

CLINICAL PERSPECTIVE

The Dart-Throwing Motion of the Wrist: Is It Unique to Humans?

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Kinematic analysis has shown a near-stationary proximal carpal row during the dart-thrower's motion, which is believed to provide a stable platform for the generation of force and accuracy during certain power and precision grip activities. This finding is consistent with evidence in the human hand of adaptations that enabled effective manipulation of stones, cylindrical wood, and bone tools for throwing and clubbing. There are at least two possible explanations for the observed human proximal carpal row kinematics. One is that it is retained from a previous common ancestor with great apes and previously adapted to some form of foraging or locomotor behavior involving the hands, but was recruited for tool use after we diverged from the apes. The second is that it evolved after our divergence from apes, in synchrony with adaptations in the human hand to the manipulation of tools, and central to the development of the human's unique ability to aim and accelerate tools and weapons. (J Hand Surg 2006;31A:1429–1437. Copyright © 2006 by the American Society for Surgery of the Hand.)

Key words: Dart-thrower's motion, wrist kinematics, human evolution, carpus, markerless bone registration.

This report details our understanding of the dart-thrower's motion in the context of carpal kinematic research and the implications that these kinematic findings have to human evolutionary development. We believe that a fundamental reshaping of our understanding of the planes of wrist motion and the functional arc of the human wrist may lead to advances in nonsurgical and surgical care of wrist injuries, implant design, and rehabilitation.

Wrist Kinematics and the Dart-Thrower's Arc

The study of carpal kinematics is highly complex because of the irregular size and shape of the multiple small articulating surfaces and the complex forces that cross the wrist. Conclusions in the literature often are contradictory, and there is disagreement among leading investigators as to the direction of rotation and the contribution of individual carpal bones to global wrist motion. It generally is agreed that the proximal row moves in synchrony throughout radioulnar deviation and flexion-extension, but

the degree of out-of-plane rotation and intercarpal motion within the proximal row is the source of considerable research efforts.^{1–5} Both planar radiographic analyses and detailed 3-dimensional analyses of cadaveric wrist motion have been performed using a variety of bone-marking techniques. The applicability of these studies to the clinical situation is limited by the difficulty in simulating normal wrist-loading conditions, the invasiveness of implanted radiopaque markers, and the mechanical obstruction of motion that can occur from protruding marker pins.

Recently, techniques of noninvasive measurement of carpal kinematics have provided data on *in vivo* carpal motion in both uninjured and injured subjects.^{6–12} The techniques share in common the positioning of the wrist in a number of static postures and rigid-body tracking with advanced imaging techniques such as spiral computed tomography scanning or magnetic resonance imaging. Quasi-static kinematic data are generated by calculating the change in carpal position in reference to a coordinate system

usually based on the stationary radius. The true real-time compilation of data can be considered the holy grail of wrist kinematics, but to the best of our knowledge has not yet been reported because of limitations in the speed of image acquisition and concerns for radiation exposure.

A common perception is that the human wrist moves as 2 rows, represented by the tightly bound trapezium, trapezoid, capitate, and hamate in the distal row, and the more mobile lunate and triquetrum in the proximal row.¹³ Whether or not the scaphoid is included as a member of the proximal row, or is a link between the 2 rows, has been debated.^{14,15} Craigen and Stanley¹⁶ challenged the traditional row theory of carpal kinematics by showing highly variable scaphoid kinematics between male and female patients during radioulnar deviation, prompting them to conclude that the wrist may behave kinematically as columns, rows, or both. Garcia-Elias et al¹⁷ similarly concluded that the degree and direction of scaphoid motion in radioulnar deviation may vary among individuals and is correlated with the degree of ligamentous laxity. In contrast, a 3-dimensional *in vivo* kinematic study from our laboratory using a technique known as *markerless bone registration* showed that the scaphoid, lunate, and capitate motion among 10 male and female healthy volunteers was strikingly uniform during wrist flexion-extension.⁹ The relative contribution of the bones of the proximal and distal carpal rows differed from that shown in previous cadaveric kinematic studies,^{2,18-20} and the marked intercarpal motion between the scaphoid and lunate led us to conclude that the scaphoid functions independently of the proximal carpal row. A 3-dimensional computed tomographic study of normal volunteers by Moojen et al²¹ agreed that the scaphoid moved independently of the bones of the proximal row and showed greater degrees of out-of-plane rotations than previously reported studies.

