cranial features (maybe this is a matter for another paper). The author justifies his use of "Neandertal" as "in the loose sense": I do not find this use correct and would prefer "early *H. sapiens*" as more appropriate.

Since there is indeed no sufficient ecological explanation of the comparative sexual dimorphism in hominoids with the present evidence, I would suggest investigating a possible phylogenetic explanation of the "complex" pattern: maybe it is not "each case" that must be handled separately, but rather each group of related taxa or evolutionary branch. My impression is that the Asiatic pongids have diverged since the Early Miocene, both ecologically and in definite evolutionary trends, from the African group of *Proconsul* with its Spanish relative *Hispanopithecus*. I think that the African group was less arboreal and is related to the origin of *Homo*.

The general conclusion cannot be argued, but I would like to see separate consideration—at this inferential level—for each of the author's subsamples, since adaptation and behavior seem to be undeniably divergent, at least between "robusts" and "graciles."

by MARSHALL JOSEPH BECKER

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Now that a large variety of early hominid specimens is available for study, the next logical general area of study has been undertaken by Wolpoff. The descriptive work which was necessarily a part of many previous studies, where few or single specimens were available, led unwary human paleontologists into taxonomic fantasy-lands. Before any significant progress can be made in understanding hominid evolution and in perfecting concepts of hominid taxonomy, scholars must go beyond the common and latent assumption that all members of a "species," regardless of sex, fall into a narrow morphological pattern. Wolpoff's study offers a necessary evaluation of the characteristics which may be used to distinguish sex in a "population." Once sexual dimorphism can be recognized, a better idea of the range of variation within a population can be gained, along with a better basis for understanding the behaviors of that population.

Wolpoff's approach to the study of dimorphism concentrates on dental variations. Since dental evidence provides the most abundant body of information regarding the early hominids, there is little wonder that Wolpoff focuses on these data. A great deal is known, however, about dental variations in living nonhuman primates, and more study of the dimorphism evident there would provide points of departure for studying dimorphism in various stages of human evolution, as Wolpoff's title suggests.

Wolpoff clearly identifies his early hominids as "australopithecines," which he describes as inclusive of but four African populations (South African graciles, South African robusts, East African "Homo," and East African robusts). Although

Wolpoff and Lovejoy (1975) have provided a fine statement on the "genus" *Australopithecus*, I would consider placing many of these early hominids, and other populations throughout the world which I believe to be related, in a single species of the genus *Homo*. Just as the present species of the genus *Pan* have been collected together from what were formerly distinct genera, various genera of the Hominidae might be more accurately placed within a single genus, and the entire range of the Hominidae might be reevaluated.

The placement of the "australopithecines" in the taxonomic unit with *Homo* has subtle support in Wolpoff's consideration of features of the os pubis, which are reliable in sexing members of the genus *Homo* (Krogman 1962, Phenice 1969), as reliable in sexing specimens of the australopithecines. Although the available fossil material does not permit significant use of the method, Wolpoff's concern for this approach suggests that he recognizes a close relationship between these populations. As in the case of the use of comparative studies of the sexual dimorphism of living nonhuman primates noted above, data on the sexing of living nonhuman primates based on comparisons of features of the os pubis would also be most useful. Such data might augment information upon which taxonomic considerations might be made. Although the comparative evidence from early hominids might not be forthcoming because of the infrequent survival of pelvic fragments sufficiently well preserved to permit analysis, research in this area would be of considerable theoretical interest.

Wolpoff has concentrated his research on the dentition, where abundant fossil evidence provides an outstanding data base and where comparative work in living nonhuman populations has been done. His data from these areas are extremely good, well presented, and well illustrated. One cannot fault him for concentrating his efforts in this most suitable area, but must applaud him for both completing the task so well and pointing out significant areas of study which might be pursued, including general review of sexual dimorphisms in living nonhuman primates and specifically the use of the os pubis in making these distinctions.

For clarity, one might place the term "Neandertal" in quotes (e.g., in the caption of table 4), although Wolpoff clearly states in the text how he is using the term. This use would then be parallel to his quotation of the term "Homo" when used for an "East African" australopithecine group.

by VACLAV HAJN
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Práce Wolpoffa je zajímavým příspěvkem k problému evoluce sexuálního dimorfismu u hominidů. Přináší nové pohledy na evoluci sexuálního dimorfismu, která byla a je zkoumána a kvantifikována mnoha charakteristikami kraniálního a post-kraniálního skeletu. Je přínosem po praktické i teoretické stránce. Kladem práce je rovněž řada přehledných srovnání fosilních i recentních skupin. Problémy evoluce sexuálního dimorfismu a otázky fyzických analogií chrupu mezi jednot-livými recentními i fosilními skupinami hominidů však zřejmě ještě delší dobu budou diskutovány.

[The work of Wolpoff constitutes an interesting contribution to the definition of the problem of the evolution of sexual dimorphism in hominids. It offers new perspectives on the evolution of sexual dimorphism, which has been and is being studied and quantified on the basis of several characteristics of the cranial and postcranial skeleton. This contribution is both practical and theoretical. Another contribution of this work is a series of comparative presentations of fossil and recent samples. The problems of the evolution of sexual dimorphism and of physical analogies of jaws among individual specimens, recent and fossilized, may be anticipated to remain a long-term topic for discussion.]

by KENNETH A. R. KENNEDY
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The primary value of this article lies in its theoretical consideration of how the emergence of certain behavioral patterns in australopithecine populations might have led to a reduction of sexual dimorphism in descendant hominids. Wolpoff notes that an evolutionary shift from patterns of bimodality to unimodality of dento-gnathic features may be evidence of such modification over time, but his intent to establish a single uniform procedure for determining sex of australopithecine fossil specimens can be realized only after more intensive testing of the hypothesis he presents. His caution in evaluating the importance of canine labio-lingual breadth measurements for sex determination of Lower Pleistocene hominids is to be commended, and the two comments which follow are offered in the spirit of encouragement.

