HYPOTHESIS

Evolution of the human hand: the role of throwing and clubbing

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Abstract

It has been proposed that the hominid lineage began when a group of chimpanzee-like apes began to throw rocks and swing clubs at adversaries, and that this behaviour yielded reproductive advantages for millions of years, driving natural selection for improved throwing and clubbing prowess. This assertion leads to the prediction that the human hand should be adapted for throwing and clubbing, a topic that is explored in the following report. It is shown that the two fundamental human handgrips, first identified by J. R. Napier, and named by him the 'precision grip' and 'power grip', represent a *throwing grip* and a *clubbing grip*, thereby providing an evolutionary explanation for the two unique grips, and the extensive anatomical remodelling of the hand that made them possible. These results are supported by palaeoanthropological evidence.

Key words handgrips; manual structure; palaeoanthropology.

Introduction

The typical primate hand is characterized by a diminutive thumb in combination with long, curved fingers (Midlo, 1934). In contrast, the human hand has a much larger, more muscular, mobile, and fully opposable thumb combined with fingers that have shortened and straightened. This striking exception to the primate pattern clearly requires an evolutionary explanation (Marzke & Marzke, 2000; Fig. 1). Although no comprehensive account has been offered, there is general agreement that the anatomical reconstruction of the hand during human evolution was somehow linked with *tool behaviour*. This approach is consistent with evidence that an early hominid (hominin) behaviour was bipedal gait, which would have 'freed the hands' for greater use of tools. However, basic questions remain: what kind of tools? In what manner and for what purpose were they used? How did such behaviour provide reproductive advantages sufficient to drive natural selection during the millions of years required to transform the ancestral ape hand into the human hand?

A proposal that offers an answer to these questions is provided in the following report. It is suggested that the tools were hand-held weapons that were hurled or swung as bludgeons at adversaries during disputes, providing the aggressors with advantages that in various ways promoted reproductive success. The resulting selection for improved throwing and clubbing prowess, prolonged over millions of years, led to numerous anatomical changes throughout the body, including those that characterize the evolution of the human hand.

The demonstration of a compelling reproductive advantage is essential to any argument that purports to identify a behaviour that leads to evolutionary change. The behaviour must be able to increase the proportion of genes in the breeding population of those who are most adept at it. There are numerous ways that aggressive use of weapons could have led to this result.

The best throwers and clubbers in a community would rise in the male dominance hierarchy and thereby obtain more breeding opportunities. Use of rocks or clubs would provide an advantage in territorial hostilities with unarmed outgroup conspecifics, yielding
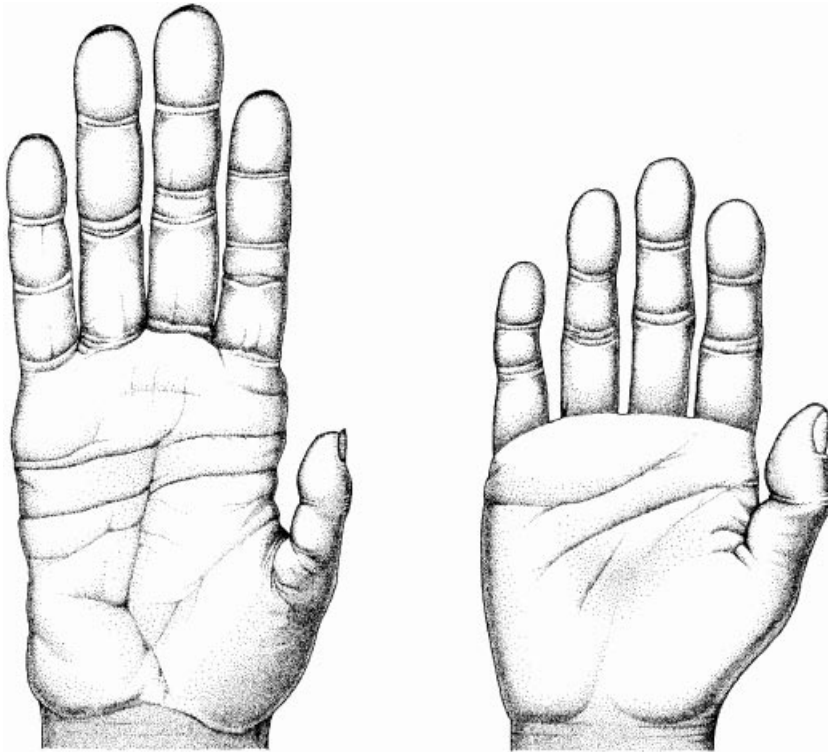
Fig. 1 Chimpanzee hand, a model for the hand of the hominid ancestor (left), and the human hand.

