SEXUAL DIMORPHISM

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INTRODUCTION

That the human species exhibits sexual dimorphism in size, shape, and be-
havior is an obvious conclusion from anyone's simple participation in society.
It is common knowledge that males have a larger stature than females, more
robust cranial and facial features, along with greater muscularity, strength, and
speed. In all human groups, male tooth size exceeds that for females, females
store more subcutaneous fat, males have proportionally more muscle fiber, pre-
and postnatal hormonal levels differ, growth rates vary, and diseases affect the
sexes differentially (122a, 278). The fact that most of these differences do not
occur in infants, children, and subadults, but are typical primarily in the adult
stage, indicates that many of the effects are the result of hormonal events
occurring at puberty (23). Like the primary sexual characteristics (i.e. differ-
ences in external genitalia), secondary sexual characteristics are largely con-
trolled or mediated by X-linked genes (247), although they differ in control
from the primary ones in that the environment has a more direct influence on
their expression. For example, muscular differences between males and
females converge when comparing an athletically active female to a nonactive
male. As another measure of plasticity, nutritionally deprived adolescent males
have a greater reduction in realized stature than females suffering similar
protein shortages. Differences in the plasticity of males and females, along
with the underlying genetic differences, provide evidence for a long-term
selection regime in which human males and females, each in their own ways,
have responded to reproductive, environmental, and cultural factors. The intent
of this review is to establish what can and cannot be said about human sexual

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dimorphism. We will examine this phenomenon in the context of primate and other mammalian dimorphism patterns and in the light of human evolutionary history. Our purpose, however, is not to document the variation but rather to attempt its explanation. Thus, our main focus will be on discussing, elaborating, and when possible testing the models that have been proposed to account for differing magnitudes of sexual dimorphism, and when possible we will use these models to help explain the human condition.

Dimorphism in the human skeletal system and in dentition is well established. It has been studied in detail because of the importance of accurate sex determination for archaeological remains (2, 20–22, 27, 30, 30a, 33, 43–45, 47, 51, 65, 66, 70–73, 75, 85, 101–105, 111–115, 133–137, 142, 145, 148, 149, 153, 154, 162, 166, 167, 174, 184, 209, 221, 225, 235, 237, 240, 248, 252, 260, 271–273, 284, 291–293, 294a, 295). These studies focus more on the determination of sex from various parts of the skeleton than on the degree of dimorphism. Even so, they provide, perhaps inadvertently, important information about the populational variability in the sex differences. This variation is great enough for the magnitude of sexual dimorphism itself to become one of the criteria used in establishing the region of origin for a skeletal sample. However, like so many other osteological criteria purporting to describe regional differences, the magnitude of sexual dimorphism may differ greatly from population to population, but it does not seem to differ on the average from region to region.

As a background to the sexual dimorphism in living groups, there is substantial evidence to show reduction of sexual dimorphism in the human lineage. Plio/Pleistocene hominids exhibit a level of dimorphism for tooth, cranial, and skeletal dimensions much greater than subsequent groups. Early *Homo* samples and other more recent Middle and Upper Pleistocene forms display levels of dimorphism intermediate between *Australopithecus* and extant groups (311). Similarly, when considered all together, European Upper Paleolithic groups have more dimorphism than their Mesolithic and Neolithic descendants (92, 93). Thus contemporary populations, as well as their fossil and more recent ancestors, consistently show sex differences. These appear to be greater in earlier populations.

Although sexual dimorphism is easily observed and well documented for fossil and extant groups, models accounting for its existence and persistence, as well as the trends for reduction, are varied and sometimes contradictory. Some of the confusion relates to the complexity of the underlying genetics and the interaction of environmental variables. As amply shown in anthropological genetics, traits of simple inheritance are much easier to analyze and interpret than those resulting from polygenic effects (200, pp. 21–22). Since the majority of sexually dimorphic traits are determined by polygenes, evolutionary explanations must consider nongenetic and genetic influences. In addition, the

capacity of culture to override biological constraints and to substitute behavioral solutions makes it difficult to apply many of the models for sexual dimorphism deriving from nonhuman evolutionary biology. Moreover, uniformitarianism aside, there is no justification for assuming that the same factors controlling the maintenance of sexual dimorphism today are the same or at least related to the ones working in the past (25, 83, 89, 156, 213, 278, 297, 302).

In a broader context, studies of mammalian dimorphism, and specifically of dimorphism in the nonhuman primates, indicate that explanatory models must be more general than the human studies by themselves might suggest. Such a broader context is dictated by studies of dimorphism in groups as diverse as amphibians and reptiles (50, 251, 265, 270, 315), bats (220), rodents (78, 79, 178), decapods (3), insects (28, 90), and birds (9, 24, 74, 76, 234, 261, 262, 264, 279). The nonhuman primate literature is particularly extensive (7, 14, 17, 29, 56, 57, 69, 77, 96, 97, 107, 108, 116, 140, 144, 146, 161, 187, 188, 193, 195–197, 212, 224, 232, 233, 238, 239, 245, 253–258, 297, 298, 308, 314). While most of these establish some degree of dimorphism in particular primate species, and many relate this to specific evolutionary models, a few workers describe primates in which dimorphism is virtually or completely absent (59, 61, 172, 173, 217, 320, 322, 323). On the face of things, this diversity of fact and hypothesis suggests that if there is a general explanation of sexual dimorphism, it is likely to be complex (62, 83, 121, 242).

The literature on human sexual dimorphism can be viewed from the separate perspectives of proximate or ultimate causation. A proximate explanation considers sexual dimorphism as a response to nutritional stress or overall improvements in the environment of growing adolescents. Such nongenetic factors account for secular trends for increases in sexual dimorphism in recent groups or over periods of nutritional changes. Ultimate causation models view sexual dimorphism as a genetic adaptation to a variety of ecological, social, or economic factors, and traditionally incorporate selection as the primary explanatory mechanism. Though ultimate causation models have occupied a greater place in the literature, they do not necessarily explain short-term fluctuations in sexual dimorphism.

PROXIMATE CAUSATION

Numerous studies have documented a decrease in male/female differences in stature under conditions of nutritional stress and an increase in dimorphism with improved diet (39, 127, 131, 147, 176, 201, 274–278, 286, 303). Males are more susceptible to fluctuations in nutritional quality and show greater impairment in long bone growth. Females are less affected by nutritional shortages and prove to be more stable under the same food deficits, presumably because of reproductive demands, storage of more subcutaneous fat, and

overall smaller body size. These differential growth vectors generally result in both a collapsing of the male and female mean adult statures and a reduction in the level of sexual dimorphism in body size. Nutritional factors, then, may explain trends for reduction in dimorphism in some horticultural and agricultural groups, since there is good documentation for the decline in dietary sufficiency in the shift from hunting and gathering to agriculture (185, 219, 228). However, we view this factor as a short-term consequence of deprivation and of little relevance for explaining patterns of reduction from australopithecines to early postglacial hunter-gatherers.

Proximate causation for sexual dimorphism changes are not without more ultimate (i.e. evolutionary) consequences. A possible long-term effect of nutritional shortages would be a shift toward smaller adult body size in both sexes. Should the dietary deficiencies become chronic, selection would operate to reduce body size with respect to energetic efficiency. Since males would be under more intense selection, sexual dimorphism should decrease. Furthermore, since body size is positively correlated with the degree of sexual dimorphism (53, 55, 195), any selection for smaller body size should result in reduced sexual dimorphism. Some evidence for this model is found for small body size and low levels of sexual dimorphism of agricultural groups in North America (40, 133), Mexico (228), Europe (94, 95, 170), India (168, 169), China, and Southeast Asia (37, 38, 205).

However, exceptions occur where nutritional patterns and sexual dimorphism are not correlated in modern populations (202) and where groups undergoing the transition from hunting and gathering to agriculture exhibit an increase in sexual dimorphism, because of greater reduction in female body size, as described by Larsen (185), or, as Tobias (286) has shown for the San, a greater increase in male stature. In the former case, Larsen argues that females have differential dependence on agricultural foods and show depressed nutritional status and growth retardation as a consequence. In the latter case, as Bushman groups become more sedentary and adopt "Neolithic" forms of subsistence, there has been a marked increase in male stature. These results present a stark contradiction to the nutritional hypothesis, given evidence for nutritional adequacies of hunting-gathering San (177, 290). As Eveleth (82) and Wolfe & Gray (305) have argued, it is difficult to demonstrate the relationship between nutritional status and sexual dimorphism in a worldwide sample. This must result at least in part from the interplay of proximate and ultimate causation for variation in sexual dimorphism. These clearly are not independent.

