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Review

Evolution of the human hand: approaches to acquiring, analysing and interpreting the anatomical evidence

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ABSTRACT

The discovery of fossil hand bones from an early human ancestor at Olduvai Gorge in 1960, at the same level as primitive stone tools, generated a debate about the role of tools in the evolution of the human hand that has raged to the present day. Could the Olduvai hand have made the tools? Did the human hand evolve as an adaptation to tool making and tool use? The debate has been fueled by anatomical studies comparing living and fossil human and nonhuman primate hands, and by experimental observations. These have assessed the relative abilities of apes and humans to manufacture the Oldowan tools, but consensus has been hampered by disagreements about how to translate experimental data from living species into quantitative models for predicting the performance of fossil hands. Such models are now beginning to take shape as new techniques are applied to the capture, management and analysis of data on kinetic and kinematic variables ranging from hand joint structure, muscle mechanics, and the distribution and density of bone to joint movements and muscle recruitment during manipulative behaviour. The systematic comparative studies are highlighting a functional complex of features in the human hand facilitating a distinctive repertoire of grips that are apparently more effective for stone tool making than grips characterising various nonhuman primate species. The new techniques are identifying skeletal variables whose form may provide clues to the potential of fossil hominid hands for one-handed firm precision grips and fine precision manoeuvering movements, both of which are essential for habitual and effective tool making and tool use.

Key words: Paleoanthropology; biomechanics; manual function.

INTRODUCTION

In 1960 an extraordinary set of hand bones was found at Olduvai Gorge in Tanzania (Fig. 1), at the same level as primitive Oldowan stone tools, dating to about 1.75 mYr ago (Leakey et al. 1964). Parts of a skull vault and mandible were associated with the hand, and from their morphology it was concluded that this specimen, OH7, was an early member of our human genus, *Homo*. Although some of the hand bones appeared to have an ape-like pattern suggesting a capacity for strong flexion of the fingers, there was evidence that the thumb was quite similar to the modern human thumb, in its range of motion and in its ability to flex strongly at the tip (Napier, 1962). The species was named *Homo habilis* ('handy man'), communicating the view of its discoverers that the hand was capable of making the associated tools. The find set off a debate about the role of tools in the evolution of the human hand, and specifically about morphological correlates of human tool making and tool using, that has persisted to the present day.

Napier published a description of the hand bones in 1962, and his publication set the direction for future research on the evolution of the human hand. Ever since Darwin, there has been a discussion of whether the evolution of tools played an important role in the evolution of human morphology. Napier used 3

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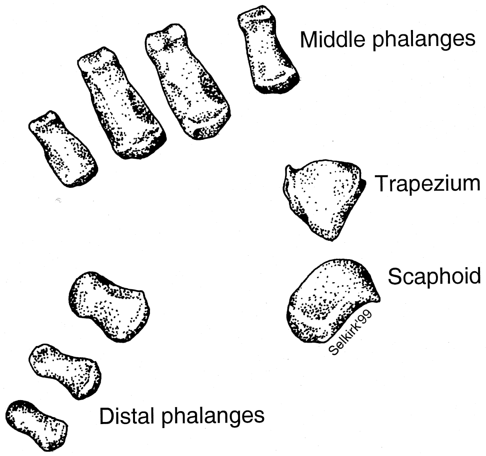

Fig. 1. Fossil hand bones from Olduvai Gorge, drawn from National Museums of Kenya casts.

