CHAPTER 9

The Human Hand

"Man could not have attained his present dominant position in the world without the use of his hands which are so admirably adapted to act in obedience to his will"
[Darwin, 1871, p. 141].

"...adaptations for manual dexterity appear well before the earliest known evidence of modified stone tools. These adaptations suggest that early hominins used or made tools...before the earliest-known stone tool record"
[Panger, et al., 2002, p. 239].

Introduction. If natural selection for bipedal use of hand-held weapons played a major role in human origins and evolution, then our hands should bear the crucial evidence. Natural selection would have acted to improve the hand's grip of those weapons. The prediction that from the earliest hominins until the emergence of *Homo* there will prove to be an ineluctable remodeling of the hands to enhance the prehension of spheroidal missiles and clubs with cylindroidal handles is a crucial test which could falsify the throwing-and-clubbing explanation or provide it with a powerful stamp of confirmation. It was once thought that the human hand was the preeminent example of benevolent design in nature—the most remarkable, most perfect combination of bones and muscles [Bell, 1837]. Darwin [1871], like Bell, marveled at the structure and capacities of the human hand, but imagined an evolutionary explanation which involved the bipedal use of hand-held weapons: "To throw a stone with as true an aim as can a Fuegian in defending himself, or in killing birds, requires the most consummate perfection in the correlated action of the muscles of the hand, arm and shoulder, not to mention a fine sense of touch. In throwing a stone or spear, and in many other actions, a man must stand firmly on his feet; and this again demands the perfect coadaptation of numerous muscles" [Darwin, 1871, p. 138]. "But the hands and arms could hardly have become perfect enough to have manufactured weapons, or to have hurled stones and spears with a true aim, as long as they were habitually used for locomotion and for supporting the whole weight of the body, or as long as they were especially well adapted...for climbing trees" [1871, p. 141].

These ideas hold true today. The evolution of the human hand can be explained in remarkable detail by the simple proposal that it is the result of natural selection for improved gripping of spheres and cylinders which for millions of years were used as weapons from a bipedal stance, a strategy that promoted greater reproductive success for those who were most adept at it. Although our signature behavior is not much use in the modern world, we are still the master throwers and strikers of the animal kingdom. Furthermore, our hands, naturally selected for a firm grip on a club and a fingertip-pad grasp on a spheroidal missile, have proved to be capable of all of the manipulatory behaviors displayed in our modern culture. The hands we inherited from our ancient ancestors, still bearing the imprint of the missiles and clubs they once used in the competition to survive and reproduce, are among the greatest gifts of our hominin legacy.

That our hand structure is the result of genetic inheritance is uncontested. It arises from a developmental process which differs from that in all other known species, living or extinct. The hands of our nearest relatives, the great apes, are adapted for an arboreal lifestyle. Ours must be adapted for something else—an innovative behavior that enhanced survival and reproduction.

What was the hand like in the hominin ancestor? The first hominins were arboreal creatures (Chapter 2); their hands were "ape-like" [Tocheri, et al., 2008] and our ancestors retained arboreal traits in their hands for several million years. In the absence of fossil hands of our last common ancestor with chimpanzees, the chimpanzee's hand has often been used as a model for the ancestral hand [Young, 2003]. Recently discovered fossils, however, have raised the possibility that after the hominin divergence chimpanzee hands may have undergone selection which accentuated their arboreal adaptation, shrinking and weakening their thumbs, lengthening their palms, elongating and increasing the curvature of their fingers, and losing their fleshy fingertip pads. Features of the *Orrorin* distal thumb phalanx suggested to Gommery and Senut [2006] that this bone in chimpanzees was a poor model for that of the hominin ancestor. Short metacarpals may be more of an ancestral condition than the long metacarpals in *Pan* [Drapeau, et al., 2005; Drapeau and Ward, 2007]. Lovejoy et al. [2009b, d] think the *Ardipithecus* hand indicates that fingers of modern apes became elongated and the thumb atrophied. Human hand proportions may be more like those of Miocene apes than modern apes [Alméija, et al., 2010]. These recent conjectures emphasize the caution required when there is insufficient fossil evidence. The hand of the hominin ancestor was ape-like, but which ape's hand it was like is unknown. With this caveat, I shall use the hand of the chimpanzee.