improved access to breeding females and food, which promote reproductive success. In conflicts between armed hominid communities, those with the most adept warriors would be more likely to prevail. Defence against predators would be enhanced, and opportunities for scavenging would increase when predators could be driven from carcasses. Weapons would have made hunting more effective. Meat obtained by males through hunting and scavenging could be traded for sex with females.

Females who aggressively used weapons would have protected themselves and their children better and increased their access to disputed food resources. A further reproductive benefit could occur through female mate selection. Because hominid males who were skilled throwers and clubbers were more likely to rise to higher ranks, wield more power, dominate other males, commandeer the best feeding sites, obtain more meat, and protect women and children better, females would be more likely to select such males for mating whenever the opportunity arose. Generation after generation, natural selection would have enhanced the anatomical basis of throwing and clubbing prowess.

This scenario accounts for the unprecedented ability of modern humans to throw missiles and swing clubs with power and accuracy. Selection for improved

throwing and clubbing produced an innovative, instinctive, whole-body motion performed from an upright stance that begins with a thrust of the legs. Improved dynamic upright balance on more powerful legs and resilient feet in the service of throwing and clubbing would have made upright *locomotion* more efficient, leading to its increasing use and eventually culminating in habitual bipedalism. (Several other unique human anatomical and behavioural features can also be accounted for by this approach: Young, 2002.)

The throwing and clubbing motion that begins in the legs progresses through the hips, torso and arms and ultimately imparts accumulated kinetic energy to the hand or hands holding the weapon. The entire body is involved, but the role of the hands is crucial. Natural selection must have acted strongly on the hands from the outset of aggressive throwing and clubbing behaviour. Indeed, analysis of the evolution of the human hand provides an opportunity to falsify or lend credence to the throwing-and-clubbing proposal.

Grasping a spheroid and precisely controlling its release, required for accurate throwing, demands a grip that differs from one that can firmly grasp a cylindrical club-handle and absorb the reaction force of impact without release of the weapon. This implies that the
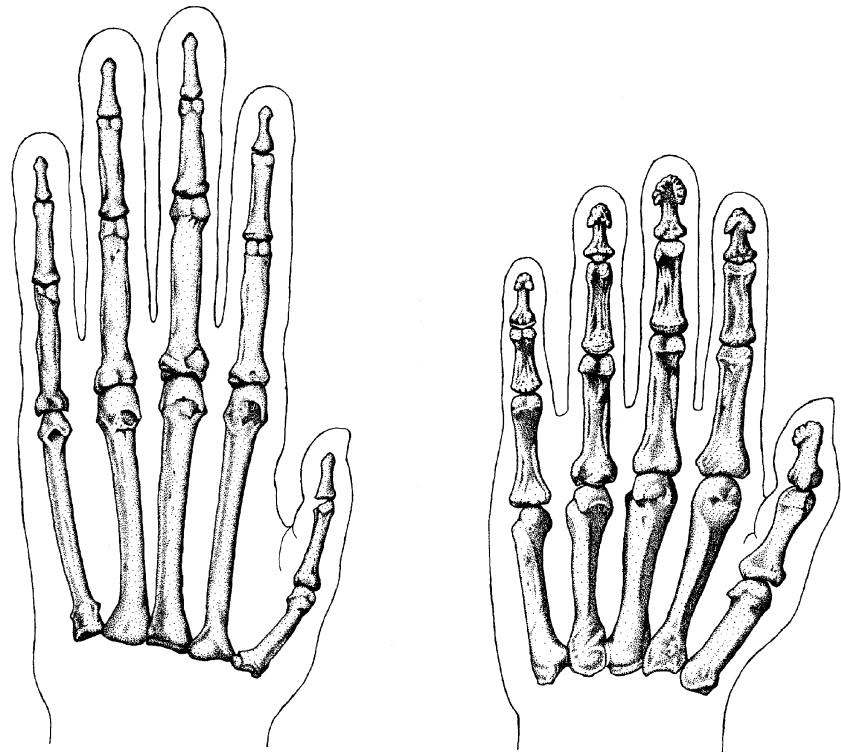
Fig. 2 Bones of the chimpanzee (left) and human hands.

human hand should manifest *two* unique grips – one specialized for throwing, the other for clubbing. The following report will show that the two predicted grips are the two fundamental human handgrips first identified by the British anatomist, Napier (1956).