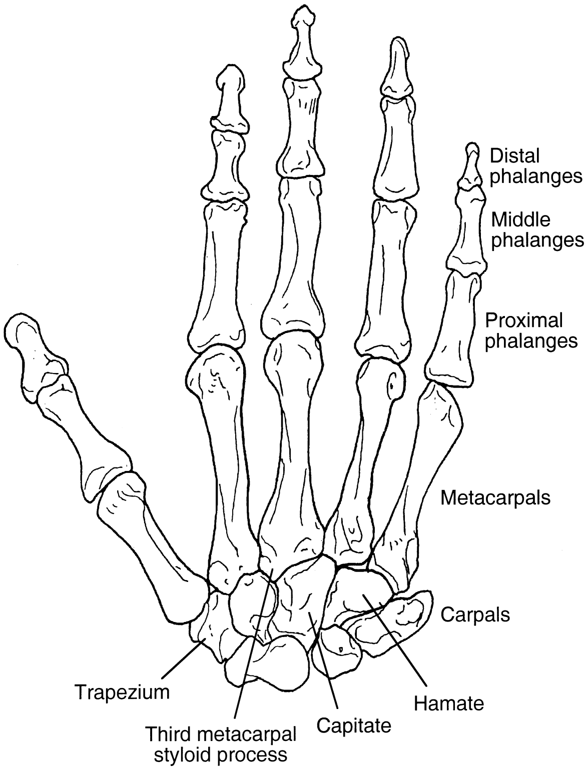

Fig. 2. Human hand skeleton with selected bones and muscles identified.

approaches to address the question. First, he compared the fossil hand with the hand bones of living human and nonhuman primate species to see whether it shared features with humans that might shed light on its capabilities for Oldowan stone tool making. He found that the fossil hand resembled ours in having a broad saddle-shaped surface on the trapezium (Fig. 2) for the thumb metacarpal, a marked cavity on the distal phalanx of the thumb in the region of the flexor pollicis longus muscle insertion, and broad distal phalanges. The saddle surface would have allowed full opposition of the thumb to the fingers. The cavity on the distal pollical phalanx is associated with the insertion of the flexor pollicis longus tendon in humans and, when considered along with the broad distal phalanges, it suggests that *H. habilis* possessed human-like capabilities for grasping objects. However, there were not enough bones to determine how long the thumb was relative to the length of the fingers. This was a major problem, because Napier's second approach had been to watch apes manipulate objects. He saw immediately that the manipulative capabilities of the apes seemed to be limited by the great distance between the fingertips and the tips of their relatively short, weak, thumbs. They were not able to control objects by the palmar pads of the thumb and fingers. He therefore came to the view that a proportionately long thumb and short fingers, facilitating precision grips by the thumb and finger pads, might have been an essential element of hand morphology for the hominids that manufactured the Oldowan tools and that, without evidence for this element, the tool-making capabilities of the fossil species could not be assessed. This motivated him to consider yet a third approach, in which he replicated the Oldowan tools using an ape-like grip by the fingers without the thumb. His reasoning was that since the Oldowan tools were quite primitive, a proportionately long thumb and short fingers might not have precluded the ability of the fossil species to make them. He succeeded in replicating the tools, and concluded that the fossil hand could have made the primitive associated tools, even if it turned out that it lacked a long thumb and a human thumb/index finger pad grip.

Since 1962 we have learned more about the morphology of human and nonhuman primate hands and about how the hands are used during locomotor and manipulative behaviour. Until quite recently, most of this knowledge has been qualitative, but it has been important in generating functional models that have attempted to link aspects of modern human manipulative behaviour with distinctive patterns of hand morphology. These models now need to be tested. They have generated new questions and have stimulated the collection of new data with recently-developed techniques that quantify features previously described qualitatively, as well as much additional information relating to muscle mechanics and the 3-dimensional (3-D) topography of bones and joints. Models using these new quantitative data should enhance our ability to glean evidence for manipulative capabilities from patterns of skeletal morphology in fossil hominid hands. A detailed review of the field at this qualitative stage, and suggested explanations for the poor performance of current models in predicting fossil hominid toolmaking capabilities, can be found in Marzke (1997).

This contribution reviews advances made since 1962 in our knowledge of hand morphology and functions associated with manipulative behaviour in humans, apes and monkeys, including the application of this knowledge to the functional analysis of fossil hominid hands. The earlier qualitative and more recent quantitative findings are presented in sequence, so that the reader may understand the current state of the debate and appreciate the potential of the new analytical techniques for reconstructing the functional capabilities of fossil hominid hands.