ULTIMATE CAUSATION MODELS

Because virtually all higher vertebrates exhibit sexual dimorphism, a great deal of effort has been made to explain the biological cause(s) and genetic mecha-

nism of this underlying pattern of life. Unlike the proximate model discussed above, these models assume that environmentally mediated growth disruptions have little direct influence on adult body size, so that sexual dimorphism is related to different selection forces operating on males and females, according to Lande (182, 183). Ultimate causation models attempt to explain the conditions and existence of sexual dimorphism in relation to underlying genetic adaptations, which are tempered by selection forces. Historically, a number of ultimate causation models proposing to account for differences in sexual dimorphism have been published. Some of these are now understood to be based on faulty biological thinking, while others, such as the idea that female preference for male traits with no functional significance is a way of reducing or eliminating male sex chromosome parasitism (31), are undeserving of further comment. We will discuss what we believe are the four main ultimate causation models that have been seriously considered in recent years. These are 1. sexual selection and mating patterns, 2. body size, 3. economic patterns and the division of labor by sex, and 4. noneconomic role differences. The models are not necessarily mutually exclusive, and indeed it is the lack of clearly defined contradictions in the predictions generated from them that has made them so very difficult to decide between. It is possible that none of the causal models discussed here may be entirely irrelevant in the causation of sexual dimorphism.

Sexual Selection and Mating Patterns

Darwin (64) was the first to suggest that certain aspects of sexual dimorphism in humans and other animals could be attributed to selection occurring between members of the same sex (231). The critical factor in sexual selection is the reproductive advantage certain phenotypes have in attracting or acquiring mates, so that sexual selection is primarily invoked to explain selection operating on males (16). For example, Darwin ascribed gaudy coloration and ornamental plumage in some male birds and larger body size in most male mammals to intermale competition for females (64, pp. 210–211). However, it is also true that selection on or between females may play an important role in this relationship (52a, 294a).

Coupling female preference for better endowed males with the greater ability of large aggressive males to limit access of other males to females, these larger, more aggressive males would be more successful in leaving offspring (234). Thus, for sexual selection to promote differences between the sexes, certain social conditions must be met (32, 81). Principally, there must be unequal opportunities of access to females by males (some individual males can potentially have more offspring than females) which is established by a dominance system, a polygynous mating system (which results in a number of individual males having few or no offspring), and, probably, some operation of female discrimination or choice (4, 52, 57a, 98, 182, 183, 211). When such conditions

are met, males compete with each other for control of females, and those with larger body size and a more aggressive personality, for example, have greater success in monopolizing their own breeding rights and territories, thereby contributing differentially to the next generation.

Numerous examples of mammals and other animals seem to corroborate these predictions, for example, a number of bird families (234), elephant seals (191), many ungulates (5, 157), langurs (150), macaques and baboons (26), orangutans (249), and other species (see 3, 4, 54, 56, 108, 122, 223) where male body size is considerably larger and more variable than body size in females, and have high male reproductive variance relative to female variance, at least when observed for individual mating seasons. The most extreme case is probably California elephant seals, where males are three times the size of females and the chance of any male leaving offspring is less than 10% (191, 192).

For mammals in general, correlations between sexual dimorphism and the mating system are also upheld when considering most monogamous species (5, 265). In monogamous groups, females are occasionally even larger than males, resulting in reverse dimorphism (241, 244), although monomorphism general-ly prevails so that body size, canine dimorphism, and other secondary sexual characteristics are not substantially different among males and females. Be-havioral differences are also similar in that females can be equally aggressive and in some cases dominant to males (176). Male investment in offspring is greater in monogamous species (151, 152, 176, 181), which according to Trivers (289) and others (63, 106, 234) would reduce the competition between males. Moreover, in most monogamous species, males and females participate equally in defending young and territory, scent marking, vocalizations, groom-ing, and infant care (176).

Among the birds there does seem to be some sort of relationship between mating system, paternal care, perhaps even body size in some families, and the magnitude of sexual dimorphism (9, 74, 234, 242, 261, 262, 279). The mating system-dimorphism relation, in particular, seems particularly well founded in a recent study by Payne (234). This may be because the range of mating systems that can be analyzed in birds extends beyond the normal mammalian range. In his analysis of bird families, Payne discusses a scale of continuous mating behavior variation, ranging from monogamy through polygyny to lek and exploded arena systems. The later two permit no paternal care of the young and involve an important degree of female mate choice. With this magnitude of mating system variation, data clearly show a higher male success variance in lekking species than in monogamous ones. Yet it is unclear how far beyond the bird families studied this observation can be used since an analysis of Payne's data (234, table 2) also shows that polygynous males do not have a significantly greater variance in reproductive success than do the males of monogamous

species (p = 0.15 using a student's *t* test). Even the basic observation that body size dimorphism differs with mating system was established only by comparing lek species with monogamous species. The more relevant comparison (for mammalian studies) of polygynous species with monogamous species shows a relation between dimorphism and these mating systems for only a few of the families discussed. Because the lekking species are characterized by more potential "causes" of dimorphism than male-male competition (for instance, an important element of female choice, the complete lack of male investment in offspring, and generally larger body size), it is unclear exactly what the bird data show. Specifically, while there might be a correlation between mating system and body size dimorphism among bird taxa, the nature of the relation (only significant between the extremes), the range of mating systems considered, and the number of independent variables make it difficult to establish cause clearly and problematic to extend the conclusions to the interpretation of mammalian variation. Thus, while these data bode well for the potential explanatory power of sexual selection in explaining the variation of sexual dimorphism among many bird species, between the lack of an unambiguous causal hypothesis accounting for the bird data and the greatly reduced variation in mammalian mating systems, it is not clear that the potential relation of sexual selection and sexual dimorphism in the primates can be illuminated.

Studies on primates have reported some weak and strong correlations between sexual dimorphism and mating systems. In numerous publications Leutenegger (195, 197–199) has argued for a small contribution of mating systems to levels of sexual dimorphism in primates, while an opposite position has been taken by Clutton-Brock (52a–56) and others (4, 16, 32, 50, 98, 107, 289). This inconsistency of interpretation is not surprising since some monogamous species (such as *Saguinus mystax*) show marked dimorphism while some polygynous species *(Propithecus verreauxi, Presbytis frontata)* show little dimorphism (52a, 54, 108). Moreover, selection acting on males and on females may be of fundamentally different origin. Even if male reproductive success is primarily a consequence of access to females, female reproductive success may be more dependent on female access to food supplies if food is a limiting resource (289). Finally, much of this difference in opinion and perspective relates to the nature of the statistics used and assumptions made, so that it is difficult to reach an easy answer to the controversy.

The problem with assuming a simple relationship between mating system and sexual dimorphsism within the primate is the breadth of the variation in the primate order. Although the common assumption is that monogamous primates are monomorphic and polygynous primates dimorphic, there are numerous exceptions to this "rule" which produce poor correlations between mating type and dimorphism (107) when all primates are considered. In some respects this should not be surprising since mating patterns are not easy to categorize nor to

compare across different taxa. For example, both Leutenegger & Cheverud (198) and Gaulin & Sailer (107) include solitary species of prosimians in their analysis as nonmonogamous, yet this form of polygyny is not comparable to the more social prosimians let alone higher primates. At the same time, there are different intensities of polygyny in Old World monkeys and apes which call into question correlations across major taxa.

We have combined the data of Leutenegger & Cheverud (198) and Gaulin & Sailer (107) and reorganized the body weight dimorphism by major taxa (Table 1). On the surface, differences between the mating systems would appear to explain much of the variation in sexual dimorphism. Thus, in apes, the monogamous gibbons and siamangs have low dimorphism ($\bar{X}$ = 103.5), while the more polygynous apes show increased levels ($\bar{X}$ = 144.4). Similarly, New World monkeys that are monogamous have low levels of sexual dimorphism, while polygynous forms express marked sex differences. In the single monogamous species of prosimians (for which data exist), the *Indri* males and females are equal in size. Nonsolitary, polygamous prosimians show an average dimorphism of 110.6.