The chimpanzee hand

The chimpanzee hand will be taken as a model for the hand of the hominid ancestor. The most ancient hominid fossils closely resemble chimpanzees, who are genetically our nearest relatives (Sibley, 1992; Ruvolo, 1997). *Pan* and human lineages diverged 5–7 million years ago (Mya), about the time the first hominid specimens appear in the fossil record (Klein, 1999). The fingers, metacarpal and carpal bones of the chimpanzee hand are elongated, but in typical primate fashion the thumb is small, weak and relatively immobile (Figs 1 and 2). The third and fourth metacarpals, which absorb the highest compression during knuckle-walking, are especially robust (Lewis, 1977; Susman, 1979). Both proximal and middle phalanges are curved toward the palm to withstand stress from gripping limbs during arboreal locomotion (Susman & Creel, 1979; Susman, 1987, 1994). The finger tips are cone-shaped, and lack

broad apical tufts (Napier, 1960; Susman, 1988b, 1991). Owing to the transverse arrangement of the meta-carpo-phalangeal articulations, there is a transverse skin crease across the palm (Napier, 1960, 1993; Lewis, 1977; Fig. 1). Thumb phalanges and metacarpals are slender and short (Susman, 1994; Fig. 2) and the intrinsic muscles of the thumb, underlying the thenar region of the palm, are small (Marzke et al. 1992).

The grips of the chimpanzee differ profoundly from those of humans (Napier, 1960). For suspension from horizontal supports, chimpanzees use a 'hook grip' of the four flexed fingers (Napier, 1960; Marzke & Wullstein, 1996). With vertical supports, a diagonal hook grip is used (Susman, 1979; Marzke et al. 1992). The thumb may touch the support, but does not squeeze it against the palm. Chimpanzees use this grip when flailing with sticks, but when the arm swings forward the hand tends to lose its grip, possibly due to weakness of the thumb and its inability to overlap the index finger (Marzke et al. 1992; Marzke & Wullstein, 1996). Because the thumb is weak and short, its distal phalanx is relatively immobile and its distal pad cannot be opposed to those of the fingers, it cannot generate a firm pinch or squeeze (Marzke, 1992a, 1997; Marzke & Wullstein, 1996).

The human hand

The human thumb is longer, the palm and fingers are shorter, and the fingers have lost their curvature (Susman, 1979). The distal phalanges have gained large apical tufts which support broad, palmar, fibrofatty pads that distribute pressure during forceful grasping and whose deformation accommodates the pads to uneven surfaces (Napier, 1965; Susman, 1979, 1988a; Marzke & Shackley, 1986). Apart from thickening of the fifth metacarpal and enlargement of its base, the balance of strength and robusticity has shifted radially, to the thumb, second and third fingers (Susman, 1979; Marzke & Shackley, 1986).

The thumb metacarpal articulates with the carpals in a saddle joint which in combination with remodelling in the metacarpal–phalangeal joint allows its distal pad to be placed against those of the other fingers, providing full opposability (Napier, 1955). The intrinsic thumb muscles are larger (Marzke, 1992b, 1997) and three new muscles add strength and control to thumb movements. The flexor pollicis longus muscle, absent in chimpanzees, is the most powerful thumb muscle in humans. It flexes the distal phalanx of the thumb and maintains the orientation of its pad toward the fingers against pressure. Also new are the deep head of the flexor pollicis brevis and the first volar interosseous muscle (Susman, 1994).