It is conceivable that the discrepancies in the wrist kinematic literature can be resolved when we consider that each cited study constrained the wrist to uniplanar motions of flexion-extension or radioulnar deviation. Our vision of carpal kinematics may be obscured by a relatively rigid adherence to the orthogonal coronal and sagittal planes of motion, when in fact most activities of daily life rarely use these planes of motion. The earliest notation of the functional use of conjoined wrist motions is attributed to Fisk,²² who noted the association of wrist extension with radial deviation and wrist flexion with ulnar

deviation “when someone is casting a fly, throwing a dart, or conducting an orchestra.” Palmer et al²³ showed that many occupational activities, exemplified by hammer use, involved an arc of motion from radial deviation and wrist extension to ulnar deviation and wrist flexion. These investigators popularized the term *dart thrower’s arc* to describe this conjoined wrist motion. Indeed, nearly all sporting activities, including pitching, racquet sports, fly fishing, javelin throw, batting, and golf also use the dart-thrower’s arc of wrist motion.

Several kinematic studies of the relative motion of the proximal carpal row during the dart-thrower’s motion arc have been performed, and the results show profound consistency between investigators. Saffar and Semaan²⁴ used direct visualization of cadavers and cineradiography to show that scaphoid and lunate intercarpal motions were minimal during the dart-thrower’s arc of motion. They observed that there was more mobility and more agility and that there was greater midcarpal than radiocarpal motion in this oblique plane. They suggested that more attention should be paid to this plane of motion, and their findings prompted several subsequent kinematic studies. Ishikawa et al²⁵ studied wrist kinematics during external fixation distraction using attached 3-space sensors, and showed kinematic changes that occurred during distraction. They also showed that scaphounate intercarpal motion was smaller in the dart-thrower’s plane than in the coronal or sagittal planes of motion. Werner et al²⁶ used a wrist motion simulator to study intercarpal motion during several combined planes of flexion-extension and radioulnar deviation and identified a dart-thrower’s plane of motion in which minimal scaphoid and lunate motions were observed. The scaphoid and lunate were shown to flex and extend with little out-of-plane motion, regardless of the primary plane of wrist motion. Moritomo et al²⁷ used magnetic resonance imaging of the wrist in several positions of radioulnar deviation and showed that rotation was confined predominantly to the midcarpal joint during the dart-thrower’s plane of motion.

By using the markerless bone registration technique to study the *in vivo* intercarpal motion of both wrists of 14 uninjured subjects, Crisco et al²⁸ confirmed that the scaphoid and lunate move almost exclusively in flexion-extension regardless of the path of wrist motion, but that the amount of scaphoid and lunate rotation is highly dependent on the direction of global wrist motion. The dart-thrower’s plane of motion identified the transition between scaphoid and lunate

flexion and extension, such that scaphoid and lunate motions were minimal along the dart-thrower's path of motion. Based on these findings, we agreed with Moritomo et al²⁷ that the dart-thrower's arc represents the most "stable and controllable" plane of motion in a kinematic sense, and represents the functional plane of wrist motion for most occupational and avocational activities.

The finding of minimal scaphoid and lunate motions during the dart-thrower's arc has several important clinical implications. Ishikawa et al²⁵ proposed that early motion exercises along this arc may be permissible during external fixation for fractures of the distal radius because carpal kinematics were the closest to normal in this plane. Based on our findings of minimal scaphoid and lunate motions within the dart-thrower's plane, we agree with Werner et al²⁶ that early wrist motion might be permissible after complex surgery of the radiocarpal joint and proximal carpal row, provided rehabilitation protocols could be devised to constrain motion to the dart-thrower's plane. An understanding of the wrist kinematics during the dart thrower's motion may help in the design of more durable prosthetic implants that more closely mimic normal carpal motion. Future kinematic studies may help to define positions and postures for partial arthrodesis procedures that will best preserve hand and wrist function.