Despite these differences, there is a range of variation among the primates that detracts from any confidence in a strong relationship between weight dimorphism and mating system. Except for the prosimians, the monogamous species within each comparison are substantially smaller in body size than the polygynous species. They also tend to be more continuously arboreal. In addition, there is an incredible range of variation within each comparison according to the species presented in the summary tables of Leutenegger & Cheverud (198) and Gaulin & Sailer (107). In these tables (not reproduced here), gibbons and siamangs show a range from 93.5 *(H. moloch)* to 113.2 *(H.*

Table 1   Sexual dimorphism in body weight for living primates[a]

Species	Weight Dimorphism	Range	n
Monogamous			
Apes	103.5	93.5–113.2	7
OW monkeys (Mentawai langur)	101.6[b]		1
NW monkeys	101.6	95.0–112.5	7
Prosimians (indri)	100		1
Polygamous			
Apes	144.4	120.0–192.7	4
OW monkeys	143.7	98.9–236.4	37
NW monkeys	123.8	95.5–155.7	11
Prosimians	110.6	100.0–126.2	4

[a]Data are from Gaulin & Sailer (107), Leutenegger & Cheverud (198a), Tilson & Tenaza (285a), and Wrangham & Smuts (316). Weight dimorphism is the index of male weight/female weight × 100.
[b]Monogamy in the Mentawai langur is of recent origin (83).

lar) and chimpanzees, gorillas, and orangutans vary between 120.0 and 192.7. In New World monkeys, the monogamous forms range from 95.0 *(Callithrix jacchus)* to 112.5 *(Sanguinus mystax).* The polygynous New World monkey species also show a great deal of variation and overlap at the bottom of the range with the monogamous forms. A similar pattern holds for the prosimians. Finally, among the Old World monkeys [which are all polygynous except the Mentawai langur (285a)], there is a remarkable spread in the range between the least and most dimorphic forms. From the data tables of Leutenegger & Cheverud (198) and Gaulin & Sailer (107), the least dimorphic is *Presbytis frontata* (98.9) and the most dimorphic *Mandrillus sphinx* (236.4). Between these endpoints is an array of arboreal and semiterrestrial, small- and large-bodied forms that show great variation. Ten species have indices, of dimorphism below 110, while in six species the index exceeds 175.0. There appears to be no simple rule for predicting the cause of dimorphism among these polygynous Old World monkeys since some small-medium forms show great dimorphism (e.g. *Erythrocebus patas*-176.9) while others (e.g. *Colobus satanus*-111.1) show little dimorphism. Furthermore, some completely arboreal forms such as *Nasalis larvatus* show very marked dimorphism (206.0), while semiterrestrial forms such as *Macaca cyclops* exhibit much smaller male/female differences (121.3).

Perhaps this lack of patterning, or of an unambiguous association between the variables, should be expected. If body size dimorphism in a polygynous species is presumed to be causally linked to differential reproductive success in the males (resulting from increased intermale competition), the fact is that unlike the case for birds in which lekking and monogamous species could be compared, the actual variation in lifelong male reproductive success in polygynous mammalian species has never been shown to exceed the variation in lifelong reproductive success for males in monogamous species (52a). The presumed cause of this difference may not exist, a possibility not diminished by the analysis of the bird data that shows males of polygynous and monogamous species also do not differ significantly in the variance of their reproductive success. Thus, although it is a common notion in anthropology that polygamous species have great dimorphism and monogamous species have only small sex differences, there is no clear rule for predicting the degree of sexual dimorphism from mating patterns.

Evidence for a relationship between sexual selection, mating patterns, and degree of sexual dimorphism in humans is even less convincing. Alexander et al (5) reviewed data for sexual dimorphism in various mammals and argued that competition among males in polygynous systems led to proportionally greater selection for body size in males (compared to females) resulting in an increase in sexual dimorphism. Applied to sexual dimorphism of stature in human

societies, they found an association between marriage patterns (monogamy and polygyny) and sexual dimorphism. In particular, those groups practicing polygyny and "socially imposed monogamy" showed greater sexual differences in stature than ones following what the authors described as "ecologically imposed" monogamous patterns, which led these authors to postulate that patterns of sexual dimorphism in humans resulted primarily from sexual selection relating to mating patterns. Subsequent, more comprehensive work by Gray & Wolfe (127, 304), using Murdock's *Ethnographic Atlas* and height data provided by a variety of sources, tested the correlation between sexual dimorphism and mating patterns in contemporary humans. Their results found only a weak correspondence between marriage patterns and level of dimorphism, so that "marriage systems explain very little of the variation of human sexual dimorphism of stature" (304, p. 226). Available nutrition shows higher correlation with sexual dimorphism than any mating form.

Although current research on modern humans and living primates refutes a strong relationship between mating patterns and sexual dimorphism, it is uncertain how appropriate these results are to fossil human samples. For example, human social arrangements in the ethnographic present probably bear little resemblance to patterns in Middle and Lower Paleolithic contexts. It is also problematic how patterns of mating in agricultural groups are at all relevant to Pleistocene hunters and gatherers, given differences in subsistence economy, diet and nutrition, and technology. We suspect that principles of uniformitarianism break down when considering human fossil assemblages, so that correlations in the present may be of little significance for fossil hominids.

It may be equally difficult to attribute patterns of correlation in a diverse group of primates (which uniformly lack a cultural adaptation) to fossil humans. For instance, variance in male investment in offspring is an important consideration in arguments that link monogamy and a low degree of sexual dimorphism in the primates. Yet "fathering," the extreme expression of male parental investment behavior, is virtually unique to humans among the primates (181, 300), and may well be fundamental to the human adaptation as it developed during the process of hominid origins (203). But fathering underlies important aspects of social relationships in all human societies, regardless of their marriage or mating patterns. Thus, if Lovejoy is correct in terms of the early appearance of fathering, the primate patterns of relationship simply may not apply at any stage of human evolution.

Similarly, if differential female access to food supplies dominates female reproductive success, the development of role expectations and the systematic reciprocal sharing of food resources would markedly reduce this differential in the hominids, and thereby reduce its potential for creating or maintaining sex differences.

Body Size

The possibility of a relation between the magnitude of sexual dimorphism and body size is one of the oldest alternatives to the mating pattern causation argument. Unfortunately, examination of this possibility is often confused by methodological considerations. The problem is how to examine the consequences of body weight differences for the magnitude of body weight dimorphism (or a measure of dimorphism related to it) and maintain the independence of the two variables compared. Recent discussions of this problem have centered on whether the ratio of means is a better measure of dimorphism than the difference between the means (107, 198, 198a), and there are numerous other ways of comparing the sexes in an attempt to describe the magnitude of dimorphism (66, 240, 246, 301). Allometry is also problematic in this context (161, 313). Finally, a possible relation between body weight and the magnitude of dimorphism may be confused by the influence of habitat differences (if arboreal primates are less dimorphic, for instance, they are likely to be smaller than terrestrial ones), and/or possibly differences in home range [there is a positive correlation between home range and diet in primates, more than likely resulting in the observation that range and dimorphism are related (222)].

Many studies indicate that with some exceptions, body size and sexual dimorphism are related to each other, but predictions concerning the amount of the contribution of body size alone varies from 83% of the variance in dimorphism (198) to less than 20% (107). Whatever the value, the generalization that a species overall size correlates with its level of sexual dimorphism has been said to hold for a great variety of animals from insects and other invertebrates [where reverse dimorphism often occurs (244)] to birds and mammals (234, 242) to primates (56, 195, 198, 198a). Although considerable variation occurs, in most animals there is a positive correlation between body size and sexual dimorphism. Among the nonprimates, when body size is large, sexual dimorphism is generally pronounced. Our review of the primate literature, however, suggests this relationship is not as strong as reported in other major taxa. We collected body size data for 80 different primate species, relying on data given by Leutenegger & Cheverud (198) and Gaulin & Sailer (107), supplemented by additional data for the common chimpanzees (161) and for pygmy chimpanzees (316). We used the ratio male/female body weight as our measure of sexual dimorphism and correlated this index with female body weight, as suggested by McCown (212). Unlike Leutenegger & Cheverud (198, 198a), we did not use the log of the absolute difference in weight between males and females, since this measure is clearly inappropriate (107).

Table 2 reviews our results, and it is clear that we find much lower correlations than are generally reported in the literature. For example, when all

primates are considered, sexual dimorphism correlates significantly with female body weight ($r = .39$), which is well below the figures given by Leutenegger & Cheverud (198) and even lower than those reported by Gaulin & Sailer (107). When the total primate sample is divided into smaller units (cf 55), considerable variation occurs in the strength of the correlation. For example, prosimians, New World monkeys, and arboreal Old World monkeys all show low and insignificant correlations (two of which are negative). These deviate markedly from the condition in the terrestrial Old World monkeys and apes which show correlation coefficients of .514 and .816 respectively. In apes, the high correlation is partly due to the effect of comparing very small body size in *Hylobates* species with very large body size in gorillas and orangutans. In addition, there are few species in the ape comparison and much greater breadth in the range of body sizes represented. The smallest species are monogamous, are the most often arboreal, and have low levels of sexual dimorphism. The largest species are nonmonogamous, are the least arboreal of the apes, and are very dimorphic. Whether these associations occur by chance or whether they reveal an underlying pattern of relationship is unclear from this sample alone, but we find it suspicious that such a pattern cannot be found in any other primate groups.

As we view these data, we see no simple relationship between body size and degree of sexual dimorphism. There certainly is not a singular relationship which exists in primates, since there is no correlation among some major groups and high correlations among others. There is also considerable variation as is easily appreciated by inspecting the raw data tables given by Leutenegger & Cheverud (198) and Gaulin & Sailer (107). With respect to humans, as we discuss later, there is little reason to suspect that body size has much effect on the evolution of sexual dimorphism since there is only minor change of body size through time in the human lineage. Thus, we find little evidence of body

Table 2   Correlations between sexual dimorphism and female body weight for various groups of nonhuman primates[a]

	Correlation	n	Significance
All primates	.390	80	.001
Prosimians	−.101	15	ns
New World monkeys	.065	17	ns
All Old World monkeys	.404	37	.05
Arboreal Old World monkeys	−.050	23	ns
Terrestrial Old World monkeys	.514	14	.03
Apes	.861	11	.001

[a]Data are from Gaulin & Sailer (107), Jungers & Susman (161), Leutenegger & Cheverud (198a), and Wrangham & Smuts (316). With the kind help of R. W. Wrangham, we were able to resolve contradictions between the data sources, and corrections were made when necessary.

size as an important contributor to sexual dimorphism in either primates or fossil humans.