The palm has several derived features. Because the fourth and fifth metacarpals are progressively shorter than the third, there is an obliquity to the hand when it is flexed. This produces flexure creases that run obliquely, from the lower ulnar side of the palm to the upper radial side (Napier, 1993). The thenar and hypothenar eminences are enlarged by fat pads which overlie the muscles. Contraction of the palmaris brevis muscle stiffens the hypothenar pad (Marzke et al. 1992). Several features increase the ability of the centre of the palm to withstand stress imposed along the second and third fingers (Marzke & Marzke, 1987). The metacarpals and bases of the proximal phalanges of these fingers are robust. A palmar fat pad in the third metacarpal region protects the deep branch of the ulnar nerve. Stability of the third metacarpal base is enhanced by a styloid process on its dorsal radial aspect. When the finger is extended, the styloid process locks the carpal and metacarpal bones together, preventing hyperextension. A ligament from the pisiform bone to the third metacarpal base further restrains hyperextension (Marzke & Marzke, 1987).

Another unprecedented attribute of the human hand concerns finger rotation. When the fingers are flexed, they rotate towards the central axis so that the fingertips can meet the tip of the thumb. The metacarpal–hamate articulation permits supination of the fourth and fifth metacarpals, whereas the heads of the second and third metacarpals allow pronation of the proximal phalanges. Rotation is more pronounced for the two outermost fingers (Susman, 1979; Marzke, 1983, 1997).

The two unique human hand grips

What was the adaptive significance of this profound remodelling of the ancestral hand? Napier (1956) provided a provocative answer: the human hand gained two new grips. 'In spite of the multiplicity of activities of the hand', he wrote, '… there are only two prehensile actions: these are called the precision grip and the power grip' (Napier, 1965).

These two patterns of movement, which are anatomically and physiologically distinct, provide the basis for all prehensile activities (Napier, 1960, 1961). The precision grip is employed where precision of movement is required, whereas the dominant characteristic of the power grip is application of force (Napier, 1960). In each of these grips the carpo-metacarpal joint of the thumb, in full abduction or adduction, is stabilized by congruent articular surfaces and tension of ligaments. In the intermediate position, the joint is most unstable (Napier, 1955).

Napier illustrated the two grips with photographs of hands grasping a ball and a cylindrical rod (Napier, 1956, 1965, 1993).

His analysis showed that the human hand is adapted for gripping spheres and cylinders (Fig. 3).

In Napier's description of the precision grip (Napier, 1956, 1965, 1993), the terminal pad of the thumb forms one jaw of a clamp, the other being formed by the fingertip pads. Large objects held in this way involve all the fingers, but smaller ones require only the thumb, index and middle fingers with the fourth and fifth fingers providing lateral stability. Marzke (1983) refers to this as the 'three-jaw chuck' grip, depicts the grip of a baseball, and notes that if the object is thrown, the fingers contribute to aim, propulsion and velocity. According to Napier, in the power grip the clamp around the cylinder is formed by the partly flexed fingers and the
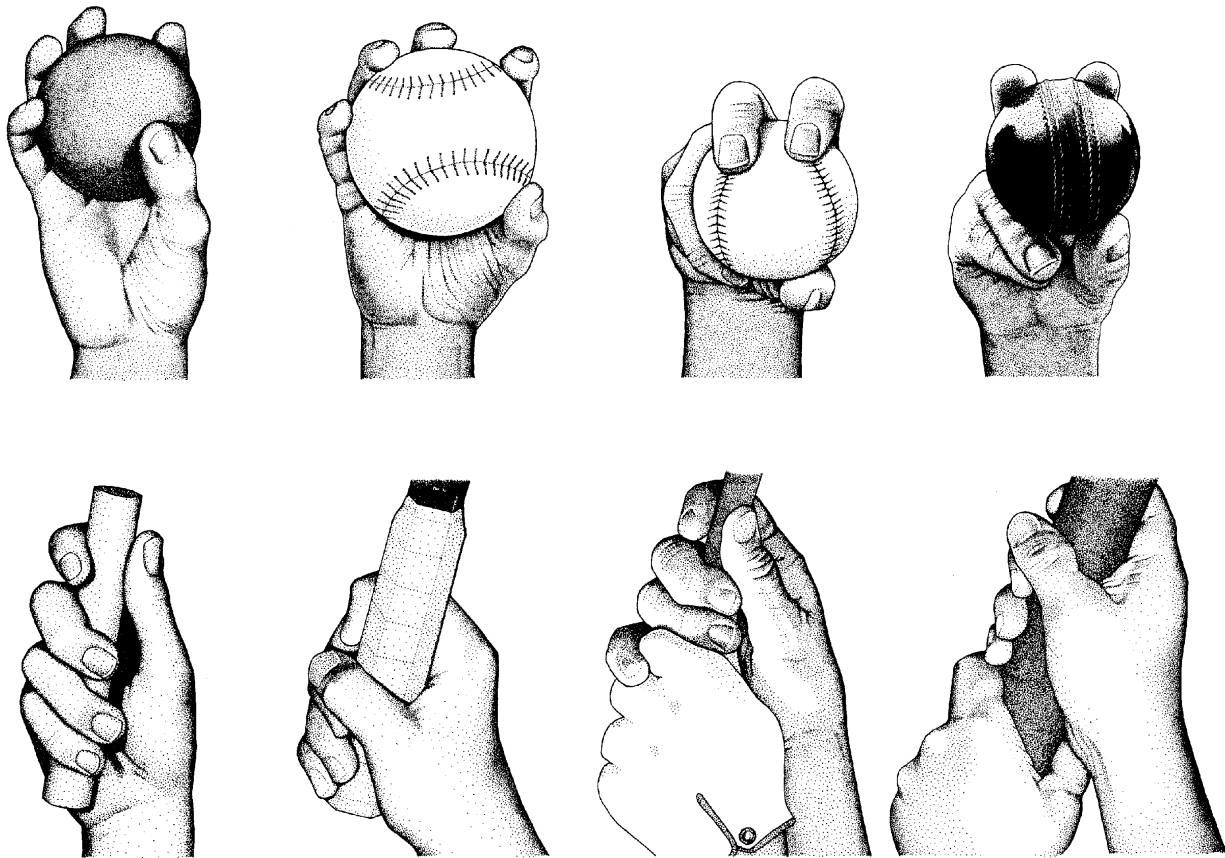
Fig. 3 During its evolution, the human hand gained two unique grips, first identified by Napier. He called them the precision grip and the power grip and depicted them by the grip of a sphere (top left) and a cylinder (bottom left) (Napier, 1956, 1965, 1993). The evolution of these grips can be attributed to adaptation of the hand for gripping missiles and clubs. This is shown (above) by the grip of a softball, baseball and cricket ball, and (below) by the grip of a tennis racquet, golf club and cricket bat.