In the face of laboratory evidence documenting wide variations of intercarpal motion, dependent in part on both the direction of motion and individual factors such as ligamentous laxity, the consistent finding of a nearly motionless proximal carpal row during a wrist motion path that is used during an array of predominantly human activities suggests that the carpus may have experienced morphologic adaptations to facilitate these activities. We propose that there was a survival advantage to a carpus that provided a stable and stationary platform for precision use of an instrument, weapon, or tool.

Anthropologic Importance of the Dart Thrower's Wrist Motion

There is a compendium of evidence to support the contention that the development of proportionately shorter fingers and other morphologic adaptations of the hand were critical determinants in the ability to use and manufacture tools, and similar to upright stance and increased cranial capacity, were defining characteristics of the lineage that gave rise to *Homo sapiens*.^{29,30} The ubiquitous presence of the dart-thrower's wrist motion in distinctively human activ-

ities involving tool use, throwing, and weaponry suggests that its development also may have played an important role in human evolution. Although the exact tool behaviors to which uniquely hominin (human) hand grips are adapted is unknown, Young³¹ has hypothesized that such grips would have facilitated accurate throwing and clubbing. Presumably, improved throwing and clubbing prowess would have provided a survival advantage to early hominin species.^{31–33} Indeed, the ability to throw rocks or wield a club effectively may have provided an advantage against competitors for food and defense against predators. Young³¹ hypothesized that natural selection "would enhance the anatomical basis for throwing and clubbing." The common denominator in effectively using either the precision 3-jaw chuck baseball grip (when holding a stone) or the power squeeze grip (when grasping a hammer or a spear) is a smooth arc of motion from an extended wrist position that is combined with radial deviation to a flexed wrist position that is combined with ulnar deviation—the dart-thrower's motion. Whether or not the dart-thrower's motion is a mechanism unique to human beings among the primates is uncertain, and is a subject of ongoing research by our team. As discussed later, determining the primitive state for the hominoid wrist in terms of movement capabilities will bear crucially on our interpretations of the adaptive importance of the dart-thrower's motion. For reference, *Hominoidea* is a taxonomic category that comprises human beings and the 4 apes (gibbons, orangutans, chimpanzees, and gorillas). Within this category, human beings (hominins) and the great apes (orangutans, chimpanzees, and gorillas) form the clade Hominidae.

Evolution of a Power Swing

When the Leakeys uncovered primitive tools at the same level as the 1.75-million-year-old fossil hand bones attributed to *Homo habilis* in the Olduvai Gorge in 1960, they elicited a profound change in the perspective of hand development in evolutionary theory. Previously, the hand was thought to have been a passive participant in evolution, reasonably well developed in early hominins, but incapable of maximizing its potential until provided with a more robust central nervous system. The finding of hand-crafted tools with hand bones that did not show the fully derived (distinctive) morphology of modern human beings prompted the theory that morphologic changes occurred in the hand during hominin evolution.^{34,35}

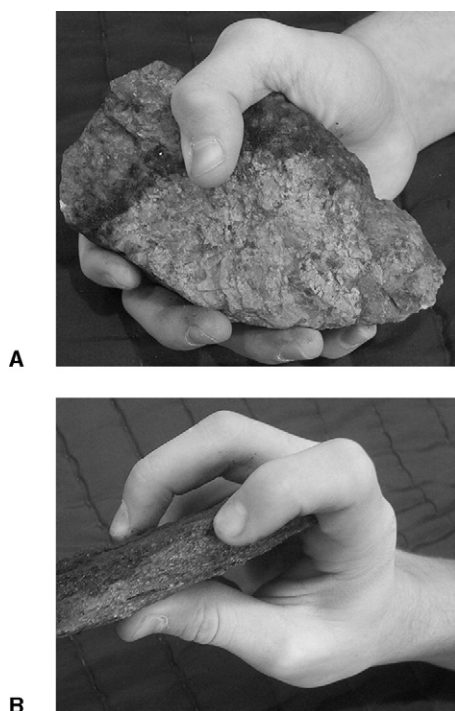


Figure 1. The 2 hand grips described by Napier.^{34,36} (A) The power grip, characterized by tight closure of the fingers around a hammerstone with the thumb adducted, and the (B) precision (or baseball) grip, wherein an object is held at a distance from the palm by 2 fingers and an opposed thumb.