Economic Patterns and Division of Labor by Sex

Several models for development, maintenance, and reduction in sexual dimorphism have considered the adaptive importance of varying economic patterns based on the exploitation of different parts of the niche by males and females (267). Mechanisms that result in sex differences include differences in selection acting on females and males, sex differences in feeding behavior (262), and competition between the sexes for population-limiting resources (250, 267). One might consider the possibility that there are dimorphic niches, or perhaps bimodal niches differentially utilized by the sexes (251). Slatkin (267) emphasizes the importance of dimorphic niches, but discounts the model of bimodal niches differentially utilized by the sexes. Selander (261, 262) has discussed this factor in birds, and Galdikas & Teleki (99) suggest that different resource exploitation in baboons, orangutans, and chimpanzees foreshadow human patterns of division of labor by sex (155, 156, 181). This partitioning of resources reduces ecological competition between the sexes, which is expected when the variance of resource utilization ability is small relative to the width of the resource spectrum (267). Moreover, it carries another advantage, that of providing for a more efficient use of economic resources *if* there is reciprocal sharing.

The roles adopted by males and females in many species of higher primates often differ dramatically, resulting in nonoverlapping economic duties, and in some cases significant dietary differences (294, 294a). Besides the obvious and well-documented differences in mothering and troop defense, a common activity of higher primate males is hunting, especially hunting that takes males away from the confines of the social unit. For example, work by Strum (138, 280) has shown that male olive baboons were much more likely to participate in predatory behavior and were exclusively involved in hunting activities which took place outside the confines of the troop. The fact that these males completely dropped the cooperative hunting behavior when it conflicted with their reproductive effort (280) indicates that the dimorphic differences were related to something more than subsistence activities, but also that these differences between males and females established the preconditions for male hunting.

Similar patterns exist among some chimpanzees (215) in that males almost exclusively hunt small mammals (283), while female hunting is restricted to smaller prey that occurs in closer proximity to the troop and does not interfere with infant care. There are also sex differences in the techniques used in hunting (229). In the Mahale chimpanzees, females often hunt juvenile ungulates, taking them by seizure, while males chase adult monkeys (282). Another important sex difference in chimpanzee food procurement lies in the fact that

females regularly share gathered plant foods with other females, but not with males (214, 216).

A parallel case for systematic sex differences in economic activities can be made for human hunter-gatherers where the economic roles of hunting males and gathering females are generally found (227, 227a), which may be closely associated with the requirements of female pre- and postnatal reproductive duties (41, 42). Thus for the higher primates, including humans, it seems there should be an association among dimorphism, economic patterns, and the division of labor by sex. Based on comparisons between hunting behaviors in nonhuman primate males, sexual dimorphism and differential reproductive factors preadapt males to more freely participate in cooperative hunting away from the social unit.

This presumed relationship between human sexual dimorphism and sexual division of labor in economic activities has been used to account for changes in the degree of sexual dimorphism in the hominid lineage (35–37, 86, 91–93, 95, 132, 310, 311). The theoretical basis for this relationship rests on assumptions concerning the separation of economic duties in hunter-gatherer groups and food-producing populations. Given the near exclusive involvement of males in long distance, multigame hunting and more equal sharing of economic duties in horticulturalists/agriculturalists (227a), Frayer (93, 95) has argued that reduction of sexual dimorphism in prehistoric European populations is related to changes in economic systems. A similar argument is implicit in Slatkin's work (267). He proposes that dimorphism will only result from differences in resource utilization when the variance in resource utilization ability for each sex is small relative to the total resource range. An important part of human evolution involves the expansion of this ability for both sexes. It follows that as the variance for resource utilization ability increases for each sex, the degree of sexual dimorphism would be expected to decrease. This explanation may account for sexual dimorphism decreases over much of human evolution, especially in the Lower and Middle Pleistocene. It would be reasonable to describe the pattern of changes in resource utilization during this time span as expanding for each sex (thereby increasing its proportional variance) because of technological improvements and increased knowledge about the habitat and the most effective means of utilizing its resources (156, 311).

However, differences in economic activities and sexual dimorphism in extant hunter-gatherers and food-producers do not corroborate this hypothesis. For example, Wolfe & Gray (305) have examined the correlation between sexual dimorphism in stature and economic patterns in a large sample of contemporary humans. They found agricultural groups no less dimorphic than hunter-gatherers, arguing against a relationship between economic patterns and sexual dimorphism. Unfortunately, Wolfe and Gray did not differentiate food-producing groups with respect to intensification of agriculture, which may be

important since Ember (80) and Burton & White (48) have shown that women's contribution to agricultural work differs substantially between horticulturalists and intensive agriculturalists. These distinctions are, however, not easy to glean from the existing literature and are obviously open to conjecture in prehistoric groups.

To further test the economic model, we assembled data on mandibular canine and second molar breadths for a series of postglacial and recent hunter-gatherers, horticulturalists/agriculturalists, and modern urban populations (Tables 3 and 4). We selected the canine and second molar since these generally show the greatest dimorphism in human and primate groups and breadths, because they are not significantly reduced by occlusal wear. Other than showing that male canine and second molar breadths are *always* larger than female breadths, and that canine dimorphism is usually greater than second molar dimorphism (the only exception to this is the British sample), there is no other clearly emerging pattern. For the canine, the most dimorphic sample is the Czech Neolithic and the least the Danish Neolithic. In the second molar breadth, the Czech Neolithic sample shows much more sexual dimorphism than any hunter-gatherer population, and two of the Urban samples also exceed these in dimorphism. Overall differences among the three broad economic groups are absolutely nonexistent for either tooth. The differences in mean dimorphism are miniscule and not significant. On the basis of these data we concur with Gray and Wolfe's conclusions—modern differences in economic pattern have absolutely no influence on the magnitude of sexual dimorphism (127, 304, 305).

In sum, we note that even with the apparent bias toward sexing skeletons as males in skeletal samples (299), there are still no differences among the three economic categories, whether the data derive from skeletal or living samples (compare Tables 3 and 4 with 5). As with mating patterns and body size, a relationship between sexual dimorphism and economic systems is not demonstrable because of the great variation in recent human groups. Although this does not mean that such a relationship was unimportant in Pleistocene fossils, it does indicate the possibility that recent variation is not particularly useful in either *predicting* patterns of the past or *explaining* them because the fact remains that there are marked changes in economic systems through the Pleistocene, and hominids do greatly reduce in sexual dimorphism during this span of time. In addition, although we do not have body size data for all these groups, we suspect that the hunter-gatherer and urban samples have the greatest statures, yet they do not exhibit more dimorphism, negating any powerful relationship between sexual dimorphism and body size. The data for dental dimensions also lack a regional patterning with respect to the expression of sexual dimorphism (contra 82, 139). For instance, among hunter-gatherers the most and least dimorphic are Amerinds. In horticulturalists/agriculturalists, the

Table 3 Sexual dimorphism in mandibular canine breadth[a]

	Male $\bar{x}$	n	Female $\bar{x}$	n	% Dimorphism	Significance
Hunter-Gatherers						
Glacial Kame	8.0	20	7.2	18	111.1	.001
Libben	8.3	19	7.5	21	110.7	.001
Australian Aborigines						
Murray River	8.8	98	8.1	81	109.2	.001
Lapps	7.6	211	7.0	190	108.6	.001
Riviere aux Vase	7.9	11	7.3	13	107.4	.01
Indian Knoll	7.7	46	7.2	48	106.9	.01
Australian Walbiri	8.1	71	7.6	79	106.6	
Vlasac	7.8	16	7.4	11	106.1	.05
Jomon	7.5	62	7.1	25	105.6	.001
Ainu	7.5	32	7.1	20	105.4	.001
Nubian "Mesolithic"	8.4	17	8.0	15	105.0	.05
Aleuts	7.9	74	7.6	57	103.9	
St. Catherine's Island	7.8	25	7.5	29	103.9	.05
Horticulturalists/Agriculturalists						
Czech Neolithic	8.1	28	7.2	30	112.2	.001
Adena/Hopewell	7.9	42	7.1	52	111.3	.001
Swiss Neolithic	7.6	16	7.0	12	109.6	.01
Yayoi	8.2	13	7.5	40	109.3	.001
Leavenworth Arikara	8.3	21	7.6	23	109.0	.001
Nubian Agriculturalists	7.6	89	7.2	82	105.6	.05
St. Catherine's Island	7.9	44	7.5	45	105.1	.001
Nasioi	8.3	58	7.9	67	104.7	.001
Canaveral Indians	8.1	17	7.8	5	103.7	ns
Ticuna	7.5	27	7.2	27	102.9	ns
Danish Neolithic	8.0	12	7.8	9	102.6	ns