COMPARATIVE SKELETAL MORPHOLOGY OF HOMINOID HANDS

Carpometacarpal and metacarpophalangeal morphology

Anatomical studies of fossil hominid hands have built upon a solid foundation of descriptive comparative hand morphology of living species, laid down by Lewis in publications beginning in 1965 and culminating in a book (Lewis, 1989). His work drew attention to features in the carpometacarpal and metacarpophalangeal joint regions of the human hand (Fig. 2) that together contribute to our apparently distinctive ability to cup the hand and accommodate it to the varying shapes of objects (Lewis, 1977, 1989). This ability also enhances the amount of information about a manipulated object that can be conveyed by the sensory system from the palm and fingers to the brain (Landsmeer, 1993). The features of the hand that allow it to be cupped include (in addition to the opposable thumb, which is shared with apes): (1) a complex of 3 articular surfaces at the base of the 2nd metacarpal for 3 carpal (wrist) bones, the trapezium, trapezoid and capitate, facilitating pronation of the metacarpal; (2) marked asymmetry of the 2nd and 5th metacarpal heads, in which protrusions of the articular surface on the outer margins cause the index finger to rotate toward the 5th finger with flexion and abduction, and reciprocal rotation of the 5th finger; and (3) a saddle joint between the base of the 5th metacarpal and hamate that contributes to 5th finger rotation toward the index finger and thumb. Lewis also noted the characteristically broad human trapezoid, which articulates with a broad capitate anteriorly, in a position to accommodate the large stresses associated with opposition of the well-developed thumb to the fingers in human manipulative activities. These features have been considered in qualitative assessments of manipulative capabilities of fossil hominid hands by Lewis (1977, 1989) and Marzke (1983, 1997) but quantification of the 3-D joint surface topographical features Lewis describes is needed to establish whether they do, and how they do in fact distinguish humans significantly from nonhuman primate species and how they differ. Techniques for obtaining images of joint surfaces such as these, with which to reconstruct 3-D models and measure joint surface areas and curvature, have become available in recent years. They include stereophotogrammetry (Ateshian et al. 1992) and laser scanning (Aiello et al. 1998), and they will be described below in the section on modeling of bone and joint surfaces.

Trinkaus (1989) found that the Neanderthal and Olduvai *H. habilis* trapezium (Fig. 2) has a significantly flatter surface for the pollical metacarpal than in modern humans (based upon his caliper measurements of arcs and chords). The difference may reflect differences in loading of the joint (Trinkaus, 1989) and also in the range of thumb opposition to the fingers (Marzke & Shackley, 1986). There are interesting additional variations among species in the shape of the trapeziometacarpal joint (Guthrie, 1991), indicating that *Australopithecus afarensis* and chimpanzees may have less potential thumb excursion in opposition to the ulnar fingers, but more stability for firm thumb/index finger pinch grips that tend to displace the metacarpal dorsally. The modern human trapeziometacarpal joint pattern seems to be a compromise, with a structure that allows full opposition to the fingers, but which retains enough mutual curvature of the trapezium and metacarpal base to stabilise thumb/index finger pinch grips (Marzke, 1992). The new techniques for 3-D analysis of surfaces will allow more precise comparisons of species in the overall topography of the joint, and therefore more insight into whether emphasis in fossil species was placed on grips requiring thumb/finger stability, or on grips requiring wide thumb excursion in opposition to all 4 fingers.

A report by Bush et al. (1982), that the distinctive styloid process on the proximal end of the 3rd metacarpal of humans (Fig. 2) is absent from the hands of *A. afarensis*, led to a comparative survey of primate hands and a biomechanical analysis investigating the possible functions of the process in the manipulative behaviour of later hominids (Marzke & Marzke, 1987). The 3rd metacarpal styloid process is absent in other hominoids, and the analysis indicates that its position at the dorsal base of the metacarpal, together with a distinctive ligament from the pisiform to the anterior base of the metacarpal (the pisometacarpal 3 ligament), may stabilise the bone against large external forces in the palmar region of the 3rd metacarpal head. The use of hammerstones for tool manufacture by later hominid species was suggested as a possible source of these kinds of forces, and therefore as one possible explanation for the origin of the feature in human ancestors (ibid). Ricklan (1987) explored other possible explanations for the feature, in connection with his description of a 3rd metacarpal from Sterkfontein (Stw 64) dating to 2.5 mYr ago. This is the earliest known fossil hominin specimen with the feature.