First, I would be interested in knowing what conclusions might be drawn from a much broader analysis of metro-morphic variables relating to sexual dimorphism in *Homo sapiens*, both anatomically archaic and modern, than is discussed in the article. The point is not whether a *single* method for sex determination of hominids has been established (a suggestion at which some skeletal biologists are going to wince), but whether the estimates of degrees of reliability of the myriad procedures already developed for sex determination of anatomically modern man can be applied appropriately to the study of australopithecines. For example, Oetteking's (1945) plotting of the pogonion-condylion superius line in relation to the nexus of the anterior border of the ramus and the superior border of the mandibular corpus has demonstrated a bimodality very closely corresponding to sexual dimorphism of other skeletal characters in series from Alaska and South Asia. Is this procedure applicable to the estimation of sexual dimorphism of australopithecine mandibular specimens? How closely might the results of this observation correlate with the morphological variables of the gonial and symphyseal regions which have been recognized for a long time now as sound markers of sexual dimorphism in terminal and post-Pleistocene hominids? Obviously, some morphological features of the mandible are less appropriate than others for sex determination of earlier hominid populations, and the median and bilateral symphyseal forms of the mandible come to mind as an example. But should methods of sex determination which have been yielding convincing levels of reliability when applied to the study of sexual dimorphism in anatomically modern man appear to be unimodal when employed in the study of australopithecine fragments, then we are opening the field to still broader speculations as to the biological history of human sexual dimorphism.

Second, it would be valuable to compare small and random samples of teeth and gnathic fragments from large mortuary sites of *H. sapiens* with analogous samples from the australopithecine fossil record, assessing both series for normal and bimodal distribution of the sorting criteria recommended by the author and using chi-square and a comparative analysis of probabilities. What is recommended here is not incorporating more comparative skeletal series on the order of the Libben Amerinds already observed by Wolpoff, but rather setting up small and randomly selected series extracted from easily assessable contexts which would serve as models for testing the author's contention that his dento-gnathic observations have demonstrated a trend from bimodal to unimodal patterns in the course of human evolution. If such experiments were conducted, how frequently might a normal distribution appear in the small series of *H. sapiens* dento-gnathic materials? Would bimodality be infrequent or even absent? In short, what

probabilities might come forth from this exercise? Certainly its execution would bring us closer to establishing the probability of sampling bias in the australopithecine series than we are after Wolpoff's comparison of those earlier hominids which he lumps under the category of "Neandertals," populations as diverse in time and space as Petralona and Spy. Yet he is aware of the difficulty in demonstrating that the canine is the most dimorphic tooth in the human skull so long as Garn's "Ohio Whites" are around to qualify our temptations to generalize.

Appreciation is due our author for providing us with an exciting paper, one which promises to remain a focus for discussion of hominid evolution for some years ahead. And for that occasional undergraduate student registered in the introductory anthropology course who wants to know why we won't skip the "picky details" and come out with the authoritative and crystal-clear theories, we now have the answer in this piece of highly recommended reading!

by TURHON A. MURAD
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I always enjoy articles that attempt, as Wolpoff's does, to bring order to complex problems of human paleontology. I agree with him that "the question of sexual dimorphism is of considerable potential importance in any attempt to reconstruct the ecology, behavior, or phylogeny of the australopithecines," and I admire him for his attempt "to establish a single uniform procedure for determining sex."

While recent information on various human groups suggests that the canine, particularly the mandibular canine, displays the greatest sexual dimorphism of any tooth (Anderson and Thompson 1973, Perzigian 1976, Potter 1972, Rosenzweig and Smith 1971), I doubt that Wolpoff's choice of canine breadth will provide the basis for the single uniform procedure he seeks. Apparently he would agree, since in the case of STS 52 he does not trust the calculated designation of male but suggests that it is female on the basis of overall size and certain aspects of its morphology. This is not to suggest that canine breadth cannot aid in assigning sex, but only that it should be considered with other criteria (e.g., overall size, sharpness of the lower nasal border, etc.) when available.

In addition, in spite of the obvious sampling problems that would ensue from treating subsamples of *Australopithecus* separately, and Wolpoff's attempt to justify their lumping, I question the validity of treating all Pliocene/Lower Pleistocene hominids together. Indeed, as he has suggested, they represent numerous biological populations widely separated in space and time, which may be as close as different subspecies or as divergent as different genera. A problem that may result from lumping can be illustrated by combining the chimpanzee and gorilla frequency data provided by Wolpoff. The result is a bimodal distribution for both maxillary and mandibular canine breadth not too different from the corresponding distributions reported for the australopithecines. That is, the lesser mode, made up of chimpanzee females and males as well as gorilla females, is more frequent, while the greater mode, made up of gorilla males, is skewed to the right. If we employed Wolpoff's suggested procedure for assigning sex to the combined data, the result would misassign several chimpanzee males to the female mode. We cannot be certain that this is not happening with the australopithecine distribution. The bimodality seen in the australopithecine data may indeed be due to biology instead of sampling as Wolpoff suggests. The question remains, however, whether the observed bimodality is due to sex alone, as Wolpoff suggests, or to the interaction of sex and subspecific, specific, or generic differences.

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Wolpoff's technical discussion of the evolution of sexual dimorphism on the basis of analysis of some hominid specimens is fascinating. Determination of sex in dry long bones—and, for that matter, in the skeleton as a whole—is an arduous anatomical exercise. Moreover, in cases of disarticulated or fragmentary skeletal remains, the determination of sex at times poses a problem even with direct study of the skeletal remains. Gender determination is likely to be vital in the assessment of archaeoanthropic and related conclusions. In this connection, I would like very much to see the establishment of authentic and clearcut criteria for sexing the osteological specimens of *Australopithecus*. Next I would ask what, precisely, are the diagnostic osteological features in *Australopithecus* attributable to sexual dimorphism. When there is a difference in a trait in male and female skeletal remains of *Australopithecus*, what is the macroscopic inventory of osteological and dental features of similarity or dissimilarity by virtue of sexual dimorphism? A further question would be how, specifically, one would relate a reconstruction of the ecology with that of sexual dimorphism.

by FRANCISZEK ROSIŃSKI
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Praca Wolpoffa dotyczy bezpośrednio niektórych tylko aspektów wczesnych stadiów ewolucyjnych dymorfizmu płciowego istot człowiekowatych, pośrednio jednak wyniki jego badań mają także duże znaczenie dla klasyfikacji taksonomicznej kopalnych Hominidae. Szczególnie w tym drugim aspekcie widzę wielką jej wartość, nadal bowiem w badaniach paleoanthropologicznych w niewystarczającej mierze bierze się pod uwagę istnienie stosunkowo dużego zróżnicowania wewnątrzgatunkowego, uwarunkowanego dymorfizmem płciowym, zmiennościa międzyrasowa i wewnątrzpopulacyjną a nawet osobniczą w obrębie danej społeczności lokalnej, jakie charakteryzuje zarówno różne odmiany Homo sap. rec. jak i małoliczne nawet stado Pongidae (Schultz 1964, Bielicki i Wanke 1965). Ponieważ różnice te, zwłaszcza płciowe zaznaczały się u wczesnych Hominidae przypuszczalnie silniej niż u dzisiejszego człowieka, stąd niełatwo ustrzec się różnym autorom, zwłaszcza dokonującym odkryć szczątków kostnych kopalnych Hominidae, przed tworzeniem w ich obrębie wciąż nowych gatunków, choć faktycznie stanowiły, być może, tylko jakieś odmiany lokalne tego samego gatunku o swoistej morfologii, etologii ewentualnie i kulturze.