The chimpanzee hand. The major features of the chimpanzee hand are depicted in Figures 4 and 5. Compared to humans, the range of wrist flexion is large in the chimpanzee, but extension is constrained by bony ridges, ligaments and the long flexors of the fingers [Napier, 1960; Tuttle, 1967; Richmond et al., 2001]. (This stiffens the wrist for knuckle-walking). Both the palm and the fingers are elongated. The third and fourth metacarpals are especially robust [Lewis, 1977; Susman, 1979]. Proximal and middle phalanges are curved toward the palm [Susman and Creel, 1979; Susman, 1994], the distal phalanges lack apical tufts [Napier, 1960; Susman, 1988b, 1991], and both thenar and hypothenar muscles at the base of the hand are poorly developed [Napier, 1960]. Bones of the thumb are slender and diminutive relative to the fingers; intrinsic thumb muscles are small and weak [Susman, 1994; Marzke, et al., 1992, 1999].

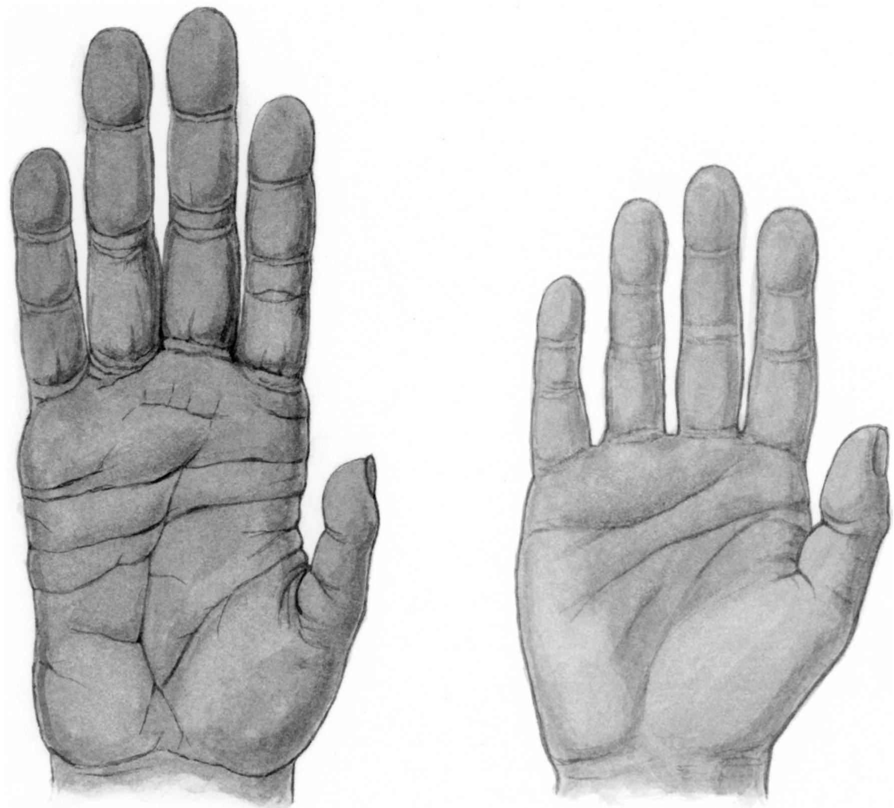

Figure 4. The chimpanzee hand (left) serves as a model of the ancestral ape hand for comparison with the modern human hand (right). The chimpanzee hand is adapted for arborealism. The human hand has a shorter palm, shorter fingers, and an enlarged, mobile thumb which can be rotated into opposition to the palmar surface of the other fingers. The thenar eminence is larger, due to increased size of intrinsic thumb muscles. There is a shift in finger robusticity from fingers 4 and 3 in the chimpanzee to fingers 3 and 2 in the human hand. The distal creases in the palm take a more oblique course in humans. These and other features of the evolution of the human hand are explicable as an adaptation to gripping missiles and clubs (from Young, 2010).

The long, curved fingers in conjunction with a small, weak thumb are characteristics of arboreal apes who are adapted to climbing vertical supports and suspension below tree limbs.
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