Lewis (1989) and Sarmiento (1994) have argued that a feature homologous with the 3rd metacarpal styloid process may be found in African apes, but as Marzke & Marzke (1987) noted and illustrated, the projection on the metacarpal to which they refer is directed anteriorly and proximally into a cup on the distal dorsal radial aspect of the capitate, rimmed dorsally by a raised border that is continuous with the dorsal ulnar border of the capitate surface. Like other irregularities in the carpometacarpal region of these apes, this capitometacarpal interlocking feature stabilises the metacarpal against sliding on the capitate as body weight is borne by the dorsal surfaces of the middle phalanges during knuckle-walking locomotion. The human styloid process lies behind the capitate and is accommodated by a distinctive beveling of the dorsal radial corner of the capitate.

Distal phalangeal morphology

Complementing these features in the carpometacarpal and metacarpophalangeal regions of the human hand are functionally differentiated and compartmentalised volar pads ('ungual pulp') on the distal phalanges, which are stabilised distally but are flexible proximally (Shrewsbury & Johnson, 1975, 1983), where they accommodate varying deformation forces from the shapes of objects held by our cup-like grips. This compartmentalisation of the pads has been found in 100 % of a sample of 15 human hands but not in hand specimens of *Cercocebus*, *Presbytis*, *Macaca*, *Papio*, and *Gorilla* (Shrewsbury, personal communication). In the humans and some Old World monkey specimens the proximal volar pads were tethered to the distal phalanx by lateral ligaments whose distal attachments leave marks (spines) on the broad apical tufts of the distal phalanges. Comparable spines were not found in the gorilla (ibid). Interestingly, similar spines and attached lateral ligaments were found at the same relative location in the halluces of human and Old World monkey specimens, but not in the distal phalanges of the remaining toes (ibid). Compartmentalisation of the pads was not found in any distal phalanges from the feet. These findings indicate that the spines may reflect tethering of the pads that is perhaps compatible with functions shared by humans and these Old World monkey genera. However, they do not confirm the previous suggestion by Shrewsbury & Sonek (1986) that the spines are associated specifically with human-like soft tissue compartmentalisation of the pads.

Susman (1998) reported similar spines in a baboon skeletal specimen, but did not indicate how they related to the ligaments and to the overlying volar pad of the distal phalanx. An extension of the study by Shrewsbury, involving a wider range of human and nonhuman primate species (Shrewsbury & Marzke, unpublished observations) could potentially identify a nonhuman species with a homologous structural complex. Its functions might illuminate the conditions under which the human compartmentalised pattern of the pad might have originated.

Perhaps the most widely used morphological feature for inferring tool-making and tool-using capabilities from fossil hand morphology has been the marking on the distal pollical phalanx associated with insertion of the flexor pollicis longus tendon (Fig. 3). The size of the area has long been assumed to reflect the size of the tendon, but it has not been well described in the literature except for humans (in which it is well-marked) and great apes (in which it is barely discernible or absent). It was only recently that dissections were made for the purpose of examining the tendon insertion, and it was found that a hollow in the phalanx formerly assumed to receive the tendon in fact accommodates a sesamoid bone or cartilagenous nodule in the distal interphalangeal joint capsule when the distal phalanx is flexed (Marzke et al. 1998). Moreover, there is a facet on the distal phalanx for the sesamoid, when it is present. The presence of the sesamoid has the effect of increasing the length of the flexor pollicis longus tendon moment arm. The occurrence of these 2 skeletal features, which reflect the presence of a sesamoid bone in the joint capsule, can therefore be used to infer the existence of an enhancement to the torque capability of the muscle through enhancement of its leverage (for an explanation of these terms, see the section below on muscle force potential, moment arms and torque potential). This morphology was found in several human and nonhuman primate specimens.