palm, counter pressure being applied by the thumb, which is wrapped over the dorsum of the fingers, where it acts as a buttress to reinforce the grip. Marzke (1992a) calls this the 'finger-active palm squeeze' grip, illustrates it with a hammer and states that it employs all the fingers to secure a cylindrical tool against the palm, so that the tool functions as an extension of the hand and forearm.

These descriptions make it clear that the 'precision grip' is a *throwing grip*, and the 'power grip' is a *clubbing grip*. 'Precision' and 'power' suggest typical uses for the grips. 'Three-jaw chuck' and 'finger-active palm squeeze' refer to the position of the hand when it forms the grips. They could be called the 'sphere grip' and 'cylinder grip' based on the shape they are best able to grasp. The terms throwing grip and clubbing grip emphasize the evolutionary context in which these grips evolved by specifying the behaviours that account for them. The unique features of the human hand can be viewed as adaptations for throwing and clubbing.

Adaptations of the hand for throwing

For efficient throwing the hand must be able to grip the missile while energy is transmitted to it, then accurately control its release. This requires a fingertip grip. The thumb must be long enough and sufficiently mobile to oppose its fingertip pad to the missile on one side while the fingers oppose their distal pads to the opposite side and adjust themselves to irregularities in naturally occurring rock spheroids. For accurate release, the fingers must be under precise neural control and able to absorb without injury the reaction force resulting from the propulsive thrust.

These adaptations are all found in the human hand. The thumb has lengthened and can be fully opposed to the fingers, which have shortened. The thumb and the

first two fingers, which play the major role in the throwing grip, are strong and robust. Thumb opposition is enhanced by addition of a muscle that flexes the terminal phalanx, and is matched by rotation of the fingers as they flex: supination on the ulnar side, pronation on the radial side – exactly as needed for a fingertip grip of a sphere. Broad apical phalangeal tufts support soft, fleshy fingertip pads that adapt themselves to irregular spheroids and provide a large friction surface. The fingertips are highly innervated with sensory endings that inform the brain about the missile and forces acting on it. Precise neuromotor control of finger muscles permits submillisecond release times needed for throwing accuracy. When a missile is released, there is only one point on the arc of the moving hand where release will result in movement towards the target (Hore et al. 1995). Abduction of the thumb and extension of the finger joints control this action. A 1-ms delay in finger extension causes a change in direction of 2.2° (Hore et al. 1996a,b). A baseball pitcher must regulate ball release with a tolerance of less than 0.5 ms to deliver the missile within the strike zone. Enhanced control of the hand, a key element in throwing accuracy, is reflected in expanded representation of the fingers in the human sensory and motor cortex (Napier, 1965).

