Darwin, sexual selection, and human evolution

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In addition to creating the foundations of modern evolutionary theory, Darwin was a pioneer in the field of sexology. Surprising and shocking as this statement would have seemed to his contemporaries in Victorian times, it is justified by a consideration of his work on *The Descent of Man and Selection in Relation to Sex*. His studies of sexual selection in animals led Darwin (1871) to posit that sex differences in body size and weaponry occur because males of certain species compete for access to mates, and thus derive a reproductive advantage from traits such as greater strength and aggressiveness. However, he also stressed that 'there is another and more peaceful kind of contest, in which the males endeavour to excite and allure the females by various charms.' It was on this basis that he sought to explain the evolution of extravagant secondary sexual adornments and courtship displays as, for example, in the Argus pheasant and peafowl. He was also intrigued by sex differences in human physique, secondary sexual adornments and behaviour; thus Darwin attempted to apply his theories concerning sexual selection in animals to questions of human evolution.

At the time when the *Descent of Man* was written, no hominid fossils were known aside from a few Neanderthal specimens. Yet Darwin, like his champion Thomas Henry Huxley (1863), was aware that the great apes constitute our closest relatives among the extant primates. Darwin considered the African apes (chimpanzee and gorilla) to be especially important in this regard, and he proposed that human beings had originated in Africa. It is now known that humans and chimpanzees share a common ancestor, which existed approximately 7–8 million years ago. An extensive tree of fossil hominids is now known, firmly rooted in Africa, including australopithecines of the genus *Australopithecus* and the genus *Paranthropus*, as well as the earliest members of the genus *Homo* (e.g. *H. habilis*, *H. rudolfensis* and *H. ergaster* – Figure 1). The first anatomically modern humans are also of African origin; fossils of *H. sapiens* from Omo Kibish in Ethiopia have been dated to 195 000 years ago.

Many of the australopithecines that preceded the emergence of the genus *Homo* are thought to have been sexually dimorphic in body size, with males being markedly larger than females. If this interpretation of fossil evidence is correct, it might indicate that inter-male competition, for access to females, was important in the mating systems of our precursors. However, it is exceedingly difficult, from fragmentary evidence, to identify the sexes of fossil hominids, and calculations of their body weights are also highly problematic. Thus, data on sexual dimorphism in body size among ancestral hominids are incomplete and the subject of continuing debate (e.g. Reno *et al*. 2003).

Comparative studies of humans and the extant non-human primates can be helpful in addressing questions about sex differences in body size as they relate to mating systems. Body-size sexual dimorphism is most pronounced in polygynous species, such as the gorilla, where a single large male associates with a small group of females for reproductive purposes. It is least pronounced in monogamous forms like the gibbons, which live in small family groups. However, many species of monkeys, as well as chimpanzees, live in multimale–multifemale groups. Intra-sexual competition has also led to increased male body size under these conditions, although it is not so pronounced as in polygynous primates such as the gorilla, the hamadryas baboon, or the gelada. There are good reasons to believe, however, that humans did not emerge from a background involving a chimpanzee-like mating system. To understand this, it is necessary to say a few words about the subject of 'sperm competition' in relation to mating systems. This is an important facet of sexual selection, which was unknown to Darwin.

Whenever a female mates with two or more males during her fertile period, there is the possibility that sperm from these 'rival' males will compete for access to her ova. This is the essence of Parker's (1970) definition of 'sperm competition,' which he formulated by studying insects, and which was later applied to many animal groups including the primates. Thus, in chimpanzees, females that are likely to ovulate will mate with most non-related males in the multimale–multifemale community (Goodall 1986). Sperm competition has resulted in selection for reproductive specialisations in males, including very large testes, in order that they can maintain high sperm counts during multiple copulations. In general, those monkeys and apes that have multimale-mating systems tend to exhibit