Urban Populations

Hungary Mediaeval (Zalavár)	7.9	49	7.2	40	109.7	.001
Koreans	8.3	11	7.6	5	109.2	.01
Ohio Whites	7.9 ·	45	7.3	35	108.4	.001
Denmark Mediaeval	7.9	34	7.3	74	108.2	.001
Norwegians	8.1	78	7.5	87	108.0	.001
San Cristobal	7.9	49	7.5	27	106.5	.001
Japanese	7.1	114	6.7	158	106.0	.001
Javanese	7.9	139	7.2	42	106.0	
Tristan da Cunha	9.0	54	8.5	43	105.9	.01
North Chinese	8.1	80	7.7	10	105.2	.01
British	7.1	30	6.8	30	104.4	
Hong Kong Chinese	7.9	29	7.6	13	103.9	

aData derive from 8, 19, 36, 37, 49, 123, 139, 185, 189, 206, 221, 226, 234a, 259, 263, 285, unpublished measurements kindly provided by C. L. Brace, and from our own measurements. The Leavenworth Arikara data were kindly provided by H. W. Case. "Ohio Whites" are from data provided by S. M. Garn, and differ significantly from the summary data published earlier (103).

Table 4 Sexual dimorphism in mandibular second molar breadth[a]

	Male x̄	n	Female x̄	n	% Dimorphism	Significance
Hunter-Gatherers						
Libben	11.3	19	10.7	20	105.6	.01
Vlasac	10.7	16	10.2	12	105.5	.01
Australian Aborigines						
Murray River	12.3	97	11.7	80	105.1	.001
Lapps	10.1	259	9.6	218	104.7	.001
Ainu	10.3	37	9.9	28	103.8	.001
Australian Walbiri	11.4	71	11.0	79	103.6	.001
Nubian "Mesolithic"	11.4	14	11.0	18	103.6	.05
Jomon	10.5	85	10.2	61	103.5	.001
Aleuts	10.6	45	10.3	37	102.9	
Glacial Kame	10.8	29	10.5	29	102.9	
Riviere aux Vase	11.0	10	10.7	10	102.5	ns
Indian Knoll	10.9	53	10.7	52	101.9	
St. Catherine's Island	10.9	23	10.7	43	101.9	ns
Horticulturalists/Agriculturalists						
Czech Neolithic	10.4	22	9.5	27	109.4	.001
Yayoi	11.0	32	10.4	13	105.8	.001
Nubian Agriculturalists	10.5	159	10.0	142	105.0	.05
Nasioi	11.0	66	10.6	65	103.9	.001
Adena/Hopewell	10.7	54	10.3	52	103.8	
Canaveral	10.8	17	10.4	5	103.4	ns
St. Catherine's Island	10.8	44	10.5	61	102.9	.01
Swiss Neolithic	10.0	13	9.7	12	102.8	ns
Ticuna	10.3	24	10.1	20	102.6	ns
Leavenworth Arikara	10.5	45	10.3	60	102.2	.01
Danish Neolithic	10.3	26	10.1	22	102.2	ns

Urban Populations

Hungary Mediaeval (Zalavár)	10.0	55	9.4	42	106.4	.001
British	10.8	30	10.2	30	105.9	.001
Ohio Whites	10.6	31	10.1	22	105.2	.002
North Chinese	10.8	94	10.3	21	104.9	.001
Denmark Mediaeval	10.0	76	9.6	99	104.2	.001
Koreans	10.8	13	10.4	6	103.8	ns
Japanese	10.5	197	10.2	194	102.9	.005
Javanese	10.5	133	10.2	38	102.9	
Tristan da Cunha	10.8	108	10.5	92	102.9	.01
San Cristobal	10.8	29	10.5	20	102.9	.01
Norwegians	10.5	58	10.3	46	101.9	
Hong Kong Chinese	10.3	21	10.2	7	101.0	ns

[a]Data derive from 8, 20, 21, 36, 37, 49, 123, 139, 185, 189, 206, 221, 226, 234a, 259, 263, 285, unpublished measurements kindly provided by C. L. Brace, and from our own measurements. "Ohio Whites" are from data provided by S. M. Garn, and differ significantly from the summary data published earlier (103).

Table 5 Dental and body height percent sexual dimorphisms in living human populations[a]

	C̄ Breadth	n (m/f)	M₂ Breadth	n (m/f)	Femur length	n (m/f)
Bambandyanalo	110.1	5/2	112.9	6/2	110.7	2/2
Libben	110.7	19/21	105.6	19/20	109.7	37/41
Vlasac	106.1	11/16	105.5	16/12	109.2	11/4
Zalavár	109.7	49/50	106.4	55/42	109.1	65/41
Czech Neolithic	112.2	28/30	109.4	22/27	108.6	22/14
Japanese	106.0	114/158	102.9	197/194	107.6	20/25
Yuendumu	106.6	71/79	103.6	71/79	107.5	209/149
Nubian Neolithic	106.3	89/82	105.0	159/142	107.3	108/93
Leavenworth Arikara	109.0	21/23	102.2	45/60	107.2	25/19
St. Catherine's Island Agricultural	105.1	23/45	102.9	44/61	107.1	47/54
Ainu	105.4	32/20	103.8	37/28	106.7	44/25
Afalou/Taforalt	105.5	18/8	102.9	20/9	106.0	20/9
Nubian Mesolithic	105.0	17/15	103.6	14/18	105.9	11/10
St. Catherine's Island Hunter/Gatherer	103.9	25/29	101.9	23/44	103.3	9/19

[a]Data are from 21, 49, 65, 100, 185, and Abbie (1) for the Yuendumu femora, with the published lengths modified to approximate skeletal femoral lengths. Additional data were provided by C. O. Lovejoy, H. W. Case, T. Brown, and the authors.

most and least dimorphic samples for both teeth are Europeans, as is the case for the horticulturalists/agriculturalists. Finally, whether hunter-gatherers or horticulturalists/agriculturalists are considered, both monogamous and polygynous marriage systems are certainly represented, but it would be difficult to determine the mating preferences from the levels of dimorphism in canine and second molar breadths.

Thus, considering the economic pattern, our data confirm the generalization that most of the prehistoric groups spanning the transition from hunting and gathering to agriculture to urbanization do *not* show a pattern of decreased dimorphism (13, 49, 60, 133, 185, 243, 269), but either stability through time or a very slight increase. The only exceptions for this are Europe (91, 93, 95, 219), India (168, 169), and a group of Amerinds from Alabama (40). It remains to be demonstrated whether these are anomalies or are part of a pattern perhaps obscured by noneconomic factors.

Noneconomic Role Differences and the Division of Labor by Sex

Differences between female and male roles that are unrelated to economic activities provide a classic explanation for sexual dimorphism. Indeed, different social roles should probably be considered a special case of a dimorphic niche, as discussed by Slatkin (267). It has been argued that the energy requirements of sex roles predominate in controlling the degree of dimorphism expressed (74). The extent of sexual dimorphism resulting from role differences can range from a marked expression in baboons, presumably because of the male role in troop defense (62), to a weak expression in late Upper Paleolithic Europeans, presumably because of a decrease in male robustness following from improvements in hunting technology (93, 95), to an even weaker expression in some living groups which have virtually eliminated the differences in strength requirements between male and female roles (35, 37).

In a more complex model, Bridges (40) attributes a decrease in sexual dimorphism for skeletal strength measures associated with the transition to Mississippian agriculture in northwest Alabaman Amerinds to a number of cultural factors that result in more similar strength requirements in male and female roles. She argues that males retain their roles as hunters and become more involved in a variety of strenuous social and political activities (particularly warfare and sports), but do not contribute to agricultural chores as intensively as females. The pattern of male skeletal change involves the legs much more than the arms (although the right-left strength differences decrease, presumably as a consequence of the replacement of the spear by the bow and arrow). In females, the requirements of numerous new agricultural chores such as planting and grinding result in significant increases in the strength of the arm bones. Bridges concludes that in general the strength requirements of agricul-

ture are greater than the requirements of hunting and gathering, and that the difference is greater for the females than for the males because their roles change more. Thus, there is a *decrease* in the magnitude of sexual dimorphism. However, the exact pattern of change differs according to whether the arms or the legs are considered, because different sorts of activities are involved in the patterns of change affecting males and females. One sure implication of Bridges' work is that the behavioral patterns underlying the magnitude of dimorphism are very complex, not necessarily reciprocal (i.e. males doing more or less of the same thing that females do), involve both economic and noneconomic roles, and affect different parts of the body in different ways.

