Knuckle Walking by a Baboon *(Papio cynocephalus)*

GLENN HAUSFATER
Department of Psychology and Biology, University of Virginia, Charlottesville, Virginia 22901

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ABSTRACT This paper describes the development of a knuckle walking mode of locomotion by a free-living yellow baboon *(Papio cynocephalus)*. Some implications of this occurrence for theories of the evolution of knuckle walking are discussed.

Knuckle walking, a mode of locomotion in which weight is supported on the dorsal aspects of middle phalanges II–IV, is considered unique to the African apes among primates. This unusual mode of locomotion figures prominently in theories of hominoid evolution, and in particular, several scientists have claimed that early man passed through a knuckle walking stage. However, after surveying the morphology of ape hands, Tuttle ('67, '69) concluded that man's ancestors did not pass through a knuckle walking stage and that knuckle walking was a secondary adaptation to terrestrial life by the chimpanzee and gorilla. Tuttle ('69) further concluded that knuckle walking probably developed either from fist walking, the variety of hand positions used by orangutans on the ground, or from some sort of palm walking, modified to allow for flexion of the digits. Recently, Tuttle and Beck ('72) and Susman ('74) have described knuckle walking by a captive orangutan *(Pongo pygmaeus)* and have argued, based on this occurrence, both that knuckle walking evolved from fist walking and that the arboreal habitat of orangutans predisposed them to such behavior. This report describes knuckle walking by a free-living yellow baboon *(Papio cynocephalus)* and considers the implications of this behavior for theories of hominoid evolution and the evolution of knuckle walking.

In early 1973, Dutch, a fully adult male yellow baboon under study in the Amboseli National Park, Kenya, received several puncture wounds on his left wrist. Apparently as a result of these injuries, Dutch began walking on the back of his left hand rather than on the palmar surface as is usual for baboons. In 1974, Dutch used the dorsal surface of both his right and left hands for walking, though his locomotion was relatively inefficient and he often lagged far behind his group. Also in 1974, Dutch frequently used his right or left hand to knuckle walk (fig. 1).

Dutch's aberrant hand positions can be classified into a dorsal support, an intermediate, and a knuckle walking position. In dorsal support, the wrist was fully flexed and the dorsum of the hand directly apposed to the ground. Dutch's weight was supported on metacarpals II–IV and probably also somewhat on the distal carpals; the middle and distal phalanges were slightly flexed, raising them from the ground. In knuckle walking, Dutch placed his weight directly on middle phalanges II–IV. The metacarpophalangeal joints were fully extended and the wrist was either extended or hyperextended. Dutch's knuckle walking hand position was thus essentially the same as that of chimpanzees and gorillas (Tuttle, '69). In the intermediate position, Dutch's weight was supported almost completely on proximal phalanges II–IV and both the metacarpophalangeal and the interphalangeal joints were flexed. The wrist was usually extended, though less than during knuckle walking. Abrasion of Dutch's hands by the ground resulted in the loss of hair from above the metacarpals and proximal and middle phalanges and thick calluses developed in these areas (fig. 2).

Dutch's usage of dorsal support and

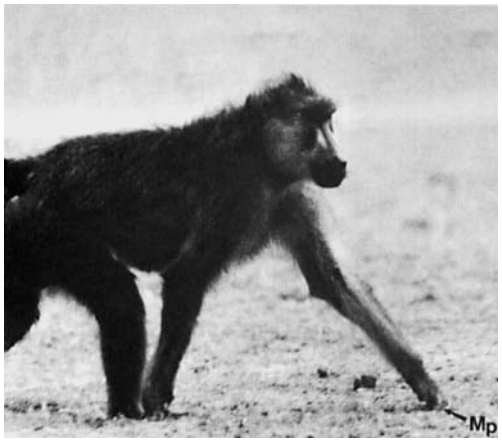

Fig. 1 Dutch knuckle walking. Note that the dorsal surface of the middle phalanges (Mp) of the left hand is in contact with the ground.

knuckle walking hand positions was relatively independent of substrate; each of his modes of locomotion was used on rocky volcanic hills, in wooded areas, and in short grass savannah. In slow casual movement, for example between food plants, Dutch usually placed his right hand in the intermediate or knuckle walking position and his left hand in the dorsal support position. When chased or harassed by other group members, or otherwise moving rapidly, Dutch usually reverted to dorsal support on both hands. Despite atypical hand positions in walking, Dutch was still able to use his fingers dexterously to groom himself or others and to pluck single berries from a bush.

Habitual knuckle walking by a normally plantigrade primate has strong implications for attempts to infer the phylogeny of knuckle walking in African apes. In particular, the possibility that knuckle walking evolved from some sort of modified plantigrade hand position, rather than from fist walking, cannot be excluded from consideration by evolutionary theorists. However, although Dutch's novel mode of locomotion clearly shows that there is more than one sequence of hand morphologies and hand positions that may lead to the development of habitual knuckle walking, the behavior of a single baboon or a single orangutan is scant and insufficient evidence on which to base any evolutionary theory. For example, Tuttle and Beck ('72) concluded that "because a highly adanced arboreal climber and arm swinger like an orangutan is able to place his hands in knuckle walking postures . . . [then] the African apes might have been similarly, or to a greater extent, predisposed to knuckle walking by their own special arboreal heritage." Were this inference valid, then one would have to conclude that knuckle walking by a baboon indicated that large bodied terrestrial primates are also predisposed to knuckle walking by their own special heritage. In sum, although isolated cases of knuckle walking baboons, orangutans or men may tell us something about the intrinsic flexibility of primate hands, these rare events, perhaps pathological abnormalities, should not be considered or accepted as major pieces of evidence in complex and often speculative evolutionary theories. Theories of primate locomotor evolution ought to be based on, or confirmed by, quantitative

Fig. 2 Calluses on Dutch's hands. Note the large hairless callus over the metacarpals (arrow) and the absence of hair from the dorsal surface of the digits (arrow).

data on locomotor behavior under natural conditions, rather than on the aberrant behavior of single individuals.

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