Trudno mi jednak w pełni zgodzić się z niektórymi wywodami i wnioskami autora. Niewątpliwie w badaniach nad prehistorycznym dymorfizmem płciowym wyniki bezwzględnych pomiarów zębów zwłaszcza kła, mogłyby odgrywać decydującą rolę, gdyby tego rodzaju kryterium odznaczało się wystarczającym stopniem pewności. Niestety jednak w przypadku najstarszych przedstawicieli Hominidae wnioskowanie tego typu oparte jest w głównej mierze na analogii ze współczesnymi formami człowieka i Pongidae, ponieważ nie ma chociażby kilka osobników owych form, których płeć byłaby bezwzględnie bezsporna a nie tylko mniej lub więcej prawdopodobna, przez co również zakres i stopień pewności takiej cechy, oparty na takim materiale, może być również tylko mniej lub więcej prawdopodobny, hipotetyczny. W takiej sytuacji zarówno w badaniach nad dymorfizmem płciowym jak i przy określaniu taksonomicznym szczątków kostnych, zwłaszcza przy próbach konstruowania modeli filogenetycznych wskazana jest daleko posunięta oględność w stosowaniu takiego kryterium; bardziej bezpieczne wydaje się w takiej sytuacji poleganie na większym zestawie cech, w

tym również opisowych niż zbytnie zaufanie jednej czy kilku cechom odontologicznym.

Niezbyt przekonywująca jest też dla mnie argumentacja Wolpoffa, iż "all of the known functions of canines in the non-human primates could be influenced by selection due to cultural behavior . . . [including] food preparation, mainte-nance of dominance, and defense." Wydaje się bowiem, iż tendencja do redukcji kłów zaznaczyła się znacznie wcześniej, bo już u *Oreopithecus, Ramapithecus* i *Gigantopithecus,* a więc znacznie wcześniej niż rozpoczęło się używanie narzędzi, przynajmniej litycznych, jak na to wskazują dane archeologiczne (por. Conroy i Pilbeam 1975, Eckhardt 1975). Wielu autorów odmawia zresztą w ogóle australopitekom zdolności wytwarza-nia i używania artefaktów kamiennych, przypisując je bardziej od nich progresywnym człowiekowatym (Leakey, Tobias i Napier 1964, Blumenberg i Todd 1974, von Koenigswald 1975). Nadto przed używaniem ognia, przy wzrastającym udziale pokarmów mięsnych w ich pożywieniu silne kły stanowiłyby raczej cechę pożądaną niż niepożądaną, podobnie też w rozdrabnianiu innych pokarmów, jak również w polowaniu i w akcjach ofensywno-defensywnych. Wątpliwe, by nawet in dominance displays silne kły były już kilka milionów lat wstecz nieużyteczne, skoro jeszcze dziś niejeden człowiek próbuje tego rodzaju problemy rozstrzygać za pomocą bru-talnej siły biologicznej. Poza tym, czy mniejszy wymiar kłów u osobników płci żeńskiej miałyby ewentualnie świadczyć o intensywniejszym u nich używaniu narzędzi?

Biorąc pod uwagę warunki otaczające, w których te raczej bezbronne pod względem biologicznym istoty żyły, raczej wysunąłbym twierdzenie: *melior est positio possidentis,* podobnie jak w przypadku innych małp. Również charakter starcia szkliwa zębów australopiteków, jak stwierdził Wallace (1975: 219) wskazuje na to, że one "seemingly crushed and ground the food mainly with the teeth and not outside the mouth with tools."

Bardziej przekonywująca wydaje mi się wręcz przeciwna hipoteza, iż najstarszym człowiekowatym o prawdopodobnie niedoskonałym jeszcze sposobie dwunożnej lokomocji, żyjącym na otwartych przestrzeniach, wydatne kły stanowiłyby, podobnie jak u pawianów, większy pożytek w przetrwaniu gatunkowym niż ich brak, nawet w sytuacji, gdyby człowieko-wate te umiały posługiwać się w szerokim zakresie i w skuteczny sposób narzędziami. Raczej zaryzykowałbym tezę odwrotną niż u Wolpoffa, iż to właśnie postępująca redukcja kłów zmuszała człowiekowate do zastąpienia ich dotychczasowych funkcji, zwłaszcza w zakresie ofensywno-defensywnym za pomocą narzędzi (Rosiński 1969) tym bardziej iż chronologicz-nie wcześniej można stwierdzić zmniejszanie się wymiarów uzębienia zwłaszcza kłów niż tool-using behavior. Ponieważ trudno wykazać nieużyteczność albo wręcz negatywną wartość selekcyjną wydatnych kłów u wczesnych człowiekowatych za pomocą doraźnych argumentów utylitarnych, świadczących na korzyść zastąpienia silnych kłów przez używanie narzędzi, a ponieważ jeszcze trudniej byłoby wytłumaczyć jakiś dziwnie szybko zachodzący proces ich redukcji, dlatego należałoby wziąć raczej pod uwagę inne czynniki wpływające na ten proces, np. zmiany biochemiczne lub w sposobie odżywiania się, jak postuluje Holloway (1967) albo też Jolly (1970).

[Wolpoff's paper directly concerns only some aspects of the early evolution of hominid sexual dimorphism. Indirectly, however, the results of his researches bear on the taxonomy of fossil hominids, and it is especially in this latter aspect that I see great value in these studies. Up to now paleoanthropologists have not made sufficient allowance for the probable existence of great intraspecific differentiation due to sexual dimorphism, interracial and intrapopulational variability, and even individ-ual variability within a given local group as these exist not only

in various races of *Homo sapiens recens,* but even in small bands of Pongidae (Schultz 1964, Bielicki and Wanke 1965). Because these differences, particularly the sexual ones, were presumably more pronounced in early Hominidae, some researchers dis-covering the skeletal remains of fossil hominids are prone to create new species of Hominidae when the newly discovered forms may constitute only local variations of existing taxa, distinguished by morphology, ethology, and eventually culture.