Role differences are a much more productive way of looking at the consequences of division of labor by sex than is the more limited case of differences in economic pattern. However, a greater magnitude of role differences does not invariably lead to increased sexual dimorphism. For instance, increasing female specialization for long child dependency periods makes sex roles more distinct in humans as well as in other anthropoid primates. Yet the increased physiological demand on females in relation to reproductive requirements can result in selection for relatively larger female postcanine teeth and therefore a reduced sex difference in postcanine tooth size (313).

The hypothesis of increasing similarities in role requirements as a cause of decreasing sexual dimorphism is unique to human evolution (35, 311). However, the hominids are not the only lineage that shows sexual dimorphism reductions, and it is unlikely that role differences are a universal explanation of these reductions when all cases are considered. Indeed, one can question this explanation for the hominids themselves, since it rests on assumptions of behavioral differences in societies that no longer exist. Moreover, if explanations such as Bridges' (40) are correct, complex models of role differences and role difference changes as an explanation of changes in sexual dimorphism will always be untestable in the hominid fossil record. The inability to test a model does not invalidate it as an explanation, but it does render it meaningless as a scientific hypothesis.

Summary of Ultimate Causation Models

Review of the models of proximate and ultimate causation for sexual dimorphism leads to the uncomfortable conclusion that several of them have never been adequately tested, and moreover none of the models seem to be particularly successful in explaining patterns of dimorphism in humans and nonhuman primates. This may mean that factors other than those that have been traditionally considered may be of primary importance or, more likely, that sexual dimorphism in various species results from dissimilar and often complex causes. It may be true, for instance, that body size influences sexual dimor-

phism in some species, as Leutenegger and others have suggested, but this is not a universally applicable relationship. Similarly, mating systems and division of labor may contribute to differences in degree between males and females, although recognizing the possibility of a relationship between these may be of only limited application. Whatever model is appropriate, there is considerable reduction of sexual dimorphism in the hominid lineage.

DIMORPHISM IN EVOLUTION

Much of the recent thinking about sexual dimorphism and its role in the evolutionary process stems from the realization that the magnitude of human dimorphism was once much greater than it is today. Indeed, many workers now believe that the decrease in sexual dimorphism over the course of human evolution is at least as dramatic and significant as the increase in brain size and the decrease in posterior tooth size. Its explanation, then, must be at least as important and its role in the evolutionary process as critical as that of tooth size.

Apart from the primates, sexual dimorphism has only occasionally been considered to be an important aspect of the fossil record (58, 60, 118, 246, 301). Dimorphism has been noted and discussed in a number of fossil nonhuman primate species (11, 88, 119, 128, 129, 163–165, 210, 298, 312). By far the most work on fossil primate material has focused on sexual dimorphism in hominid evolution (6, 15, 34, 35, 37, 40, 46, 68, 84, 87, 91, 93–95, 109, 110, 143, 152, 158–160, 171, 175, 179, 180, 185, 186, 194, 207, 208, 228, 236, 268, 287, 288, 299, 306–312, 318, 321).

Among the primate fossils, the study of sexual dimorphism often focuses on whether the systematic differences between two specimens or two samples found at a site, or within an alleged taxon, differ because of sex or because of taxonomy. This question is often not resolved, and the sex vs taxonomic variation argument plagues the interpretation of the Proconsuls (compare 128 with 11), the ramapithecine remains (compare 129, 130, and 312 with 12, 163, 317), and many of the australopithecine fossils (compare 158 and 159 with 67, 190, 218, 230). Moreover, in those cases when the dimorphism itself is the object of study, there is often a similar lack of agreement. Even the fundamental issue of whether sexual dimorphism has changed substantially over the course of human evolution has evidently not been settled (compare 15, 37, 93, 309–311, with 194, 196, 319, 321).

In the primate fossil record, sexual dimorphism has been examined in the earliest unequivocal anthropoid fossils, and in the Fayum species most likely ancestral to the living hominoids—the *Aegyptopithecus zeuxis* remains from the later Oligocene of Egypt (88, 164). This is fortunate for an understanding of the evolution of sexual dimorphism since it provides insight into what may be the primitive condition for all anthropoid primates. This condition is one of

very marked sexual dimorphism for all three of the Oligocene anthropoid species examined.

For the purposes of comparing sexual dimorphism in a number of fossil and living hominoid species, we settled on a limited number of metric features. These were dictated by our desire to make valid comparisons between different groups and to maximize the sample sizes for those individuals whose sex could be ascertained with reasonable likelihood. We have used the breadth of the mandibular canine, the breadth of the mandibular second molar, and the height of the mandibular corpus measured between the first and second molars in these comparisons.

Canine size is a traditional measure of sex difference in primates (73, 102, 103, 141, 296) because the canine is invariably the most dimorphic of the teeth (10, 120, 309). The second molar also shows a relatively considerable degree of sexual dimorphism in most human populations (102, 309), and dimorphism in the mandibular second molar is highly correlated with dimorphism in body size (104). The second molar also provides a measure of masticatory adaptation (306, 308, 309). Mandible corpus height was chosen because it is one of the best correlates of body height that is likely to be preserved in the fossils (117, 128). However, because of masticatory differences that characterize the course of human evolution, it is not clear that mandible height variation unambiguously reflects body size alone. In the recent and living human populations, femur length is substituted for mandibular corpus height as a more exact measure of body size.

Several authors have argued that there are really a number of quite different dimorphisms (83, 232, 233, 321), and thus that different measures of sexual dimorphism may reflect very different phenomena. To some extent this must be the case. For instance, when using multivariate procedures to examine numerous features simultaneously, patterns of skeletal dimorphism revealed in the primates are often different (197, 212, 232, 233, 314). Nevertheless, we believe that there is an important common factor underlying the sexual dimorphisms we have observed, and, minimizing variation in factors that strongly affect their independent variation, they covary to a surprising degree. With regard to the four characteristics we examined in living apes for comparisons with the fossil hominids (Table 6), there is generally covariation among the metric traits. Thus, the pygmy chimpanzees were found to be least dimorphic for all features, while the gorillas are most dimorphic for canine breadth, mandible corpus height, and femur length. Orangutans are most dimorphic for M_2 breadth. In the 14 human populations for which we could gather reliable data on three variables by sex (i.e. excluding mandibular height because femur length provides a better measure of body size dimorphism), using the small sample size modification, the correlation between dimorphism in femur length and dimorphism in the breadth of the mandibular canine is .763 while the femur

length–M_2 breadth sexual dimorphism correlation is .770 (Table 5). These are high correlations, significantly different from 0.0 at better than the 0.001 level. We conclude that while these three characteristics in part reflect differing aspects of sexual dimorphism that may vary independently to some degree, they also strongly reflect a more general aspect of sexual dimorphism. To an important extent, then, these different measures actually measure the same thing.

In all the characteristics we examined (Table 7), *Aegyptopithecus* shows a dramatic magnitude of sexual dimorphism. Because the sample size is very small it is likely that the values we have determined are not exactly correct, but we believe it probable that this marked expression of sex difference is not merely an accident of small sample size. Canine dimorphism and the dimorphism reflected in mandible corpus height are extraordinary. The canine dimorphism cannot be matched in any living or fossil anthropoid species, while the mandibular height dimorphism may only be exceeded by several of the ramapithecine species. Because of the small sample sizes the conservative conclusion is that as a group the ramapithecines all reflect the primitive condition and probably do not actually differ substantially. Among the ramapithecines, the Ravin sample has the greatest likelihood of representing a real biological population. Mandibular corpus height dimorphism in this sample is the same as in *Aegyptopithecus*–the primitive state.

The dimorphism in M_2 breadth is also marked in *Aegyptopithecus*, although its absolute magnitude is not as great as the magnitude of dimorphism in other features. It is matched by the same level of dimorphism in *A. afarensis*, in the Ravin ramapithecines, and in living orangutans. One must assume that this too is the primitive condition. Thus, the *Aegyptopithecus* data indicate that the primitive condition for the anthropoids would seem to be very marked sexual dimorphism in the features we have chosen to examine. Interestingly, if no *Aegyptopithecus* were known, the dimorphism in this ancient species could be accurately reconstructed from the pattern of dimorphism in its fossil and living descendant species. If this were done, the only error would be an underestimate of the magnitude of canine dimorphism in the ancestral condition. Other than arguing that this level of dimorphism is the primitive state in the earliest apes, we offer no explanation for the degree of sexual dimorphism given the small size and arboreal habitat reconstructed for *Aegyptopithecus*.

For the earliest hominid species, *A. afarensis*, the magnitude of dimorphism is also considerable, exceeding all other hominids in measures of dental dimorphism. Mandibular body height dimorphism for this species, in contrast, does not appear to be the maximum for the hominids. However, we believe this reflects the small sample sizes, and we strongly suspect that dimorphism in this feature is the same for three of the australopithecine species *(afarensis, africanus, habilis)* and *H. erectus,* first reducing substantially in the Neandertals.