Napier^{34,36} identified 2 discrete patterns of prehensile movements, the power grip and the precision grip, distinguished by the relative thumb position and palm involvement. In the power grip the flexed fingers hold the object against the palm with the thumb adducted. The precision grip holds the object away from the palm using the volar aspect of the fingers and the opposed thumb (Fig. 1). Examination of the limited fossil remains of the *H habilis* hand by Napier³⁵ prompted him to conclude that the hominin had the capacity for a forceful power grip, which enabled him not only to use, but also to manufacture, the associated stone tools. Although the precise timing of the acquisition of certain distinctive precision and power grips by our hominin ancestors is the source of some controversy, several important hand adaptations separate human hands from our closest nonhuman primate relatives, and their appearance over several million years enabled the inclusion of these grips in our food-gathering, food-processing, and tool-making repertoire.^{29,30} Key developments include shorter fingers relative to thumb length, broader tufts on the distal phalanges for grasp, a hypothenar pad that absorbs impact during forceful grip, and topographic features at the carpometacarpal

and metacarpophalangeal joints that facilitate rotation of the second, fourth, and fifth rays. These developments allowed cupping and control of round stones by a 3-jaw chuck baseball grip for throwing, forceful knapping of stones in tool manufacture, and accommodation of the hand to the shape of cylindrical bone and wood tools. In addition, relative shortening of the fourth and fifth metacarpals, the more robust fifth metacarpal, and the more radial orientation of the fourth and fifth metacarpal joints with the hamate, enabled a cylindrical object to be tightly held obliquely in the palm by a modified or squeeze form of the power grip,²⁸ such that the axis of the tool became collinear with the axis of the forearm in the swing phase of tool use (Fig. 2). The effect was to lengthen the tool's lever arm and the force of the tool's impact. From an analysis of fossil remains, Marzke et al³⁰ concluded that it is unlikely that *Australopithecus afarensis* (the species to which the famous fossil Lucy is attributed) had an appreciable power squeeze grip, but that elements of the power grip, including a more robust fifth metacarpal, were present in later skeletal remains dating to approximately 2.5 million years ago. The acquisition of a modern power squeeze grip, however, is thought to be a relatively recent development.³⁰



Figure 2. The modified power grip, or squeeze grip.³⁰ The squeeze grip enables a cylindrical tool or weapon to be tightly grasped against the palm by the closed fingers, and tightly reinforced by an opposed and clasped thumb. Use of this grip in conjunction with the swing phase of tool use effectively magnifies the force of the tool by the leverage of the concentrically aligned forearm.

Although morphologic changes in the hand are required to control stones during throwing, pounding, and stone knapping, and to position a tool obliquely in the hand and forcefully grasp it with the fingers and thumb, the grasp alone is insufficient to effectively use the tool. We propose that forceful and accurate use of a 3-jaw baseball grip for throwing, or a power squeeze grip for clubbing, was dependent on the simultaneous facility for a power swing. This power swing is generated by a cocking phase of wrist extension and radial deviation, and a swing phase of ulnar deviation and flexion. This smooth, stable, and reproducible wrist motion accelerates the tool and in clubbing it amplifies the wrist torque generated from the powerful forearm musculature by the added leverage of the tool handle. A question of interest to anthropologists is whether the capability for a power swing was acquired in human ancestors before our divergence from apes, or after our divergence as an adaptation to tool use in throwing and clubbing.

From a biomechanical perspective, the ability of the wrist to move through a large range of wrist motion while grasping a club greatly increases the impact power that can be delivered with the club. Cocking the wrist in extension while holding the club reduces the initial inertial resistance of swinging the club. This allows the upper-extremity musculature to contract quickly, thus generating large velocities that are crucial to increasing impact power. As the upper extremity moves through the swing phase, the 3 aligned primary articulations (wrist, elbow, and shoulder) can contribute to accelerating the club, maximizing its velocity just before impact. The dart-thrower's motion allows the upper extremity to coil into this optimal cocking position and continuously extend during the swing. This coiling and uncoiling minimizes the inertial resistance in the early phases of the swing, which in turn maximizes the final velocity. The biomechanical advantage of this coiling can readily be appreciated by noting how little impact power is generated if one limits wrist extension or elbow flexion during a swing.