Nevertheless, I cannot fully accept certain of the author's arguments and conclusions. Undoubtedly, absolute measure-ments of teeth, especially of canines, could be decisive in studies of prehistoric sexual dimorphism if this criterion were sufficiently reliable. Unfortunately, when we are dealing with the earliest forms of the Hominidae, conclusions are based principally on analogies with contemporary forms; we do not have at our disposal even a few representatives of the earliest hominids whose sex can be stated with absolute certainty rather than probability. Consequently, the range of variability of any trait studied in such materials can be defined only approximately and cautiously. In this connection, extreme caution is to be advised in the use of any such criterion for the determination of sexual dimorphism and for taxonomic analy-sis, particularly when attempting the construction of phylo-genetic models. Therefore the use of several traits, including descriptive ones, seems safer and more effective than an over-estimation of the importance of one or another odontological trait.

I am not convinced by Wolpoff's argument that "all of the known functions of canines in the nonhuman primates could be influenced by selection due to cultural behavior. . . . [in-cluding] food preparation, maintenance of dominance, and defense." The tendency towards the reduction of canines seems to have appeared significantly earlier, in *Oreopithecus, Rama-pithecus,* and *Gigantopithecus,* i.e., long before the archeologically attested use and production of tools or, at least, lithic artefacts (cf. Conroy and Pilbeam 1975, Eckhardt 1975). After all, some authors deny that the Australopithecinae were capable of producing and employing stone artefacts and attribute the artefacts found to more advanced hominids (Leakey, Tobias, and Napier 1964, Blumenberg and Todd 1974, von Koenigs-wald 1975). Moreover, before the use of fire and parallel with an increase in meat eating, strong canines would have been useful for crushing food, in hunting, and in offensive-defensive behavior. It also seems to me disputable that strong canines were unsuitable for early hominids' dominance displays, since even nowadays some people try to solve similar problems by means of brute biological force. Regarding the ecological situation in which these rather biologically defenseless creatures lived, I would rather say *melior est positio possidentis,* on the analogy of other apes. Also, the wear of *Australopithecus's* teeth, as Wallace (1975:219) states, indicates that he "seeming-ly crushed and ground the food mainly with the teeth" and not outside the mouth with tools.

I prefer an opposite hypothesis: that the progressive reduc-tion of the canines, chronologically earlier than the use of tools, was the cause which compelled the Hominidae to perform hitherto canine functions with tools (Rosiński 1969), especially in offensive-defensive actions and in the change from a vege-tarian to a partly animal diet. Because it is difficult to demon-strate the uselessness or negative selective role of prominent canines in the early hominids through immediate utilitarian arguments of tool use and even more difficult to explain the relatively rapid reduction of the canines, it should be preferable to consider other factors influencing this process, e.g., bio-chemical or dietary changes, as proposed by Holloway (1967) and Jolly (1970).]

by MICHAEL I. SIEGEL
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Wolpoff is to be congratulated for his excellent discussion of canine sexual dimorphism in the hominoids. Surely a report so well documented will be of great value to students of human evolution for years to come. The documentation of the validity of using "socket" measurements is also a worthwhile contribution. However, such an abundance of data, and thoroughness, does, I feel, lull the reader into a false sense of security, making him more willing to accept some of Wolpoff's less accurate manipulations of the data and consequent conclusions.

Perhaps the weakest point, and one which must be substantiated before drawing any conclusions, is that concerning the bimodality of the australopithecine (*sensu* Wolpoff) canine-breadth distributions. Most readers will agree that for the samples of *Homo* the breadth distributions approximate normality. I am quite willing to agree with the author that for *Pan gorilla* "there is virtually no overlap between male and female distributions." The histograms for both maxillary and mandibular canine breadths are quite clearly extreme platykurtic distributions. A number of class-intervals which contain few observations separate the two modes. Though this is the case to a much lesser degree for the *Pan troglodytes* sample, I still might be convinced that this distribution is also bimodal. The australopithecine canine-breadth data are an entirely different matter. For both maxillary and mandibular distributions, only one class-interval separates the two modes. The mandibular distribution, for example, has one mode (class-interval containing ten observations) separated from the other (class-interval containing six observations) by a single class-interval containing only two observations. If the defining limits of the class-intervals are altered slightly, the apparent bimodality disappears and we are left with a perfectly normal distribution. The same can be demonstrated for the maxillary distribution. In other words, what is clearly visible from fig. 6 is that the distributions are not even mildly platykurtic, but normal, and simply reflect the small number of observations in all but a few of the class-intervals. All of the subsequent conclusions hinge on acceptance of this nonexistent bimodality. With this obvious difficulty in convincingly demonstrating bimodality in the "lumped" sample, it becomes ludicrous even to consider such an attempt for any of the smaller groups (e.g., South African graciles).

Several other points deserve mention, at least briefly. Given the obvious differences in sexual dimorphism between the two species of *Pan* (*P. gorilla* and *P. troglodytes*), one wonders whether it is valid, for purposes of analysis, to lump all australopithecines, particularly when considering canine sexual dimorphism. One also wonders why Wolpoff considers *D. africanus* "to represent the ancestral condition for both living pongids and hominids." It would appear to be more parsimonious for the "common ancestor" to have had small canines with little or no sexual dimorphism. This being the case, we would see canine dimorphism increasing in the pongids (as the author points out) and little or no dimorphism with small canines being retained in the hominid lineage. This explanation better fits the data presented by Wolpoff once we realize that bimodality of canine breadth does not exist for the australopithecines.

by FRED H. SMITH
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Except for the efforts of Brace (1973) and a few other isolated examples (e.g., De Lumley and De Lumley 1971), the possible effects of sexual dimorphism on morphological variation in fossil hominids have remained virtually uninvestigated. This is especially unfortunate in the case of the australopithecines,

because these hominids should, at least theoretically, exhibit more sexual dimorphism than any subsequent hominid form. For this reason I believe Wolpoff's article to be a significant contribution, providing sound insights into the understanding of australopithecine morphological variation. Wolpoff presents very convincing evidence that significant sexual dimorphism is exhibited in the australopithecines and thereby adds quantification to the theoretical base laid by Brace. In addition, Wolpoff further clarifies several points of misunderstanding among critics of the application of sexual dimorphism to the australopithecine sample (e.g., the impression that all females come from one site, etc.). Thus, I believe that Wolpoff's article has laid the groundwork for inquiry as to what other features of australopithecine morphology may ultimately be due to difference in sex.

Two specific points seem important to mention: First, Wolpoff (and earlier Brace) points out that the orangutan is somewhat of a contradiction to the supposed correlation between terrestrial adaptation and pronounced sexual dimorphism, as the orang is very sexually dimorphic and supposedly highly arboreal. Though her results are obviously very tentative, Galdikas-Brindamour (1975) reports that orangs are much more terrestrial than previously believed. Apparently, the more accustomed the animals become to strange humans in their midst, the more time they spend on the ground. Thus, although obviously more research is needed to be certain, it appears that orangs may not constitute an exception to the rule. Second, the similarity of the bimodal pattern of early hominid canines to the pattern of ancestral pongids would seem to be further evidence against Kinzey's (1971) suggestion that canines have not undergone reduction in human evolution, since australopithecine canines still exhibit some degree of the dimorphism present in the dryopithecines. Wolpoff's data appear to place the australopithecines in an intermediate position (between the dryopithecines and *Homo erectus*) with respect to patterns of canine reduction.