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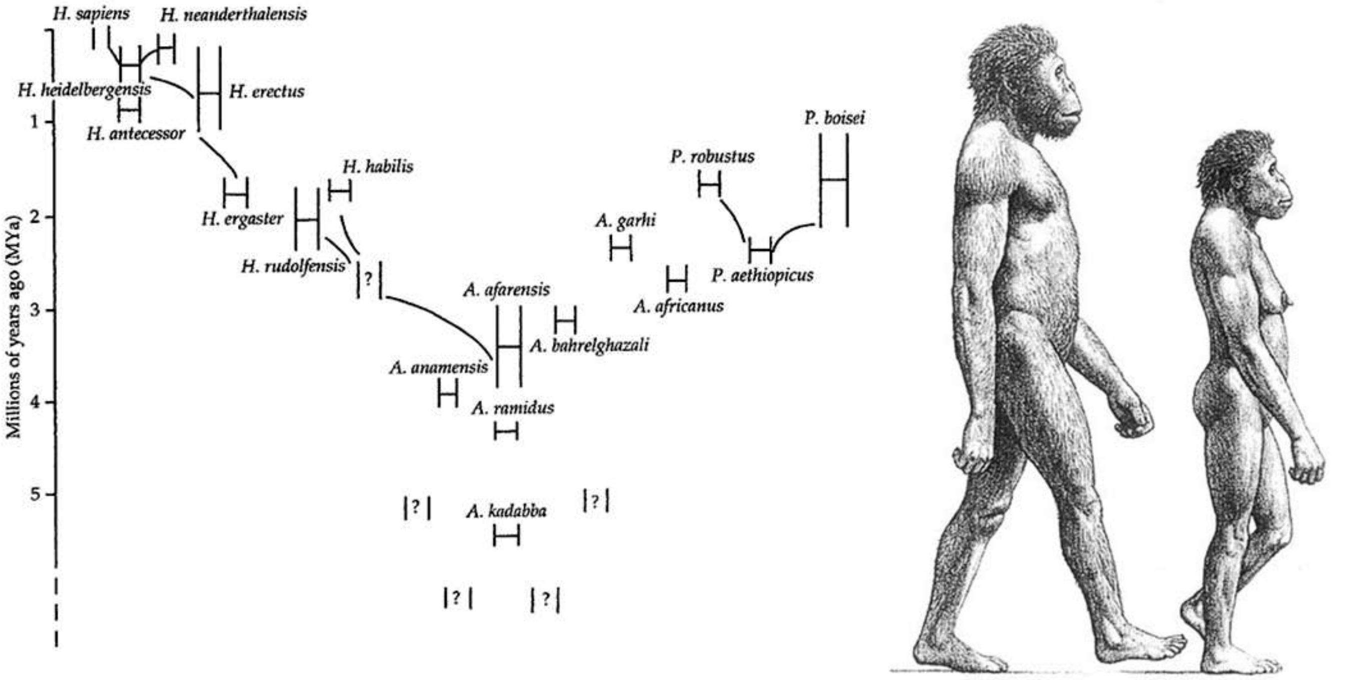


Figure 1. ***Approximate time spans and evolutionary relationships of the main hominid taxa. Note that the abbreviation "A" is used for the genus*** **Ardipithecus** ***(i.e.*** **A. kadabba** ***and*** **A. ramidus*****) as well as for*** **Australopithecus**. ***A reconstruction of*** **Australopithecus africanus** ***is also shown; the larger individual on the left is the adult male. From Dixson 2009.***

the largest testes sizes in relation to body weight. Conversely, among primates whose females mate primarily with single partners (i.e. monogamous and polygynous species), sperm competition pressures are low, and relative testes sizes are reduced (Harcourt *et al*. 1981).

Human relative testes size is quite small (Figure 2), as is consistent with an evolutionary past involving either polygyny or monogamy (or both) and a relative absence of significant sperm competition. Although some evolutionary psychologists argue that sperm competition has played an important role in human evolution (e.g. Baker & Bellis 1995; Shackelford & Pound 2006), a large body of evidence derived from work on comparative anatomy and physiology does not support this conclusion. Thus, a range of traits including sperm morphology, and the structures of the accessory reproductive glands and the penis, align *H. sapiens* with those primates that display the least evidence of sexual selection via sperm competition (Table 1).

