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Knuckle-Walking Signal in the Manual Phalanges and Metacarpals of the Great Apes (Pan and Gorilla)

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Abstract
The "Knuckle-walking Hominin Hypothesis" postulates that there was a knuckle-walking phase during the transition from quadrupedalism to bipedalism. To address this question, previous research has focused on the search for a "signal" within the wrist, and metacarpals of extant knuckle walkers that can be used to infer this locomotor pattern in extinct hominins. To date, the examined features have not yielded a clear, non-contested signal. I explore the Knuckle-walking Hominin Hypothesis in two ways: 1. by examining the hand postures and the manual pressure application of Pan and Gorilla during knuckle walking to determine whether there are species specific differences and 2. by examining the internal and external morphology of the manual phalanges in an attempt to isolate a clear "knuckle-walking signal". Chimpanzees are more variable in their preferred contact digits, and use both hand positions with equal frequency ("palm-in" - palm facing toward the body and "palm-back" -

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palm facing posteriorly). In contrast, gorillas consistently make contact with all four digits 2-5, maintain a pronated arm, and use the palm-back hand position. In both taxa, hand position affects which digit acts as the final touch-off element and therefore receives maximum pressure in a given step, and digit 5 receives significantly less pressure than the other rays. Gorillas are, in effect, practicing a refined subset of the variety of knuckle-walking postures used by the more arboreal chimpanzees.

A clear knuckle-walking signal is seen in both the external and internal morphology of the phalanges. Chimpanzees and gorillas have the same middle phalangeal curvature profile with the greatest curvature found in digit 5 ($5 > 2 > 3 > 4$), the element that receives the least amount of pressure. This phalangeal curvature profile is a feature not shared with any of the included taxa practicing different modes of locomotion. They also have similar Indices of Relative Curvature (IRC-middle phalangeal curvature/proximal phalangeal curvature) for digits 2-5 that clearly delineate them with "flatter" middle phalanges and more curved proximal phalanges (IRCs = ~ 0.85), from quadrupeds with more curved middle than proximal phalanges (IRCs > 1), and suspensory primates with higher and more equal curvature values for both elements (IRCs = ~ 1). This ability to differentiate between locomotor groups holds if the IRCs are composed of elements from different rays of the same manus and from elements of different individuals. Within the trabecular bone structure, knuckle walkers are differentiated from quadrupeds and suspensory primates in 3 locations: the metacarpal head, and the proximal ends of the middle and proximal phalanges. In particular, the metacarpal head shows distinct differences between the groups: knuckle walkers have a palmar-dorsal alignment of trabeculae and disc-like shape, suspensory taxa have a proximodistal alignment and rod-like shape and quadrupeds have a proximodistal alignment and disc-like shape. The ability to differentiate between locomotor categories using isolated zones increases the applicability of these signals to a fragmentary and limited fossil record. The morphological similarities, specifically the shared curvature profile, and the similar knuckle-walking kinematics employed by chimpanzees and gorillas point to a shared origin of knuckle walking.

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