In sum, whether or not one agrees with his interpretations, Wolpoff's quantification of sexual dimorphism in the australopithecines will certainly help to focus much-needed attention on this phenomenon as a source of variation for early hominids.

by ERIK TRINKAUS
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Wolpoff has once again presented a large body of quantitative data to support the hypothesis that the large ranges of variation seen in the African Plio-Pleistocene hominids are due to factors other than specific distinctions between the specimens. In this case the factor is sexual dimorphism. There is little reason to doubt that sexual dimorphism was greater among the Plio-Pleistocene hominids than among modern humans. The available data from sites yielding several individuals of Neandertals or *Homo erectus*—e.g., La Ferrassie (Heim 1972), Krapina (Gorjanović-Kramberger 1906), and Choukoutien (Weidenreich 1936, 1943)—suggest a high degree of body-size sexual dimorphism. The Plio-Pleistocene hominids undoubtedly exhibited equal, if not greater, levels of sexual dimorphism. It is not reasonable to expect, however, that one can correctly identify the sexes of the individual specimens on the basis of one morphometric trait, canine breadth. Wolpoff uses other traits (e.g., mandibular dimensions and noncanine dental dimensions) to sex some of the specimens. The mainstay of his argument, however, is the assumption that canine breadth can be used to assign sex accurately to members of the Plio-Pleistocene hominid sample.

Wolpoff interprets the distribution of the "australopithecine" canine breadths as bimodal, largely on the basis of the scarcity of specimens in the 9.5–9.9-mm range. He attempts to sub-

TABLE 1

Wolpoff: EARLY HOMINID SEXUAL DIMORPHISM

CHI-SQUARE VALUES FOR "AUSTRALOPITHECINE"
CANINE-BREADTH DISTRIBUTIONS

	"FEMALE"	"MALE"
Maxillary		
Chi-square............	4.15**	21.76***
N.....................	24	19
Degrees of freedom.......	1	3
Mandibular		
Chi-square............	9.18**	3.44*
N.....................	22	12
Degrees of freedom.......	2	1

* $p < 0.10$, ** $p < 0.05$, *** $p < 0.001$.

stantiate his interpretation by demonstrating for the maxillary sample that the "australopithecine" distribution is significantly different from normal. It should be emphasized that this does not prove bimodality; it only proves a skewness from a normal distribution, which may take a variety of forms. Furthermore, if one computes the chi-square value for the maxillary sample deleting the contribution of the 9.5–9.9-mm interval, the sample is skewed from normal at the same level of significance as with that interval included. This suggests that the deviation from normal is due, not to the dearth of specimens between 9.5 and 9.9 mm, but to the skewness of the total sample.

Yet, if the distributions are bimodal and the two modes represent the male and female modes with minimal overlap of the sexes, as Wolpoff maintains, one would expect the male and female portions of the mandibular and maxillary canine-breadth samples to approximate normal distributions. This is clearly the pattern for the gorilla, chimpanzee, and modern human samples (see figs. 1, 2, and 3). This does not appear to be the case for the "australopithecine" sample, as can be seen from the histograms of canine breadth (fig. 6). To test statistically the null hypothesis that the "male" and "female" canine-breadth distributions were drawn from normally distributed populations, I computed chi-square values for each of the four distributions, using the data given in Wolpoff's table 2 in 0.5-mm intervals and deleting the data points between 9.5 and 9.9 mm (see my table 1). As is evident from the chi-square values, one of the distributions is highly skewed and the others are moderately so. Given that only one of the combined male-female "australopithecine" canine-breadth distributions is significantly skewed from normal and that one only at the 5% level, would not the conclusion that a large, heterogeneous, normally distributed sample is represented be more reasonable than imposing highly skewed bimodal distributions on the data?

Further analysis and discoveries of Plio-Pleistocene hominids may well substantiate Wolpoff's contention that much of the variation in these hominids is due to sexual dimorphism. However, I do not feel that assignment of sex to specimens on the basis of a trait which has not been sufficiently shown accurately to separate the sexes and the subsequent use of these sexual designations to speculate on early hominid evolutionary processes is warranted at this time.

by B. A. WOOD
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This paper, which is an attempt to unravel the broad biological implications of hominid sexual dimorphism, starts objectively, but the eventual conclusions are predetermined by a priori assumptions about the nature of the fossil sample.

The evidence for using canine dimensions as an indicator of sex and the results of applying this test to hominid remains are clearly set out. However, because sexual dimorphism can

produce a bimodal distribution of dental measurements it is not axiomatic that all bimodal distributions have their basis in sexual dimorphism.

When the discussion turns to sexual dimorphism in other features, it becomes increasingly difficult to discern whether sexual attributions are being made on the basis of the whole australopithecine sample, geographically separate parts of it, or the four separate subsamples. At some stage in the argument the categories of East African "Homo" and Robust groups are discarded and all are grouped into one sample. While there are certain exceptions, due to mixing material that may be as much as $1\frac{1}{2}$ million years apart in time, most of the "Homo" specimens come out as small females, whereas the robust material is classified as male. This scheme produces a roughly 50–50 "sex" distribution in the fossils, but this cannot seriously be taken as underpinning the argument.

It is at this point that the danger of treating the anterior and posterior teeth separately is exposed, for a notable omission from table 17 is KNM-ER 729, a mandible hitherto classified as a robust australopithecine. Its canines are almost identical in size to those of KNM-ER 992 (which has been classed as female), but its molar-crown area is large (twice the molar-crown area of KNM-ER 992) and therefore would presumably put it in the male category.

The discussion about the evolutionary significance of molar-area dimorphism may also not be as firmly based on fact as it would appear. While there may be significant intragroup correlations between body weight or body size and posterior-tooth size, intergroup comparisons show no consistent relationship. In data recently collected in a study of allometry in modern primates (Wood 1976), dimorphism in the molar-crown area (a more satisfactory measure than one including the "area" of sectorial premolars) was about 90% for *Homo, Gorilla,* and *Pan,* groups which show a range of body-size and body-weight dimorphism. Even if it were true that australopithecines showed excessive molar-area dimorphism, it is not necessarily a corollary that body-size dimorphism would also have been excessive.