Table 6 Percent sexual dimorphisms in living ape species[a]

	C̄ Breadth	n (m/f)	M₂ Breadth	n	Femur length	n	Mandible height	n
Pan paniscus	118.3	23/25	100.0	24/33	101.2	10/10	100.0	12/17
Pan troglodytes	123.3	84/90	103.7	124/124	104.9	38/58	108.7	22/20
Pan gorilla	138.0	153/95	107.0	170/107	120.9	84/54	123.8	47/22
Pongo pygmaeus	126.6	48/59	112.0	69/73	115.0	32/29	117.0	12/16

[a] Dental data were collected by the authors. Mandibular data were provided by W. L. Jungers, A. Kramer, and measured by the authors. Postcranial data are from Schultz (253) and provided by W. L. Jungers.

Table 7 Percent sexual dimorphisms in fossil hominoid species[a]

	$\bar{C}$ Breadth	n (m/f)	M_2 Breadth	n (m/f)	Femur length	n (m/f)	Mandible height	n (m/f)
Aegyptopithecus	149.9	3/1	111.4	4/6			135.1	4/7
Ravin Ramapithecines	130.3	3/2	112.3	5/3			136.4	2/1
Australopithecus afarensis	127.5	11/5	111.2	6/10			118.4	5/5
Australopithecus africanus	117.3	9/6	109.1	7/3			119.6	4/4
Homo habilis	125.4	4/7	107.9	4/8			126.9	5/10
Homo erectus	113.6	6/15	106.0	10/22			119.6	10/17
European Neandertals	115.8	13/9	104.8	12/10	108.1	4/1	115.5	7/8
European Early Upper Paleolithic	109.8	7/6	105.5	7/8	108.4	5/3	115.3	8/8

[a] *Aegyptopithecus* data are from Fleagle, Kay & Simons (88). The remaining data were measured by the authors.

Variation in mandibular corpus height dimorphism among the earlier hominid species confounds differences in both body size and in mastication. To the extent that these are independent of each other, the resulting variation is bound to be difficult to interpret.

The differences between the *afarensis* sample and the other australopithecine grade species are not great, and except for the decrease in M_2 breadth dimorphism, the differences among the australopithecine species are not statistically significant. If the dentition of *A. afarensis* seems to be the most dimorphic of the australopithecines, it should be seen in the context of the fact that all of the australopithecines are very dimorphic compared with later hominids. While it is possible that the magnitude of sexual dimorphism decreases through australopithecine grade evolution, such a decrease can only be demonstrated statistically for the M_2. If this decrease also occurred in other features, its extent was probably not great.

Finally, although the sample sizes are quite small, the differences in postcranial remains that seem to be attributable to sexual dimorphism appear to be large in both *A. africanus* (306, contra 194) and *A. afarensis* (158, 204). The data suggest that body size dimorphism was as marked in these australopithecines as one would expect from the dental and gnathic dimorphism. One of us (306) estimated that the sexual dimorphism in weight for *A. africanus* indicated males were twice the size of females. The larger postcranial sample now known for this species provides no basis for retracting this claim. Moreover, limb dimension comparisons at Hadar show *A. afarensis* to be equally dimorphic and comparisons of *H. habilis* postcranial remains from individuals as large as ER 1472 with remains from individuals as small as OH 13 also suggest marked dimorphism. Dimorphism in the earliest hominids may not be limited to size. It has been proposed that the Hadar australopithecines were also characterized by very significant sex differences in postcranial morphology which are said to reflect sex differences in locomotor behavior and habitat utilization (281). If true, this would be a good example of adaptation to a dimorphic niche, as discussed by Slatkin (267).

In the much larger *H. erectus* sample there is a drop in the magnitudes of dental sexual dimorphism. Canine breadth dimorphism is well below the australopithecine grade condition although still above most of the modern human populational means, while the dimorphism in M_2 size does not decrease as much (relative to the late australopithecines) although it falls to near the modern populational mean (about 105). In contrast, the mandibular corpus height dimorphism remains marked, and in fact is only exceeded by the *H. habilis* corpus height dimorphism value. Of course, all of the australopithecine mandibular sample sizes are small, and there is no reason to believe that any of the dimorphism values are significantly different. Thus, the conservative conclusion is that *erectus* mandibular corpus height dimorphism is probably

unchanged from the australopithecine condition. The implications of this fact for estimations of body size dimorphism are unclear because there are too few postcranial remains known to be associated with or attributable to *H. erectus*. It is interesting that the newly discovered juvenile from west Turkana (WT-15000) is much larger than many workers expected. This probably does not indicate elevated dimorphism for the species, however, because an earlier discovered female of equal antiquity, ER 1808, is also very tall. If anything, these data would suggest that body size dimorphism in *H. erectus* is reduced compared with the australopithecines.

The European Neandertals are virtually identical to *H. erectus* in the magnitudes of dental sexual dimorphism, and the differences are not significant statistically. Here, body size dimorphism can be estimated by dimorphism in femur length. The value is well within the human populational range (143, 287), although according to the data we summarize here, it is above the mean. This might help confirm the suggestion of reduced body size dimorphism in *erectus* made above.

Looking at the European earlier Upper Paleolithic sample, the molar, femoral, and mandibular dimorphisms are virtually identical to the dimorphism values for the European Neandertals. In contrast, the canine dimorphism is much lower. Unlike the Neandertals, dimorphism of the canine in this European sample is within the range of modern populational means, although at its upper end.

We contend that these data show evidence for the persistent reduction of sexual dimorphism over the course of hominid evolution. The hominid lineage is not the only one showing reduction of sexual dimorphism. In making evolutionary comparisons, there is the inevitable problem of which similarities reflect the same condition in a common ancestor and which happened in parallel. Fortunately, the reinterpretation of phylogeny in the anthropoid primates makes it easier to distinguish these alternatives. The evidence that forces the particular interpretations of where the parallelisms in the hominoid radiation lie comes from a series of new evaluations of protein and DNA level variations as well as a reevaluation of morphological and paleontological information (18, 124–126, 130, 266, 312). These data combine to indicate clearly that it is humans and chimpanzees that form a sister group (i.e. that diverged most recently). This is a very differently composed sister group than the group defined by "great apes" (i.e. chimpanzees, gorillas, and orangutans), or even the group defined by "African apes" (gorillas and chimpanzees).

Without the fossil record (i.e. only comparing living species) one might suppose that the ancestral condition for this sister group is one of reduced sexual dimorphism. While this interpretation is possible, it leaves the pattern of variability and the systematic changes in this pattern over the course of human

evolution as revealed by the fossil record inexplicable. If the bimodality in size (and to some degree morphology) was interpreted as the result of two sympatric hominid species with low levels of dimorphism and marked degrees of similarity, study of the course of Plio-Pleistocene evolution would show these "species" becoming more and more similar to each other. Such an interpretation is unlikely, and it is much more reasonable to interpret the differences as the result of dimorphism. This would mean that reduction of dimorphism in the chimpanzee and human lines is a homoplasy. The last common ancestor of these two lines, as well as the earlier ancestor of the monophyletic group of African hominoids, would both be markedly dimorphic on this interpretation. Thus, the reduction of sexual dimorphism in the hominids does seem to be parallel to the specific reductions in some of the other anthropoid primates. In the hominids this reduction seems to take place in three stages.

In the australopithecine grade, canine dimorphism is markedly reduced from the primitive anthropoid condition, although it remains very high compared to younger hominids. There is little difference in the canine breadth dimorphism between the australopithecines and common chimpanzees and orangutans (compare Tables 6 and 7). Breadth dimorphism is only slightly greater than this for the Ravin ramapithecines. Examination of the few unworn canines indicates that the same might also be true for the dimorphism in canine crown height. Parsimony, then, suggests that the degree of canine dimorphism in the early australopithecines, common chimpanzees, and orangutans reflects the primitive condition for the later hominoids, and that the expanded canine dimorphism of living gorillas is a characteristic unique to them. The idea that the early australopithecines show a reduction in sexual dimorphism of the canine (for instance 318) cannot be confirmed. This misinterpretation probably comes from a confusion of *dimorphism* reduction with *size* reduction, an entirely different matter! The subsequent reduction of canine dimorphism in the hominids is paralleled by a reduction in the pygmy chimpanzee lineage. These reductions are parallel and do not indicate that the reduced dimorphism in *Pan paniscus* is the primitive condition for the African hominoids (contra 61, 320). Indeed, it has become quite evident that little is primitive about the pygmy chimpanzee, and that it cannot validly serve as a model for the predivergence hominoid (186, 312).