Osteology and Knuckle Walking

Understanding the wrist arthrokinematic mechanism in nonhuman primates is an important area of research for understanding the evolution of the human wrist. Whether or not particular wrist movements are unique to human beings will bear on our adaptive interpretations of the dart-thrower's motion. If the pattern of carpal motions during the human dart-thrower motion is not unique, then we must under-

stand the phylogenetic distribution of particular mechanisms to understand the sequence of changes, and this is a subject of ongoing research by our research team.

A comparative analysis of nonhuman primate wrist osteology identifies a large number of bony variations, most of which are related to particular feeding and locomotor requirements of individual species. Great apes (orangutans, chimpanzees, and gorillas) share a triangular fibrocartilage complex with human beings that separates a short ulnar styloid process from the triquetrum and pisiform.³⁷ This morphology contrasts with the proximal wrist joint morphology of monkeys and other primates, in which a long ulnar styloid process articulates with a cup-like surface formed by the pisiform and triquetrum. The exact adaptive importance of this configuration is debated, but it may contribute to the ability of certain species to feed in the slender branches at the periphery of the tree canopy by manually suspending the body and pivoting around the wrist to retrieve fruits³⁷ or by allowing for a more diverse range of hand postures during slow-climbing behaviors.³⁸

In the Asian apes (gibbons and orangutans), which use a high frequency of manual suspensory locomotor and postural behaviors, the capitate and hamate resemble a ball-and-socket configuration with the proximal row—a feature shared via convergent evolution with the New World spider monkeys.^{39,40} This ball-and-socket morphology probably allows a substantial degree of midcarpal rotation, a movement that may be beneficial for below-branch suspensory locomotion and hang-feeding by permitting rotation of the hand about a fixed hold.³⁹ The triquetrum has a broad articular facet on the dorsum of the hamate, onto which it rotates nearly 90° by the conclusion of the swing.³⁹

African apes (the closest living relatives of human beings) spend more time on the ground than the orangutan and gibbon, and use a form of locomotion known as knuckle walking, during which weight is borne on the dorsal aspects of the middle phalanges, with the long axis of the hand held approximately vertical to the surface. Overall, wrist mobility (especially in extension) is drastically restricted in the African apes relative to the Asian apes and human beings, which is probably an adaptation to knuckle walking. Although Lewis^{37,41} argued that the extension-limiting features of *Pan* and *Gorilla* are adaptations to manual suspension, they more plausibly constitute an adaptation to knuckle walking given

that the more suspensory orangutans do not show this morphologic complex.⁴²

At the radiocarpal joint of chimpanzees (genus *Pan*) and gorillas (genus *Gorilla*), a prominent ridge along the dorsal aspect of a deeply concave distal radial articular surface is thought to contact a corresponding concave facet on the scaphoid, resulting in a close-packed configuration and limited extension at the radiocarpal joint.^{43–45} At the midcarpal joint, the capitate is stout and has a waisted neck as a result of lateral expansion of a broad head that achieves a highly stable close-packed position with the scaphoid and lunate at maximum extension.⁴¹ This close-packing mechanism in the African apes may be aided by the near 100% occurrence of early fusion of the os centrale to the scaphoid in *Pan* and *Gorilla* (a characteristic shared with hominins).^{42,44–51} The os centrale portion of the scaphoid forms a broad, stable articular surface for the trapezium and trapezoid. In wrist extension, the os centrale becomes lodged within an embrasure formed by the capitate head and the trapezoid,^{42,44,50} and scaphoid-centrale fusion might provide increased resistance to extension moments at the midcarpal joint.⁴² The midcarpal joint is prevented from further extension by contact with a distinct ridge on the concave aspect of the capitate head⁴⁴ with the proximal scaphoid-centrale facet. Extension of the midcarpal joint also appears to be limited because of the proximal expansion of the nonarticular surface of the dorsal capitate in *Pan* and *Gorilla*, which shortens the articular path of the distal carpal row.⁵⁰ The lunate and triquetrum articular orientation appears to be somewhat more proximodistally oriented than in the Asian apes—possibly to allow for more efficient load transmission—an adaptation that would lend stability to a weight-bearing posture by allowing for more efficient load transmission.⁴⁸