Table 1. Summary of genital traits which have undergone sexual selection in males of those primate species that exhibit large relative testes sizes and pronounced sperm competition, but which are poorly developed in **H. sapiens*****. It is thus unlikely that sperm competition has played any significant role in human evolution.***

Trait	Effect of sexual selection	Source
sperm midpiece	increased volume and mitochondrial loading	Anderson & Dixson 2002
vas deferens	increased muscularity	Anderson et al. 2004
seminal vesicles	increase in size	Dixson 1998a
seminal coagulation	more pronounced	Dixson & Anderson 2002
penile morphology	increased complexity	Dixson 1998b, 2009

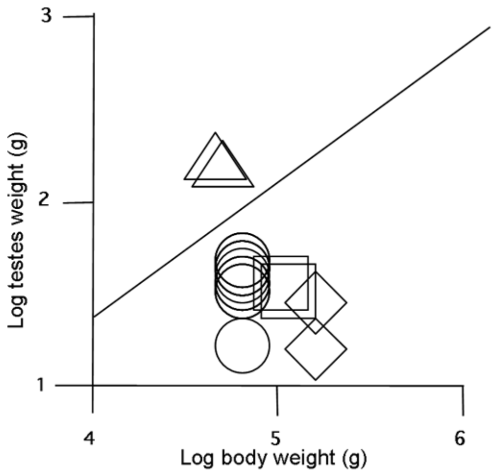
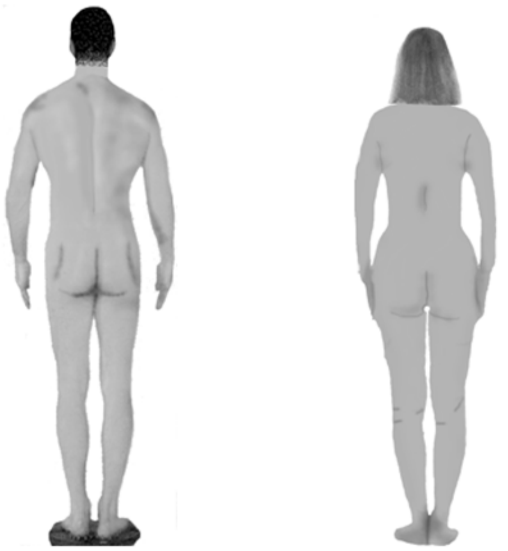


Figure 2. ***Relative testes sizes in human populations worldwide, as compared to the great apes.*** **○ = Homo**. ***Data are for 14 populations and more than 7000 men;*** **◊ = Gorilla**. ***Both the lowland and mountain forms are shown;*** **□ = Pongo**. ***The Sumatran and Bornean species are plotted separately;*** **∆ = Pan**. ***Both the chimpanzee and bonobo are shown. From Dixson 2009.***

It is most unlikely, therefore, that human ancestors would have had multimale–multifemale mating systems like those of chimpanzees. Monogamy and/or polygyny are much more likely candidates as regards the origins of human mating systems; indeed, in the majority of recent cultures, these types of mating systems have been documented (Ford & Beach 1951; Murdock 1981). The likely importance of polygyny during the evolution of human sexual behaviour becomes clearer when we revisit the classical approaches to sexual selection formulated by Darwin, in the light of modern research on human sexual dimorphism and mate choice. As can be seen in Figure 3, men and women are sexually dimorphic in a variety of traits, including body size and composition, as well as having distinctive secondary sexual adornments, including prominent breasts in females, and facial hair in males. It is likely that both natural selection and sexual selection have impacted on the evolution of many of these sex differences.