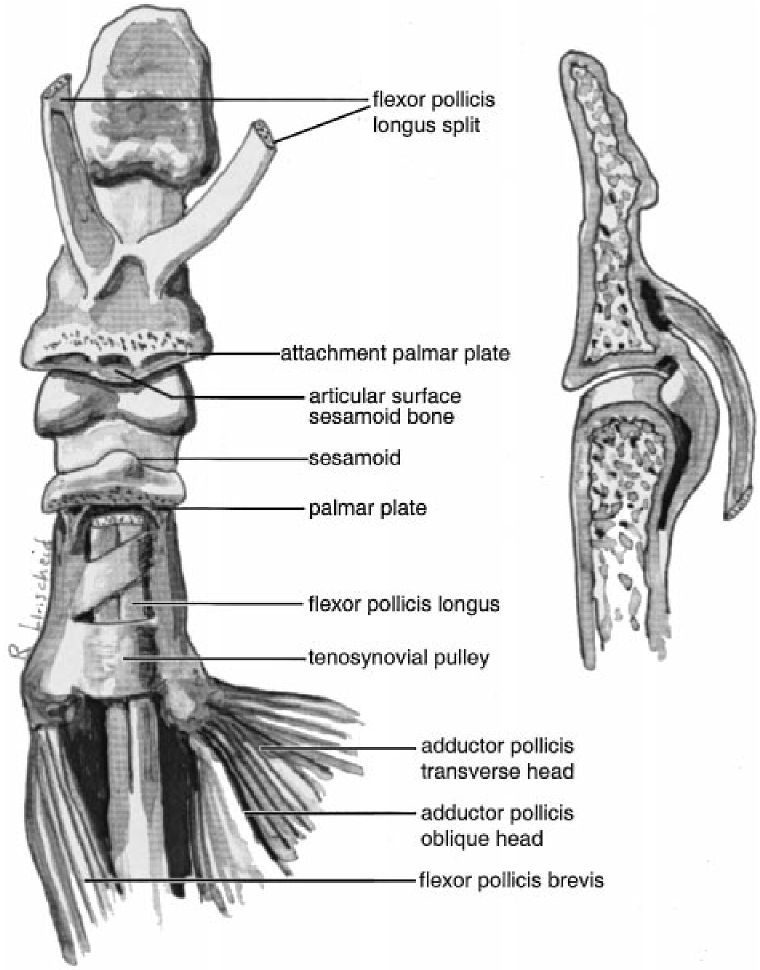

Fig. 3. Distal phalanx of the human thumb with the flexor pollicis longus tendon, shown attaching to a horseshoe-shaped crest on the distal phalanx of the thumb.

Skeletal proportions and phalangeal curvature

Humans have been compared with other primates in the length of the thumb relative to the index finger, because the ratio affects the ability to control objects by the thumb and fingers. Humans have the longest mean thumb length relative to index finger length, with a ratio of 60, followed closely by baboons and mandrills whose mean ratio is 57–58 (Napier, 1993). Other monkeys have shorter thumbs relative to index finger length, and in chimpanzees the thumb ratio is only 42. The high human ratio is an important element of the morphological pattern described above, allowing the thumb and fingers to accommodate to a variety of shapes and either to secure them firmly, or to translate and rotate them by the distal thumb and finger pads.

Although the full complement of hand bones is rarely available for fossil species, it may be possible to estimate relative thumb length on the basis of the dimensions of elements within the thumb and finger skeleton. For example, thumb and finger metacarpals and proximal and middle phalanges from hands of *A. afarensis* indicate a relative thumb length between that of chimpanzees and modern humans (Marzke, 1983). This facultatively bipedal species dates to about 2.8–3.2 mYr ago, before the first appearance of manufactured stone tools in the prehistoric record. Ricklan (1990) estimated relative thumb length for the Sterkfontein hominids on the basis of measurements relating metacarpal lengths to total thumb and finger lengths in living hominoid species. His conclusion was that the Sterkfontein ratio would have been within the human range, assuming that their metacarpophalangeal proportions were similar to ours.

Humans also appear to be distinctive among hominoids in the shape of their distal phalanges. Susman & Creel (1979) emphasised the broad apical tufts of the distal phalanges, which they found in a multivariate distance analysis were shared by humans and the Olduvai *H. habilis*. Susman (1988) also found this condition in fossil hominids from Swartkrans dating to about 1.8 mYr ago. The tufts would have supported broad distal finger pads, which these authors associated with human precision grip capabilities. Smith (1995) measured radiographs of chimpanzee and human hand bones and in a pattern profile analysis found that modern human distal phalanges are distinctive in their proportionately broader bases relative to tuft breadth. She reported that, although the Olduvai and Swartkrans hands have broad distal phalangeal thumb tufts, the base width relative to tuft width is small. This ratio is also characteristic of chimpanzees, suggesting that different thumb loading patterns may be indicated. She also suggested that body size may be a factor in determining tuft width.