In terms of molar size dimorphism, the primitive condition of marked dimorphism is evident in the *Aegyptopithecus* remains. This extreme is shared by the living orangutan, its likely ramapithecine ancestors, and the early australopithecines. Although all of the australopithecine species have marked dimorphism in molar size, this dimorphism does seem to decrease through the australopithecine span, and the latest species is considerably smaller in its molar sexual dimorphism than is the earliest species. At its largest the degree of australopithecine sexual dimorphism is equivalent to that of the orangutans,

and it is very likely that this represents the primitive condition. Unlike the distribution of australopithecine canine breadth dimorphism, even the greatest molar breadth dimorphism is within the modern human range. At its smallest, the magnitude of sexual dimorphism in the australopithecine molars is slightly greater than that in gorillas and much greater than that in chimpanzees. Thus, the australopithecines are not the only lineage to show reduction in molar breadth dimorphism. The two African ape lineages also show a reduction in dimorphism, which is not only parallel to the hominid reduction but, according to the most recent phylogenetic reconstructions, must be parallel to each other because the earliest hominids have the greater magnitude of dimorphism that reflects the primitive condition. Interestingly, the orangutans (and the rama-pithecines, which either are their ancestors or at least reflect the ancestral condition) show no such reduction.

Finally, the magnitude of sexual dimorphism in mandibular height varies among the australopithecines. This is almost certainly a consequence of small sample size, and it is likely that mandibular corpus height dimorphism in all of the australopithecine species does not differ significantly. In the Ravin rama-pithecine sample, corpus height dimorphism is very marked, closely approx-imating the primitive condition as seen in *Aegyptopithecus*. By comparison, all of the later anthropoid primates are reduced in dimorphism. Gorillas and orangutans approximate the australopithecine condition, but if the Ravin rama-pithecines reflect the ancestral condition for orangutans, this must be a parallel reduction. The further reduction in the two chimpanzee species is certainly a parallelism. Thus, mandibular corpus height, like canine breadth, is more dimorphic in the australopithecine grade than any living human population. There is some evidence that dimorphism in postcranial size is similarly extreme in this group.

Among the australopithecines, *A. afarensis* is the most dimorphic for the dentition. The differences in dimorphism within the australopithecines are not great. Yet it is interesting that if this early primitive species were unknown, variation in the other species would indicate that the earlier form should have been the most dimorphic in the genus.

The second stage is reflected by *H. erectus* and earlier populations of *H. sapiens*. It is characterized by an intermediate position for canine sexual dimorphism (between the australopithecine and the modern *H. sapiens* condi-tions), a reduction of molar sexual dimorphism to within the modern human range, but a retention of the australopithecine level of sexual dimorphism in mandibular corpus height. Comparison of these two stages provides some insight into other changes in sexual dimorphism that these variations reflect. In particular, sexual dimorphisms in other aspects of cranial morphology would seem to follow (i.e. be reflected in) the pattern of change in canine sexual dimorphism (212) better than these dimorphisms conform to the pattern of

change in molar breadth or mandibular corpus dimorphism. Thus, sexual dimorphism in the cranial and facial features of the earliest australopithecines is dramatic (171, 311), and remains little changed in *H. habilis,* as comparison of male and female specimens such as ER 1470 and ER 1813 would indicate. The sexual dimorphism in *H. erectus* and Neandertal crania is reduced from this magnitude, although it remains well above the modern human range (208, 310, 311). Thus, like modern human crania, there is disproportionate sexual dimorphism in earlier hominid facial variation (153). In contrast, it is interesting that postcranial sexual dimorphism, insofar as it can be determined, seems to parallel sexual dimorphism in the molars. This dimorphism, at least in the Neandertal sample, is well within the modern human range (143, 287).

The third stage is the modern human condition, with its marked reductions compared with earlier human populations, its marked variability, and its unpatterned, intrapopulational variations. The sample of earlier Upper Paleolithic Europeans is really part of this stage in terms of reduction in sexual dimorphism, although it resembles the Neandertals in all but the reduction of canine dimorphism. Reduction in molar and body size dimorphism in humans and chimpanzees must be parallel evolutionary trends and cannot be due to their common ancestry. Reduction in canine dimorphism is unique to the human line, just as expansion in canine dimorphism is unique to the gorilla line. Explanations of the patterns of sexual dimorphism variation in humans and chimpanzees therefore need not be the same, while at the same time, explanations in both cases are required.

Patterns of sexual dimorphism for postglacial hunter-gatherers, agriculturalists, and modern groups were previously presented in Tables 3 and 4. Other than showing that male canine and second molar breadths are *always* larger than females and that the canine dimorphism is nearly always greater than the second molar breadth, there was no other clearly emerging pattern. Differences among the three broad economic types were not striking, nor statistically significant. In addition, although we do not have evidence for body size in all these groups, we suspect that the modern populations have the greatest stature, yet they show the least dimorphism which negates any powerful relationship between sexual dimorphism and body size. Finally, whether hunter-gatherers or agriculturalists are considered, both monogamous and polygynous marriage systems are represented, yet it would be difficult to determine the mating preferences from the levels of dimorphism present in the samples. Thus, when sexual dimorphism is considered in postglacial human samples, it is apparent that no consistent pattern appears and, moreover, that no single model is successful in describing the variation among and across samples. It may be that cultural factors interfere with biological (selection) forces that previously operated on the human fossil lineage.

SUMMARY

Explanations for these evolutionary trends, as is true for explanations of all paleontological phenomena, should be based on functional and/or adaptive models that can be tested. We have discussed a number of models that purport to account for differences in sexual dimorphism. Not all of these could account for the reduction of dimorphism in the hominids, and in fact primate dimorphism has proven to be more complex than is often realized (83). For instance, even if there were an important relation between sexual dimorphism and body size, the fact is that there is little change in average body size over most of the course of post-australopithecine hominid evolution. A rather different problem lies in applying the relation of sexual dimorphism to economic systems, since it was necessary to examine this relation over a range of economic systems that do not characterize most of the fossil hominid groups. All of these prehistoric populations were hunter/gatherers to some extent (although differing vastly in the relative importance of different food-procurement approaches). Habitat and dimorphism failed as an explanation for primate variation, and there are no arboreal humans to apply a primate-based habitat model to. Finally, dimorphism and mating system, however potentially explanatory in either primates or in living human populations, must always remain a speculative relation for fossil hominids (213). While some workers have argued for an early and perhaps critical appearance of monogamy as the original mating pattern in the hominids (203), others have argued that a polygynous system was more likely (6), while still others emphasize the idea that bonding, even if short lived, was the important aspect of male-female relationships early in hominid evolution (87). We simply shall never know. Nor can we easily clarify basic issues such as whether canine dimorphism reduced because of a reduction in aggression (presumably a reduction in male-male competition over mates or the replacement of the canines by improved technology during such competition—if it ever occurred), or whether canine dimorphism reduction is no more than a reflection of the reduction in sexual dimorphism related to a completely different cause. Similarly, there are no real prospects for linking warfare-related technology or aggressive behaviors to the magnitude of dimorphism. As in the cases above, if there was such a relationship, it was likely complex and interrelated with other factors that influence dimorphism as well.

One interesting complication results from the independent reduction of sexual dimorphism in the chimpanzee and human lineages. The fact is that the chimpanzees show a definite division of labor in how they acquire foods—a division that many think could act as a precursor for a human hunting/gathering adaptation. Yet little dimorphism in body size is shown in the two living chimpanzee species (the differences between them is not important in this regard). The differential resource exploitation is a common adaptation in

chimpanzees and hominids, and this suggests that at least some of the dimorphism reduction in both of these lineages may be a consequence of the resource exploitation pattern; that is, of the economic adaptation that reduces the competition between the sexes.

Our tendency is to suspect that the systematic reduction in dimorphism over the course of human evolution is a consequence of a convergence in the requirements of male and female roles. We do not limit this contention to economic roles. This is because role requirements are complex in humans and involve far more than just those activities that can be directly related to the procurement and preparation of foods, as Bridges (40) and others (152, 213) have argued. Thus we contend that the hominids have adapted to a dimorphic niche which, over the course of human evolution, has become increasingly monomorphic. Males and females have each come to utilize a greater proportion of resources available to the population as a whole. Thus both the roles and the activities of the individuals change in such a way that would ultimately act to reduce the magnitude of sexual dimorphism and the extent of overlap between the sexes, according to this interpretation. Simply put, the problem with this contention is that we cannot test it in a convincing manner. If, as we believe, the causes of dimorphism are complexly interrelated, it is probable that specific changes in causation may never be discernible.

For some, conclusions which come to noncommittal positions may seem disconcerting and fruitless. Although we are convinced that sexual dimorphism reduces within the hominids, as well as in many other primate lineages, we are unable to determine any simple pattern of ultimate cause(s) and are unwilling to force the data into a particular model. Indeed, the models we presented in the first half of this paper are not particularly successful in explaining patterns of sexual dimorphism in the limited cases they cover. Applying them to fossil samples requires the acceptance of numerous assumptions about unknown factors of essentially unreconstructable social behavior. It is apparent from this review that sexual dimorphism reduces, but specifically why this takes place is still a unanswered problem. Most likely, simplistic, single cause models will not be effective in accounting for this common trend in evolution.

of Michigan computer system (MTS) by using TELENET and logging on to the same ID from our terminals over 750 miles apart. This is an experience we urge our colleagues to try.

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