Equality for the sexes in human evolution? Early hominid sexual dimorphism and implications for mating systems and social behavior

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Since the publication of Charles Darwin’s *The Descent of Man and Selection in Relation to Sex* in 1871 (1), there has been a vigorous debate about the meaning of sexual dimorphism for a range of physical attributes in numerous animal species, including primates and humans, extinct and extant. Key points of discussion are how to interpret size dimorphism in past humans and human-like ancestors and what inferences can be drawn about the evolution of human mating systems and social organization. In this issue of PNAS, Reno et al. (2) report on their investigation of sexual dimorphism in the three-million-year-old *Australopithecus afarensis*, an important and well-known hominid, ancestral to the genus *Homo* (3). Insight into dimorphism in this taxon has important implications for social behavior and organization in later and present-day humans.

Body mass dimorphism varies dramatically among primate species, both present and past. For most anthropoids, males are bigger than females (4–8). Humans today display relatively limited sexual dimorphism (∼15%), whereas some of the other hominoids (gorillas and orangutans) are highly dimorphic (∼50%) (5, 9). Body mass is easily determined in living species. For past nonhuman primates and human ancestors, mostly represented by fragmentary fossil remains, body mass is far less accessible. Recently, the femur head (the ball of bone at the top of the femur that fits into the hip joint) has been invoked as a source for estimating body mass in early hominids, *Homo*, and its evolutionary predecessor, *Australopithecus* (10, 11).

Comparisons of body mass in fossil hominids reveal that general levels of dimorphism have likely remained more or less the same for most of the evolution of *Homo*, or most of the last two million years to the present (9). In hominids predating *Homo*, namely the multiple species of *Australopithecus*, the consensus among paleoanthropologists that has emerged over the last two decades is that pre-*Homo* species are characterized by high levels of sexual dimorphism (4, 5, 12–15). Close scrutiny of the fossil record, however, suggests that this consensus is built on a data set complete with limitations, especially in regard to reconstructing size dimorphism in *Australopithecus*. First, the sample used to estimate dimorphism is very small (fewer than six individuals for *A. afarensis*). Second, estimates of dimorphism are based on the assumption that sex identification in fragmentary fossil remains used to derive these estimates is accurate. Indeed, the secondary sex characteristics exhibited in the bony pelvis, by far the most reliable of the indicators for humans (16, 17), are largely missing. Thus, investigators are left with size of skeletal elements alone (males have big bones and females have small bones), a poor proxy for pelvic sex identification. Third, accuracy in determination of sexual dimorphism is predicated on correct taxonomic identification. This is especially problematic given that level of sexual dimorphism shows substantial intertaxa variation. Fourth, levels of dimorphism can shift over broad expanses of time (potentially hundreds of thousands of years) or even relatively narrow expanses of time involving hundreds or tens of years (18). Finally, sexual dimorphism levels across broad geographic areas and ecological variation therein may be exaggerated in comparison with contemporary members of a species living in the same place (9).

Reno et al. (2) draw on advances made in statistical modeling to circumvent these limitations of the early hominid fossil record. They apply a new and robust method of simulating dimorphism to an assemblage of *A. afarensis* representing the remains of individuals who likely died simultaneously in a single catastrophic event some 3.2 million years ago at site A.L. 333, Hadar, Ethiopia. Using the 40% complete skeleton (“Lucy”) from site A.L. 288 as a morphometric template (she has a relatively well preserved femur head and other long bones; Fig. 1), they calculated femoral head diameters from measurements for the postcranial elements from A.L. 333 and other *A. afarensis* remains. In contrast to the consensus, their analysis...
revealed only slight to moderate levels of sexual dimorphism, more like Homo
and chimpanzees than gorillas.

How to interpret this interesting result? By using models derived from
study of living nonhuman primates and humans, analysis of sexual dimorphism
provides a window onto behavior in earlier hominids and added perspective
on the evolution of human social behavior and mating systems. Monomor-
phic species of living primates (those
taxa exhibiting low levels of sexual di-
morphism) tend to express minimal
male–male competition, whereas di-
morphic species tend to express rela-
tively high levels of competition (19–
21). Baboon males, for example, are
highly intolerant of one another and
aggressively compete for access to fe-
male mates; simply, success in fights
results in greater access to females.
For this and other dimorphic primates,
sexual selection is only one explanation
for high levels of dimorphism, and may
not be the best one (22). However,
new analyses indicate associations be-
tween dimorphism and competition
levels (6, 7): where dimorphism is high,
levels of dimorphism in single- and
taxa exhibiting low levels of sexual di-
morphism). This would seem to be one
possible conclusion. However, A. afa-
rensis has lower canine dimorphism
than chimpanzees (5–7, 12–14, 27),
which suggests a different kind of so-
cial organization for these early homin-
ids altogether. The findings of Reno et
al. (2) and interpretations based on
a range of evidence suggest that A. afare-
ris had a monogamous and not a
polygynous mating system with strong
intermale competition as was implied
from previous reconstructions of great
body size dimorphism. However, the
data are interpreted, their findings do
not contradict what would be expected
in a monogamous mating system. In-
deed, the relatively low amount of di-
morphism is more consistent with pair
bonding (and the behaviors associated
with it), more so than with the higher
levels of dimorphism in single- and
multimale extant primate genera (28).

We will never know what the social
organization and mating systems were
for early hominids; past behaviors do
not preserve. However, innovative doc-
umentation of morphometric variation
in the context of informed study of be-
havior in living species provides essen-
tial perspective on behavior in extinct
species. In addition to charting new
directions for future analysis, these
new findings suggest that earlier be-
havioral models based on supposedly
highly dimorphic pre-Homo taxa are
not the most appropriate, and that the

**Early hominids may have been more human-like in their basic social behavior.**

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