The ratio of male:female body weight averages 1.1–1.2 in human populations; this sex difference is larger than in monogamous non-human primates, but much smaller than in highly polygynous species such as the gorilla, in which males are more than twice as large as females. Human body *composition* is highly sexually dimorphic, however, so that the proportions of muscle and adipose tissue (fat) differ markedly between men and women (Clarys *et al*. 1984). Men have up to 50% more muscle in their bodily constitution than women, and they are physically much stronger. Cross-cultural studies of female preferences for male somatotypes show that mesomorphic (muscular) and average physiques are rated as most attractive by women (Figure 4). Women also show a fundamental preference for a male partner taller than themselves (Pawlowski 2003) and there is evidence that taller men have greater reproductive success (Pawlowski *et al*. 2000). Thus, although traits such as male height and muscularity may have been profoundly influenced by natural selection in relation to endurance running and persistence hunting during emergence of the genus *Homo* (Bramble & Lieberman 2004), it is also probable that sexual selection has played an important role in their evolution. Sexual selection may have favoured such traits because they served as 'honest signals' of a male's ability to protect and to provide for his prospective mates.

The overall distribution of fat in the female physique has also been subject to sexual selection as well as natural selection during evolution of the genus *Homo*. From puberty onwards, fat is laid down, under the influence of oestrogen, in the breasts, hips, thighs, and buttocks of young women. This produces a 'gynoid' fat distribution and an 'hourglass' female body shape, reflective of health, youth, and reproductive potential. These fat reserves are essential to support the heavy physiological demands women experience during pregnancy, lactation, and protracted periods of infant care. Women with narrow waists and large breasts have significantly higher levels of salivary oestradiol than others during the mid-phase of the menstrual cycle (Jasieńska *et al*. 2004). The waist-to-hip ratio (WHR), measured by dividing the circumference of the waist by the hips, provides a simple index of fat distribution in relation to female health and attractiveness (Singh 2002). Healthy young women in their reproductive years tend to have a low WHR, in the range 0.67–0.8 (studies in Finland: Marti *et al*. 1991). It is probably significant, therefore, that in many human cultures men rate images of women with low WHRs (0.6, 0.7, or 0.8) as being most attractive (Fig. 4). These findings apply to diverse populations: in Africa (Marlowe *et al*. 2005; Dixson *et al*. 2007b), China (Dixson *et al*. 2007a), New Zealand, and the USA (Dixson *et al*. 2009), as examples. Again, the possibility exists that sexual selection has favoured the evolution of the female hourglass shape, because it provides cues concerning female reproductive potential. Men attend to such cues in making their *initial judgments* of female attractiveness.



Height
Body weight
Body composition
Body shape
Sexual bimaturism
Facial morphology
Hands and feet
Skin colour

Facial/head hair
Body hair
Pubic hair
'Adam's apple'
Breast morphology
Axillary organ
2nd/4th digit ratio
Forearm length

Figure 3. ***Images depicting a mesomorphic masculine somatotype and an hourglass feminine somatotype (waist-to-hip ratio, WHR = 0.7) together with a list of the morphological sex differences that occur in*** **Homo sapiens.** ***From Dixson 2009.***

Sex differences in human facial morphology are also relevant to discussions of the origins of human mating systems, and the likely importance of polygyny during hominid evolution. In women, the jaw and chin tend to be smaller than in men, the eyes are larger in relation to surrounding features, and the complexion tends to be lighter. Law-Smith *et al*. (2006) have shown that these features are related to oestrogen levels, so that women whose faces are rated as most attractive also have higher follicular phase levels of oestradiol 17β. In men, by contrast, higher levels of testosterone, secreted by the testes from puberty onwards, result in greater growth of the jaw and chin, while the brow ridges often enlarge somewhat, so that the eyes appear narrower and more deep-set. Moreover, growth of the male beard accentuates the size of the lower face. Darwin considered that the beard had evolved owing to sexual selection in human ancestors and that 'our ape-like progenitors acquired their beards as an ornament to charm or excite the opposite sex'. Research currently in progress at Victoria University of Wellington is examining these questions. However, work to date indicates that the beard is probably much more relevant to judgments of male age and social status, than it is to attractiveness (Barnaby Dixson pers. comm.). Interestingly, comparative measurements of sexually dimorphic visual adornments in monkeys, apes, and humans have shown that the most striking masculine adornments occur in species that have polygynous mating systems. The human male also scores highly for such traits, and this may be indicative of sexual selection acting within ancestral polygynous precursors (Dixson *et al*. 2005).