Kinetic energy transferred to the missile is channelled through the index and middle fingers of the throwing hand. At release, the thumb drops away, these fingers extend and their apical tips provide the final thrust. An equal and opposite reaction force acts to hyperextend these fingers, particularly the third finger, which due to its length is the last to lose contact with the missile (House, 1994; Hore et al. 1996b). Stress travels down the phalanges through the metacarpals in the palm to the carpal bones where it is dissipated. The robustness of the second and third fingers which absorb stress, the styloid process and ligamentous stabilization of the third metacarpal which prevent hyperextension, and the deep palmar fat pad which shields the ulnar nerve all contribute to protecting the hand against throwing injury.

Adaptations of the hand for clubbing

Effective clubbing requires a secure grip, especially during impact, so that the time during which force is applied is maximized, diversion of energy into elastic recoil is minimized and the clubber may use the weapon again immediately. Fingers and thumb form a vice, squeezing the clubhandle against the palm. For added force and grip strength, both hands may be used.

Several features that contribute to the throwing grip also facilitate the clubbing grip. Supination of the fourth and fifth fingers during flexion aids the grip of a large spheroid and acts to apply the palmar surface of these fingers to a clubhandle orientated obliquely across the palm (Marzke & Shackley, 1986; Marzke et al. 1992). Distensible fingertip pads which maximize surface contact with spheroids perform the same function on clubhandles (Marzke & Shackley, 1986). A longer, fully opposable thumb, essential for the throwing grip, also facilitates gripping a club by enabling the thumb to overlap the ends of the index and middle fingers. The flexor pollicis longus muscle is effective in both grips, as is the deep palmar fat pad.

Other adaptations are specific to the clubbing grip. One of these is the slant of the metacarpal–phalangeal articulations. When the fingers are partially flexed, they form an oblique line. Together with the partially flexed thumb, a corridor is formed – a cylindrical cavity lying diagonally across the palm. When a club is squeezed tightly against the palm, this anatomical configuration assures that it is positioned in an oblique manner. On the ulnar side, the implement is clamped against the hypothenar fat pad, stiffened by contraction of the palmaris brevis muscle, while the thenar musculature and its subcutaneous fat layer buttress the radial side. When a club is swung, the wrist deviates in the ulnar direction just before impact. Combined with the oblique angle of the grip, this aligns the club with the forearm, increasing the radius of arm-plus-club and the velocity of the club, thereby providing maximal mechanical advantage (Marzke et al. 1992).

At impact, the reaction force acts to drive the club in a direction opposite to its former trajectory. The base of the handle exerts pressure on the base of the fingers on the ulnar side of the hand, whereas the apical end of the handle is driven against the radial side. If the grip is to be maintained, these two parts of the hand must be capable of withstanding the stress of impact. On the ulnar side, the base of the fifth finger absorbs much of the impact. Its metacarpal has thickened and its base has enlarged. The thumb stabilizes the clubhandle on the radial side. Modified carpal bones on the radial side help dissipate stresses generated in the thumb during clubbing (Lewis, 1977, 1989; Marzke

et al. 1992). The thumb is critical for 'hanging on tight' (House, 1994; Ohman et al. 1995; Welch et al. 1995). Its robustness and muscularity are adaptations for power clubbing.