Wolpoff's discussion also takes no account of allometric relationships. Intergroup plots of molar-crown area and canine-base area are both positively allometric when related to body size, but their slopes are such that canines increase in size at a faster rate than the molars in larger forms (Pilbeam and Gould 1974, Wood 1976). Despite this positive allometry, however, the food-preparation area represented by the molar-surface area does not keep pace with energy requirements (Kay 1975). Although functional correlations within the dentition related to diet have been observed (Kay 1975), there seems to be no reason to assume, as Wolpoff does, that molar-crown area was necessarily the factor being selected for in primate and hominid evolution. Differential body size is an integral part of the social organization of many primate groups, and molar-area changes may have been secondary to selection for body size.

Either way, there is currently a sufficient scarcity of data that even the most fanciful theories can, at least temporarily, escape refutation. In summary, although Wolpoff's a priori assumptions are well disguised in the first part of the paper, they come to the surface when variables other than canine size are discussed.

by SRBOLJUB ŽIVANOVIĆ
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Sex determination of primate fossil skeletons is undoubtedly very important. Unfortunately, it is an extremely difficult procedure because of the very poor state of preservation of the

skeletal remains. I agree with the author that the best results are obtained by studying the pelves. The pubic bones show quite clear sexual dimorphism (Phenice 1969, Genovés 1959), but it is very rare to find these bones intact. For this reason we (Jovanović and Živanović 1964, 1965) have developed a new method for the determination of sex in normal and pathologically deformed human pelves by measurement of the great sciatic notch, usually the only surviving part of the hip bone found at an archaeological site.

The author describes sexual dimorphism in terms of the values of the breadth of primate canines, which may be significant in establishing the sex of a specimen. Experience has shown, however, that it is not sufficient to consider only one feature when studying fragmentary skeletal remains. It would be useful and important to seek further indicators in a manner similar to that described in this article to establish an accurate method of sex determination.

Reply

by MILFORD H. WOLPOFF

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While I thank the many correspondents who support the hypothesis set forth (Aguirre, Becker, Hajn, Kennedy, Murad, Rao, Rosiński, Smith, and Živanović), I am also in sympathy with the skeptics. I have presented a model which I believe accounts for certain distributional data in a consistent and parsimonious manner—criteria for a useful hypothesis, but not evidence of its correctness. It is important to discuss the current state of the model in the light of these comments. It would be useful, however, first to clarify some of the points raised. It is true, as Wood suggests, that with a scarcity of data "even the most fanciful theories can, at least temporarily, escape refutation." Witness the attempts to determine differences in locomotor patterns of Lower Pleistocene hominids as inferred from the functioning of the lower limb, in turn inferred from the functioning of the foot, as inferred from metric analyses of the very few complete and fragmentary isolated tali! The problems here, however, result from an embarrassment of data rather than from its scarcity. The following questions have been raised and should be considered:

Is it valid to attempt sex determination from a single skeletal element (Kennedy, Murad, Rosiński, Trinkaus, Živanović)? This question is answered by Becker. It is of necessity, rather than by choice, that I have attempted to rely on a canine dimension. Undoubtedly, greater accuracy could result from more criteria, but there is a trade-off which must be considered in a sample such as this; the more the criteria, the smaller the sample they can be applied to. There is no question that the use of canine breadth will result in individual inaccuracies (such as those discussed in the text). I would still argue that it is the separate sex distributions as determined by canine breadth, and their statistics, that are accurate. The best evidence supporting this can be found in the chimpanzee distribution analysis, where the dimorphism characteristics established in a manner parallel to that used for the early hominids are a very accurate estimator of the true dimorphism, in spite of the considerable overlap between sexes and the commensurate misidentification of many specimens. The procedure would be fallacious only if the early hominid distributions were, like those of living humans, lacking in both bimodality and any significant degree of non-overlap between the sexes. The aim was never to establish a single unique and completely accurate dental determiner of sex, but rather to establish the best dental determiner of sex and then discover the likely limitations to its accuracy.

Is the early hominid distribution really bimodal (Kennedy, Siegel, Trinkaus)? There is no direct test for bimodality, but the distributions are not normal and appear to be bimodal.

While this appearance may be deceiving, no other specific explanation has been offered. Trinkaus is incorrect in arguing that one would expect the separate distributions for each sex necessarily to be normal when the combined distributions are bimodal. Use of the chi-square in the separate sex distributions in the gorilla sample does not disprove normality. In the chimpanzee sample, however, both male and female mandibular distributions deviate from normality, the male to a more significant extent. For the australopithecines, my data differ somewhat from those Trinkaus presents, since determination of normality should not be made in the absence of part of the data (he deletes data points falling in the 9.5–9.9-mm span). The only significant deviation from normality is in the male maxillary sample. Thus, in this regard the australopithecine distribution is somewhat like that of the chimpanzees; the combined distribution is not normal, and at least one of the component distributions is not normal.

Trinkaus's statistical argument does not disprove the contention that the australopithecine distributions may be sampled from a bimodal distribution, just as his demonstration that deleting the data points between 9.5 and 9.9 mm results in high chi-squares for the total remaining sample does not disprove it. Although the latter procedure indeed suggests that the deviation from normality is not due to the low frequency of specimens in this interval, this absence of normality in the separate sex distributions also seems to characterize chimpanzees.

Only one class-interval separates the australopithecine modes (or, more accurately, the extremes of the modes), contrasting with the wider separation in gorillas. One interpretation raised is that this demonstrates that the distributions are really normal "and simply reflect the small number of observations in all but a few of the class-intervals" (Siegel). Trinkaus's chi-squares indicate, however, that this is not the case. Moreover, the size of the interval between sex modes may instead reflect the lower canine-breadth variance (table 10).

Finally, Siegel's claim that a shift in the defining intervals for the classes in the early hominid sample would cause the bimodality to disappear, leaving "a perfectly normal distribution," is incorrect. This can be demonstrated by plotting the cumulative frequency distribution, thus eliminating any possible bias provided by particular class-intervals. The apparent bimodality also characterizes the cumulative distribution, in this case appearing as a horizontal portion between curve segments that descend fairly steeply. Additional specimens will surely help clarify whether or not the deviation from normality demonstrable in this sample really characterizes the distribution from which it was drawn and whether or not this deviation is the result of a bimodal underlying distribution. Statements that the existing data were inaccurately treated provide no insight into these problems.