Finally, it is useful to note Darwin's (1871) views on sex differences in the human voice and the size of the larynx. He noted that 'man appears to have inherited this difference from his early progenitors. His vocal cords are about one-third

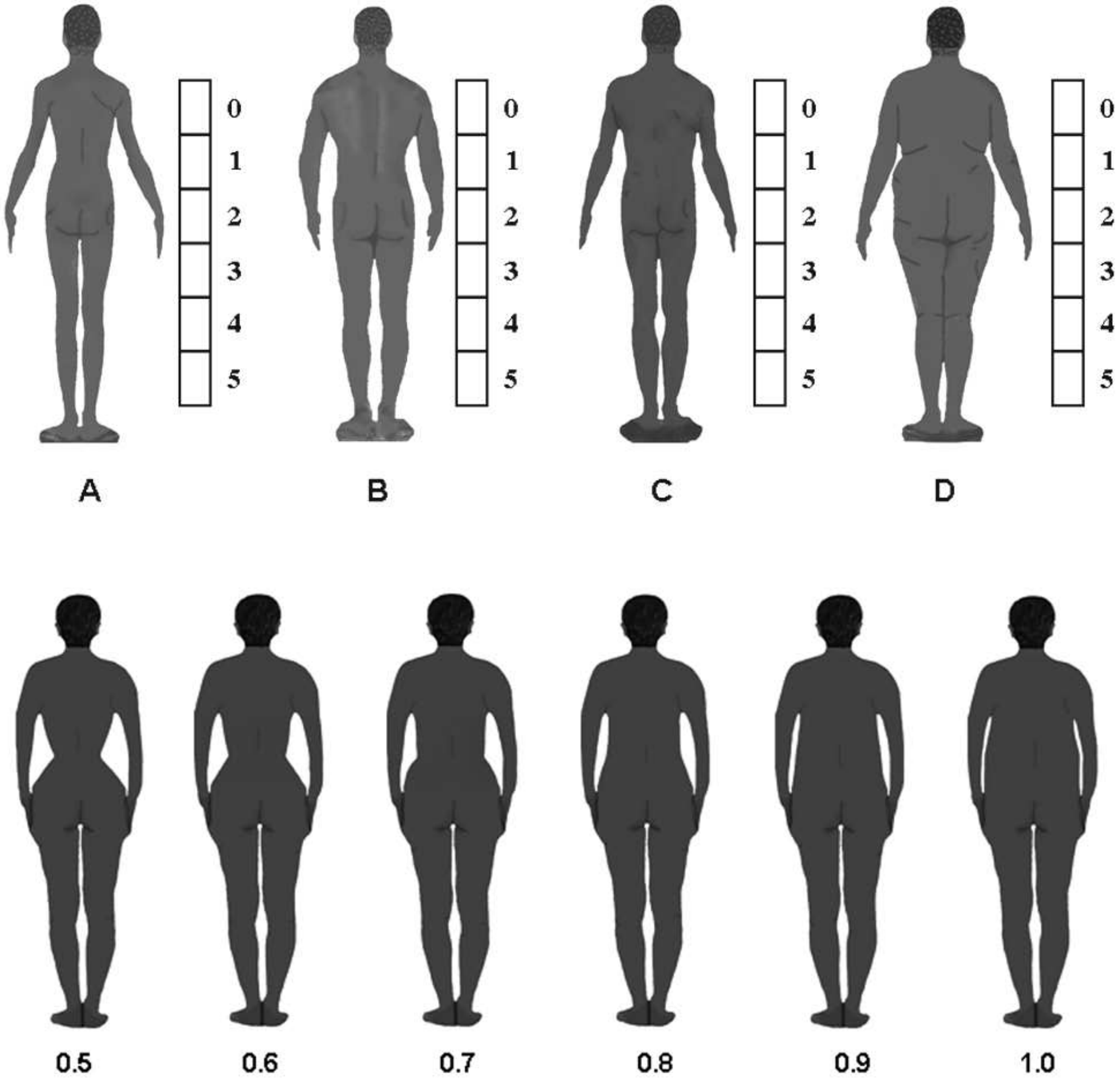


Figure 4. ***Upper:* *Back-posed images of male somatotypes (A, ectomorphic; B, mesomorphic; C, average; D, endomorphic) used in cross-cultural studies of masculine physique and sexual attractiveness. These particular images were used for work in Cameroon. Lower: Back-posed images used in cross-cultural studies of female waist-to-hip ratio (WHR) and attractiveness. This version of the images, varying in WHR between 0.5–1.0, was used in Cameroon. From Dixson 2009.***

longer than in woman, or than in boys.' It is now known that individual variation in pitch of the male voice correlates with differences in circulating testosterone (Nieschlag 1979). Women find deeper male voices to be pleasant and attractive, as well as more dominant (Feinberg *et a*l. 2005; Puts *et al*. 2006). Again, the non-human primates provide us with a valuable comparative perspective. Specialisations of the male vocal tract (larynx, hyoid, and vocal sacs) are most pronounced in monkeys and apes that are polygynous rather than among those that have monogamous or multimale–multifemale mating systems (Fig. 5). Males of polygynous species also have