The wrist

Derived changes in the human wrist can be explained as adaptations for throwing and clubbing. In throwing, the wrist moves from extension to flexion. During clubbing, it moves from radial to ulnar deviation. These movements in humans far exceed the capabilities of the chimpanzee wrist (Napier, 1960). Restricted capacity for wrist extension in the chimpanzee has been ascribed to an adaptation for both quadrupedal and arboreal locomotion (Tuttle, 1967; Dainton, 2001). Bony ridges on the radius at the radioscaphoid articulation, several ligaments and shortening of the long flexors of the fingers constrain extension of the chimpanzee wrist (Napier, 1960; Tuttle, 1967). Greater extension in the human wrist increased the acceleration path for throwing. Expanding the range of ulnar deviation improved the clubbing motion by permitting alignment of the club handle with the forearm to provide added leverage. Ulnar deviation was facilitated by changes in the pisiform bone and the ulnar flexor and extensor muscles (Marzke et al. 1992).

Previous explanations of human hand evolution

Among hand authorities, the general view is that the human hand is adapted for tool behaviour (Susman, 1994). Special emphasis has been given to the fabrication and use of stone implements (Kortlandt, 1986; Marzke & Shackley, 1986; Marzke, 1992b; Napier, 1993; Marzke & Marzke, 2000). Stress from pounding with hammerstones might account for many features of the hand (Marzke & Marzke, 1987; Marzke, 1992a; Marzke & Wullstein, 1996). However, the throwing grip is not recruited during stone tool-making (Marzke et al. 1998), submillisecond control of the release of a hand-held rock is irrelevant for such purposes and the clubbing grip is useless for flaking stone in the manner used by early hominids (Marzke & Shackley, 1986; Marzke, 1992a, 1997). Furthermore, the hand of *A. afarensis* (described below), which is dated at 3.2 Mya, shows many features of the modern human hand, yet antedates the earliest identified stone tools (2.6 Mya).

When such artefacts first appear, the hominid hand had already closely approached its current state (Susman, 1988a,b, 1991, 1993). Adaption for improved throwing and clubbing would have *pre-adapted* the hand for stone tool knapping.

Kirschmann (1999) linked throwing and the precision grip. Marzke has often noted that evolutionary changes in the hand would have facilitated throwing and clubbing (Marzke, 1983, 1992a, 1997; Marzke & Shackley, 1986; Marzke & Wullstein, 1996; Marzke et al. 1998).

Darwin (1871) believed that use of hand-held weapons from an upright stance would have enabled hominids to defend themselves, hunt and fight with enemies. Dart (1959) concurred that a prime benefit of freeing the hands from locomotion was their use for manipulating clubs and missiles. Neither author, however, associated this behaviour with hominid hand evolution.

Palaeontological evidence

If the primordial hominid specialization was aggressive throwing and clubbing, anatomical changes reflecting selection for this behaviour should be discernible in the most ancient hominid hand specimens, and later fossils should reveal the persisting influence of such selection.

The earliest known hominid hand bones are assigned to *Ardipithecus ramidus kadabba* from Ethiopia (5.8 Mya). They consist of the distal portions of an intermediate and a proximal phalanx (Haile-Selassie, 2001). There are already derived changes visible. The bones are said to be similar to those of a younger species, *Australopithecus afarensis* (described below).

Specimens of *Australopithecus anamensis* from Kenya (3.8–4.2 Mya: Leakey et al. 1995, 1998; Ward et al. 1999) include parts of a capitate and manual phalanx. The capitate has several ape features, including a facet for the second metacarpal that faces laterally, preventing rotation of the second metacarpal at this joint, and it lacks a facet for the third metacarpal styloid process. The incomplete proximal phalanx is similar in size and shape to some specimens of *A. afarensis*. That is, the curvature is less than in apes (Leakey et al. 1998).

In fossils from Ethiopia and Tanzania (3.2–3.5 Mya), designated *A. afarensis* (White et al. 1993; Johanson et al. 1994) the hand retains chimpanzee-like features and would still have been effective for tree-climbing