The evolution of knuckle walking is an important factor in interpreting the adaptive significance of the dart-thrower's motion. For example, it is theoretically possible that orangutans might share with human beings the capability of a dart-thrower motion, but the terrestrially knuckle-walking African apes (chimpanzees of the genus *Pan* and gorillas of the genus *Gorilla*) do not. This would indicate that the dart-thrower's motion predated hominin evolution and that hominins retained the capability whereas African apes lost it; however, if fossil evidence suggests that early hominins descended from a terrestrially knuckle-walking primate, such that the primitive state for hominins is limited wrist mobility, then it is

plausible that human beings may have evolved the dart-thrower motion secondarily, possibly for tool-using or weaponry behaviors.

Several investigators^{44,45,47–49,52} have suggested that there are hints of knuckle-walking human ancestors. For example, using linear and angle measurements of the radiocarpal joint, Richmond and Strait⁴⁵ suggested a temporal regression of African-ape-like extension-limiting features of the joint from early species such as *Australopithecus anamensis* and *A. afarensis*, whose radii retained a distinct distally projecting dorsal ridge, to *A. africanus*, whose radial contour and articular facets were more similar to the modern human radius. Fusion of the *os centrale* in hominins may be further evidence of a knuckle-walking ancestor.^{44,47,49} Several investigators,^{53–55} however, dispute the evidence for a knuckle-walking hominin ancestor and some argue for a more arboreal model for the prebipedal hominin. A major source of controversy has been the lack of agreement in identifying morphologic adaptations to knuckle walking in the wrist, and this is the dissertation topic for one of the authors (C.M.O.).

If the earliest hominins did descend from a knuckle walker, then the gradual regression of African-ape-like mechanical constraints to wrist extension in later hominins might be related to the “emancipation of the hands”³⁴ that occurred with bipedality,³¹ and increased demands for wrist extension with tool use,⁵⁶ for defense, or for throwing.⁴⁷ This is reflected further by the marked diminution in length and size of the pisiform, which is elongated in the African apes and projects in a palmar direction from the carpus. This orientation increases the leverage of the flexor carpi ulnaris when the wrist is extended slightly, providing an advantage during the propulsive phase of knuckle walking and possibly while climbing large vertical supports.⁴⁸ Its smaller size in human beings is thought to facilitate ulnar deviation during functional activities.³⁰ The morphologic characteristics of the pisiform shared by *Homo* and *Pongo* are unlikely to be homologous (ie, because of shared ancestry) because early hominins such as *A. afarensis* have longer, rod-like pisiforms that more closely approximate the condition seen in *Pan* and *Gorilla*.⁴⁴

Muscular Forearm Adaptations

One would anticipate that differences in forearm musculature would be necessary to use the wrist as a mechanism for accelerating the hand when grasping tools, stones, or clubs. In fact, the muscle mass of the forearm flexors is greater than that of the extensors in

apes, whereas the reverse is true in human beings.⁵⁷ This may be reflective of the more robust wrist extensor requirements of uniquely human activities, such as throwing and tool use, and the decreased use of wrist flexors during activities such as climbing, suspensory feeding, and knuckle walking. A comparison of muscle volumes on the ulnar side of the forearm in chimpanzees showed a ratio of flexor carpi ulnaris to extensor carpi ulnaris volume of 2.4, compared with a reported ratio in human beings of 1.9.^{30,58} It is thought that the increased balance between flexors and ulnar deviators in human beings may be related to the requirements of upper-extremity functions for improved coordination. Although a chimpanzee has the capability of holding a stick or a club in a threatening posture using a pseudo-power grip with the flexed fingers, he is unable to effectively strike with the weapon for 2 reasons. Despite his adequate range of passive wrist flexion and ulnar deviation,⁴² his lack of a proportionately long, strong thumb restricts his ability to stabilize the object sufficiently against his palm during the swing phase of wrist flexion and ulnar deviation.³⁰ In addition, we speculate that the radial and midcarpal skeletal constraints to wrist extension and relatively weaker wrist extensor musculature limits his ability to position the wrist in extension and radial deviation during the cocking phase of a power swing.