Even assuming that the australopithecine distributions are bimodal, is this necessarily the result of sexual dimorphism in canine breadth (Aguirre, Kennedy, Murad, Wood)? In the virtual absence of postcranial remains which can be sexed and which are associated with canines, it is impossible independently to verify this assumption. Yet, what other explanation is there? Wood suggests that this scheme, when applied to the East African sample, makes "most of the 'Homo' specimens come out as small females, whereas the robust material is classified as male." Lest this lead to a resurrection of the idea that somebody believes "graciles are females and robusts are males," it should be pointed out that table 20 indicates nothing of the sort. The 38 East African robusts have an exactly 50–50 sex ratio. While it is true that females are more prevalent in the (smaller) East African "Homo" sample, one must consider the very real possibility that this results from the placing of specimens with small dentitions in this taxon because of small tooth size.

The fact remains that if this distribution results from mixing

a small-canined with a large-canined taxon, as Murad and Wood suggest, the former taxon must include specimens as diverse as the Natron mandible and OH 13, while in the latter fall OH 5 and ER 1470 and 1590. I do not deny that species-level taxa may be mixed, but *regardless of the number of species present these data indicate that they do not differ significantly in canine size or its dimorphic distribution.* Put another way, marked sexual dimorphism and a bimodal canine-breadth distribution seem to characterize this Pliocene and Lower Pleistocene sample, whatever the lowest level of organization within which the entire sample can be included. It was not my purpose to discuss whether this level is species, genus, subfamily, or family, but rather to indicate the extent and distribution of the sexual dimorphism.

Finally, is it justifiable to use the entire early hominid sample in the determination of possible sexual dimorphism (Aguirre, Siegel, Wood)? It is true, as Wood suggests, that ultimately a priori assumptions "come to the surface" with regard to this approach. Yet, were they ever submerged? I never meant to disguise the fact that, in my view, the conservative approach is to assume a sample includes only one taxon until proof to the contrary is brought forward. Rhetoric should not be used to sanctify one viewpoint when there are honest differences in interpretation. Thus, continually characterizing adaptation and behavior in graciles and robusts as "undeniably divergent" ignores the work of those who have denied this for adaptation and behavior as inferred from the cranial (Wolpoff 1973) and postcranial (Lovejoy, Heiple, and Burstein 1973) morphology, as well as for sexual dimorphism (this paper), delayed maturation (Mann 1975), direct association with artifacts (Bishop and Pickford 1975), etc. Right or wrong, these interpretations will not disappear as a result of being ignored or misrepresented.

There may be a very real problem of obscuring differences by lumping specimens from differently adapted taxa, as some commentators suggest. An equally critical problem, however, is inherent in the opposite procedure. A sample as finely divided as is sometimes proposed for the australopithecines can result in subsamples so small that a demonstration of differences between them becomes, in effect, a demonstration that no two individuals are the same. A sample should be constituted in the light of the question being asked of it. If variation through time is being studied, the time levels cannot all be lumped. Conversely, if marked sexual dimorphism seems to characterize all of the early hominid samples, there is no reason they cannot be considered together in a study of early hominid sexual dimorphism. A high level of dimorphism may not be species-specific in the early hominids, but rather may characterize whatever number of species it is ultimately decided existed. In sum, lumping the specimens is justified because of the similarities seen in canine size and breadth dimorphism. It makes no assumptions concerning the number of species present, and if it turns out that the sample consists of more than one species lumping is still justified on this basis. If species could not be lumped for various comparisons, what would be the purpose of having higher taxonomic levels?

A few minor points: The criteria underlying the composition of the East African "Homo" sample appear contradictory and confusing to others besides Aguirre (see Wolpoff and Brace 1975). The recent discovery of an undoubted *H. erectus* cranium in the latter portion of the East African early hominid sequence (Leakey and Walker 1976) detracts little from the contention that "Homo" can only be delineated from relatively complete cranial and dental remains. The specimens referred to as "Neandertals" could just as well be called "archaic *H. sapiens*," "early *H. sapiens*," or anything else that meets with general agreement. "Neandertal" is not the name of a formal taxon, and in my view a lot of type has been wasted on discussions of what to call this group, since the group remains the same whatever label is given to it. However, I believe Kennedy misses the point of my use of this group for comparison. I picked it precisely because it lumps specimens as diverse in time and space as Petralona, Skhūl 5, and Spy 1. This, I argued, would make for a more valid basis for comparison with australopithecines, also temporally and spatially diverse. Both these fossil samples differ fundamentally from Garn's "Ohio Whites" in that it must be assumed that each of the fossils is drawn from a different biological population, whereas many "Ohio White" individuals are drawn from a single one. Contra Wood, neither ER 729 nor ER 992 was mistakenly omitted from table 17. This table suggests assignment of sex on the basis of molar size for specimens without canines, and both these specimens have canines. Applying the information in table 12 to the canine dimensions of these individuals (table 2) indicates that the former can be regarded as male and the latter as female, precisely the results that would be obtained if molar size *were* used in this determination. The breadth dimensions of the two canines, described by Wood as "almost identical in size," differ one standard deviation from the combined-sex sample and two standard deviations from the male sample.

With regard to the current status of the sexual dimorphism model, I believe now, as I did when the paper was written, that early hominids have marked sexual dimorphism and that this can be estimated by the observed bimodal canine-breadth distribution. Two subsequent developments, however, lead me to regard the problem of *individual* assignment of sex with even more caution. First, the Miocene and Early Pliocene hominids from the Afar and Laetolil in East Africa provide evidence of some degree of canine-size reduction during the time span represented by the early hominid sample. Second, as Wood correctly states, I did not take allometry into account.

Wood states that, when related to body size, the allometric constant for canine area exceeds that for molar area in primates. By inference, the power curve of canine area (dependent variable) related to molar area should have a positive exponent exceeding 1 (the linear relation). The basis for this inference is as follows: If C = canine area, M = molar area, and W = body weight, Wood's claim can be written $C = A_1 W^{b1}$, or $\mathrm{Log} C = \mathrm{Log} A_1 + b_1 \mathrm{Log} W$; $M = A_2 W^{b2}$, or $\mathrm{Log} W = \mathrm{Log} A_2 + b_2 \mathrm{Log} W$; $b_1 > b_2$. It follows from eliminating W that $\mathrm{Log} C/b_1 - \mathrm{Log} A_1/b_1 = \mathrm{Log} M/b_2 - \mathrm{Log} A_2/b_2$. Replacing the constant term by K, $\mathrm{Log} C = K + b_1/b_2 \mathrm{Log} M$, or $C = KM^{(b1/b2)}$. Since $b_1 > b_2$, the allometric exponent must exceed 1. The question