(Marzke, 1983; Stern & Susman, 1983). Nevertheless, throwing and clubbing grips are well advanced. The carpo-metacarpal joint allows the range of thumb movement necessary for both grips (Marzke, 1983). The fingers were shorter than those of the chimpanzee and the thumb is longer (Marzke, 1983, 1992b; Stern & Susman, 1983), but the fingers are long relative to the thumb when compared to modern humans (Marzke et al. 1992). Unlike the situation in *A. anamensis*, the second metacarpal could be pronated during flexion (Marzke, 1983). Combined with the other changes, this would have facilitated a throwing grip (Marzke, 1983, 1992a,b). The third metacarpal lacked a styloid process (Bush et al. 1982), but there are signs of ligamentous changes that stabilize the palm (Marzke, 1983, 1992a; Marzke & Shackley, 1986). The longer thumb would have improved the clubbing grip (Marzke & Shackley, 1986). However, both human grips were still incomplete. The apical tufts on the terminal phalanges were expanded (Bush et al. 1982), but not sufficiently to support large fingertip pads (Marzke et al. 1992). Restricted supination with flexion of the fifth metacarpal would have limited the grip used for throwing large spheroids and the effectiveness of the clubbing grip (Marzke, 1983, 1992a; Marzke & Shackley, 1986; Marzke et al. 1992). Compared to later hominids, the thumb was less robust, may have lacked some muscular attachments and shows less metacarpo-phalangeal joint expansion (Stern & Susman, 1983; Susman, 1994).

A. africanus lived in South Africa 3.2–1.8 Mya (Klein, 1999). Ricklan (1987) concluded from examination of 16 hand bones that *A. africanus* had a firm power grip and a strong capacity for ulnar deviation of the wrist, as occurs in clubbing. Well-developed muscles were present that could stabilize the wrist to prevent rebound of a club at impact. Wrist extension comparable to modern humans (Richmond & Strait, 2000) would have aided throwing efficiency. A styloid process on the third metacarpal, appearing for the first time, would have protected against hyperextension from throwing, and the capacity to rotate the second and fifth metacarpals during flexion (Ricklan, 1987) would have improved the throwing grip. A distal thumb phalanx with a broad apical tuft for support of a fingertip pad and a site for insertion of the flexor pollicis longus muscle (Marzke, 1997) would have aided both clubbing and throwing grips.

Paranthropus occurred in East and South Africa 2.3–1.2 Mya (Klein, 1999). Susman (1988a,b, 1991, 1993,

1994) described hand bones from South Africa which he attributed to *P. robustus*. The pollical distal phalanx has a fossa for the flexor pollicis longus muscle and an enlarged apical tuft. It is robust, with an expanded proximal joint surface to absorb stress. The metacarpal head is also expanded and the carpometacarpal joint supports opposition of the thumb. The fingers are straighter, with apical tufts implying broad, fleshy, fingertips.

Napier (1962) first described the hand bones (1.9–1.6 Mya: Klein, 1999) of *Australopithecus habilis* (formerly assigned to *Homo*: Wood & Collard, 1999). The sturdy thumb has an advanced saddle joint, and the distal phalanges of the thumb and fingers have marked apical tufts (Susman & Creel, 1979). Some features remain ape-like. The proximal and middle phalanges are curved toward the palm (Tuttle, 1967; Susman & Creel, 1979). The two human grips are well developed (Napier, 1993; Marzke et al. 1992; Marzke, 1997).

A. habilis gave way to *Homo ergaster* (African *H. erectus*) about 1.8 Mya. Verified hand bones from this taxon are unavailable. Those of *H. neanderthalensis* (200–30 kya: Klein, 1999) are similar to those of modern humans, except for greater robustness, and the range of manipulative movement was also comparable (Trinkaus, 1983; Trinkaus & Villemeur, 1991).

It can be predicted that as additional hominid hand bones are discovered and described they will prove to be consistent with the conclusion that the human hand, ape-like at the outset, subsequently underwent an extended adaptation for grasping spheroids and cylinders, as required by throwing and clubbing.

Conclusion

It has been proposed (Young, 2002) that the earliest hominid specialization was aggressive throwing and clubbing, and that this behaviour increased reproductive success during a prolonged period, driving natural selection that progressively improved its effectiveness. If these assertions are correct, the evolution of the human hand should provide evidence of this process in its anatomical structure.

The fossil record indicates that adaptation for throwing and clubbing began to influence hand structure at or very near the origin of the hominid lineage and continued for millions of years thereafter. During this prolonged period of evolution, the hand underwent a profound remodelling that increasingly adapted it for

grasping spheroids in a manner that allows precise control of release and for gripping clubhandles with strength sufficient to withstand a violent impact. Two unique human handgrips were thereby produced. Called the 'power' and 'precision' grips by Napier (1956) who identified and described them, they can also be referred to as clubbing and throwing grips on the basis of their evolutionary origins.

Acknowledgments

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