The squeeze grip has been shown to place the handle of the cylindrical object oblique to the palm in

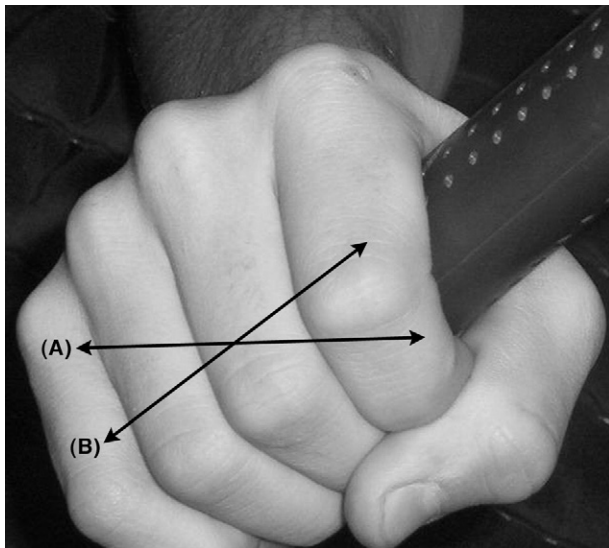


Figure 3. The closed fist when viewed from distal to proximal, in line with the forearm. The bi-directional obliquity of a tool within the enclosed fist positions the tool in a plane oblique to the trans-styloid axis of the radius (A), collinear with the radial-extension to ulnar-flexion dart-thrower's plane (B).

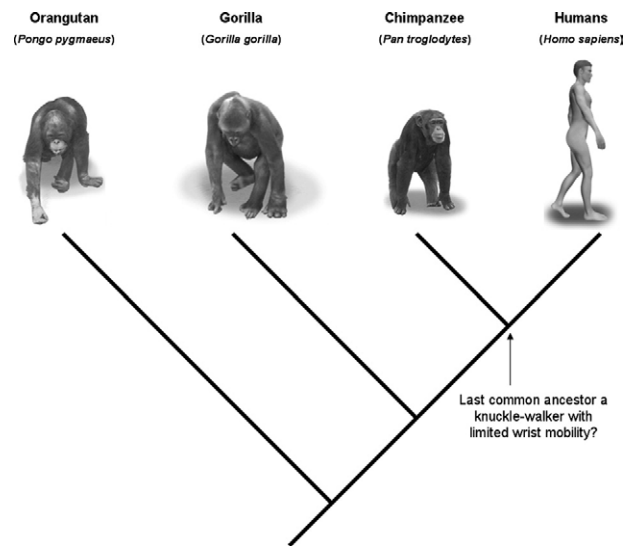


Figure 4. A cladogram illustrating the evolutionary relationships between the great apes and human beings as supported by molecular genetics. Future studies will be necessary to determine whether the carpal adaptations that enabled the dart-thrower's wrist motion are unique to human beings or retained from a previous common ancestor of the great apes and human beings.

the coronal plane. A well-developed hypothenar fat pad and a more robust fifth metacarpal diameter help to stabilize the object against the palm, tightly secured by a strong thumb.³⁰ Because of the relatively shorter fourth and fifth metacarpals, and the topography and orientation of the hamate-metacarpal joints, the object also is aligned obliquely in the axial plane. When viewing the clenched fist end-on while holding a hammer, the tool is aligned in a dorsal-radial to palmar-ulnar obliquity (Fig. 3). The net effect of the bidirectional palmar obliquity is to place the handle of the tool, club, or spear precisely in the dart-thrower's plane of motion, and consequently in the power swing plane of the forearm and upper extremity.

There is ample evidence that hominin species gradually acquired the morphologic attributes of the hand that were necessary to attain the power (squeeze) and precision grips after our divergence from the African apes.^{30,34,35} What is unknown is whether the corresponding morphology of the carpus,⁴² radius,⁴⁵ and forearm musculature³⁰ that facilitated the effective use of the power squeeze and precision 3-jaw chuck grip in the dart-thrower's plane of motion evolved in synchrony with the hand and is thus unique to the human race, or was retained from an earlier adaptation to foraging or locomotor behaviors shared with other primates (Fig. 4). Testing of both hypotheses is currently underway.

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