TABLE 21

ALLOMETRIC DATA FOR THREE HOMINOID SAMPLES

	MALES				FEMALES				COMBINED SAMPLE			
	A	*k*	*r*	*N*	*A*	*k*	*r*	*N*	*A*	*k*	*r*	*N*
Orangs..................	25.28	0.40	0.313	45	1.66	0.85	0.572	49	0.01	1.61	0.682	94
Gorillas................	8.20	0.65	0.428	171	4.70	0.64	0.474	87	0.01	1.87	0.593	258
Chimpanzees...........	6.71	0.67	0.404	75	10.30	0.50	0.316	83	1.38	0.97	0.409	158
Living humans..........	3.50	0.59	0.507	68	5.63	0.46	0.321	86	1.57	0.74	0.505	154

NOTE: Coefficients were determined through a least-squares fit and are of the form Y (canine area) = $A \cdot X$ (lower first-molar area)^k. The correlation (r) of the tooth areas and the sample size (N) are also indicated. The living human sample consists of Libben Amerinds, skeletally sexed.

of possible allometric effects is important, since it bears on the relation of the anterior and posterior dentition. Gould (1975: 359), however, states that "there is a general trend in higher primates for allometric reduction of the canines and incisors in large animals."

The contradiction between these statements can be resolved by taking sexual dimorphism into account. Allometric (power) curves for canine area as a variable dependent on first-molar area were derived for the mandibular dentitions of the three great-ape species and a living human sample. The data for males, females, and the combined sample vary systematically with degree of sexual dimorphism (table 21). The allometric exponent is highest for species with the greatest dimorphism and exceeds 1 for both gorillas and orangs. In all cases the combined-sample exponent exceeds those in the separate sexes, and the latter are always less than 1. Thus, the combined samples in dimorphic species support Wood's statement, while the others support Gould's. These allometric relations show that within-sex relative canine size decreases as molar size increases. In other words, larger males will have relatively smaller canines than smaller males.

Determining the allometric relations for the australopithecines is bound to be inaccurate, since the fossil specimens all probably represent different populations. Moreover, if the allometric relation is to be used in a taxonomic context, taxonomy cannot enter into the determination of allometry. Finally, the small sample sizes further reduce the validity of any conclusions, no matter how cautiously drawn. An attempt to determine mandibular allometry for the mandibular sample, again relating canine to first-molar area, results in an exponent not significantly different from 0 for the combined sample of all taxa. Restricting analysis to subsamples most workers would agree represent a single lineage, the exponent for all robust females is -0.89 ($N = 7$), not very different from the exponent for the South African robust females alone, -0.74 ($N = 5$). The robust male exponent ($N = 5$) is -0.50. *These exponents, as well as those for virtually every other combination of specimens, are negative* when sex is held constant. Thus, in the australopithecines, *absolute* canine size is smaller in the larger-molared specimens within each sex. That the combined sample has an exponent of 0 can thus be seen as a result of larger canine size in the males compensated for by the negative allometric relation between the canine and first molar.

The effect of allometry on the analysis of these specimens depends upon which model is thought to apply. Virtually any higher-primate model, however, results in *relatively* smaller canines in specimens with larger molars within each sex. In other words, that robust males have relatively smaller canines than gracile (or perhaps "Homo") males is a consequence of allometry and not necessarily a reflection of differing adaptation, behavior, etc. Moreover, if the negative allometry which describes restricted samples of each sex is a true reflection of the taxon, larger males might be expected to have absolutely smaller as well as relatively smaller canines. Smaller females might be expected to have absolutely larger canines. The effect of this phenomenon on the data presented here can be seen in the analysis of specimens recovered since the paper was written. The very large Rudolf mandible recently published by Leakey (1976) should be a male on the basis of corpus height and molar area. Yet, ER 3230 has a 9.2-mm canine breadth, which places it in the upper end of the female range. The molars are so large that the negative allometric effect could result in a lower male range for the extremely large specimens, such as this, ER 802, or Omo L7-125. If the *robust male* allometric curve is applied to the new specimen, the predicted canine area is 74 mm², not much different from the actual area of 72 mm². Thus, the lower boundary for the male range is probably too high for the largest specimens. In the Laetolil and Afar samples (Johanson and Taieb 1976), specimens with smaller molars are found. In the females, the smallest-molared individuals might be expected to

have canines in the male range (and the males with smaller molars might be expected to have *very* large canines). For females with small canines, the boundary separating males and females might have to be shifted upwards for more accurate sexing.

In sum, if allometry is taken into account, relative canine size very likely decreases in the specimens with larger molars within each sex. Moreover, early hominid allometric exponents appear to be negative, utilizing robust specimens only to maximize taxonomic agreement. This negative relation is highly predictive in terms of recently discovered specimens and, if valid for the entire sample, suggests that at the ends of the molar-size range the section point separating sexes must be shifted upwards for the smaller specimens and downwards for the larger ones.

Only a few commentators discussed the wider phylogenetic implications of this model. Siegel questions the use of *D. africanus* to represent the ancestral species. I could respond that it was convenient, since specimens have been sexed and the dimorphism already studied by Greenfield. A more compelling basis for this choice, however, is that the other well-published African Miocene dryopithecine species, combining *D. major* with many of the *D. nyanzae* specimens (*D. nyanzae/major*), appears to have been equally dimorphic. The likelihood is that one (or perhaps both) of these early dryopithecine species represent the common ancestor of hominids and the living African pongids, a view apparently agreeable to Aguirre. Only in the absence of fossils is it parsimonious to create common ancestors from expectations.

Rosiński questions whether cultural behavior could alter the selection acting on all of the known canine functions in the nonhuman primates. This point is difficult to demonstrate, but is not contradicted by trends toward canine reduction in certain hominoid lineages. Thus, in a continuum of taxa from *Ramapithecus* and *Rudapithecus* to *Bodvapithecus*, *Dryopithecus macedoniensis*, and *Gigantopithecus bilaspurensis*, all show canine reduction, while probably no more than one of these, if any, represents the lineage leading to hominids. That culture can result in canine reduction is not contradicted by the fact that other behaviors can accomplish the same effect. Moreover, only the hominids underwent selection to alter the entire functional complex involved. While it is far from impossible that initial canine reduction led to selection favoring tool use, increasing efficiency of tools would have altered selection acting on the canines and affected their subsequent further reduction and morphological change. There is no reason the hypothesis proposed by Rosiński must be considered "opposite" to mine.

I thank the commentators for their help in discussing this hypothesis. Ultimately, it should stand or fall with the accumulation of additional data. Whether it is right or wrong, however, I hope that this discussion will help sexual dimorphism become a topic of more research activity in evolutionary studies. Since in many respects it clearly represents an interface between morphology and behavior, I believe that there is much to gain from the analysis of trends in the evolution of hominoid sexual dimorphism.

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