deep-pitched vocal displays (e.g. the 'long-call'of the male orang-utan and the 'roaring' of the male king colobus). It is likely that sex differences in the human larynx and vocal pitch were also affected by sexual selection in polygynous ancestors, early in hominid evolution, well before the advent of language.

The fundamental contribution made by Darwin to our understanding of sexual selection and human evolution is still relevant today. However, we now possess much more information, and insights gained from studies of the fossil record, modern developments in molecular genetics, reproductive physiology, anthropology, sexological research, and evolutionary psychology. Collaborations between workers in these disciplines will be required to achieve greater knowledge of the evolution of human reproduction. Cross-cultural studies of human sexual dimorphism, sexual selection and mate choice are essential if we are to have any hope of establishing which traits are derived from the shared African ancestry of modern human populations.

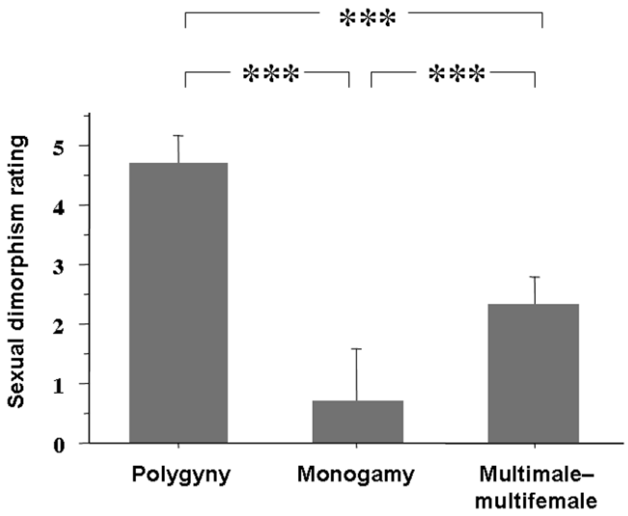


Figure 5. ***Sexual dimorphism in the vocal apparatus (larynx, laryngeal sacs, and hyoid) and its relationship to mating systems in primates. Data (from Dixson 2009) are ratings of the degree of sexual size dimorphism (male > female) for 24 genera including*** **Homo.** *** $p < 0.001$.

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