Phalangeal curvature is of particular interest in the analysis of fossils, since the degree of curvature probably reflects stresses to which the hand was subjected during locomotor and/or manipulative activities (Richmond, 1997). Stern & Susman (1983), calculating an included angle to measure phalangeal curvature (see also Stern et al. 1995), found that the phalanges of *A. afarensis* were more curved than in modern humans, resembling apes, indicating that this early hominid species might have used its hands for arboreal climbing. This ape-like curvature is part of an interesting mosaic, incorporating features relating to metacarpal rotation in the radial side of the hand that could have enhanced the manipulation of natural objects as tools (Marzke, 1983, 1997).

First metacarpal robusticity

Susman (1994) suggested the possibility of predicting a capability for 'refined, humanlike precision grasping (and its correlate, tool behavior)' in fossil hominid species using a ratio of thumb metacarpal head breadth to length of the metacarpal. In a comparison of humans, chimpanzees and bonobos he had found a significantly larger relative head breadth in humans, which he attributed to large muscle contraction forces at the metacarpophalangeal joint. However, Hamrick & Inouye (1995) and Ohman et al. (1995) found that humans are not distinctive in having a large metacarpal head ratio; the gorilla ratio is within the human range of variation. They also note the lack of predictable links between tool behaviour and precision gripping capabilities.

The identification of morphological predictors of manipulative behavioural capabilities, even in this small region of the hand, requires the quantification of more variables and the identification of significant correlations among variables. For example, measurements should be made of muscle force potential, tendon moment arms (whose length affects the amount of muscle force required to rotate bones at joints), joint surface areas and joint ranges of motion, and compared among all hominoid species. In addition, the species should be compared in the ranges of thumb and finger movements associated with grips elicited by their varied tool behaviours.

In summary, comparative anatomical studies of hand skeletal morphology in living apes and humans have identified numerous features that together appear to distinguish the human hand from the hands of apes, and which facilitate our ability to cup the hand and accommodate it to the shapes of objects. However, 3 factors should be taken into account before applying this knowledge to the functional interpretation of morphology in fossil hominid hands. First, the effectiveness of this kind of grip depends upon the presence of all the morphological components set out above, yet rarely are sufficient fossil hand bones recovered to establish the presence of the total morphological pattern (Marzke, 1997). Secondly, few of the morphological features have been screened for statistically significant differences among species. Thirdly, experiments are needed to determine how these morphological features contribute to human manipulative behaviour. How can we test these form-function hypotheses? Are these functions essential in order to fashion early artefacts? Are there alternative morphological patterns that could accomplish the same behaviours?

PATTERNS OF MORPHOLOGICAL VARIABILITY ASSOCIATED WITH PATTERNS OF VARIABILITY IN THE REGIONAL DISTRIBUTION OF OSTEOARTHRITIS: CLUES TO STRESS FOCI ASSOCIATED WITH TOOL ACTIVITIES

One source of new data relevant to understanding the workings of the modern human hand is the distribution of osteoarthritis. Some regions of the hand today sustain high frequencies of this degenerative joint disease (DJD), a pathological process that has been attributed to forceful and repetitive loading in manipulative activities (Radin et al. 1972). Since the locations of DJD indicate the location of manipulative stresses, it is not unreasonable to assume that these may be the most likely to have undergone morphological change during human evolution in response to stresses associated with the manufacture and use of tools.

For example, DJD at the base of the thumb (in the

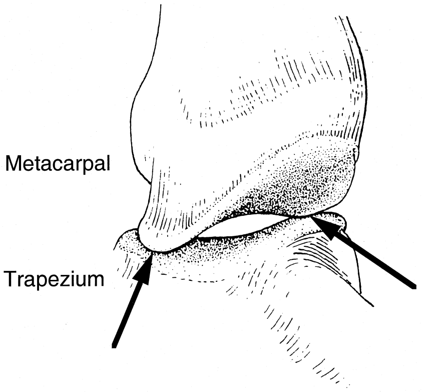

Fig. 4. Human trapeziometacarpal joint, drawn after Koebke (1983). Arrow points to the anterior beak of the first metacarpal, which rides up on the convex anterior surface of the trapezium in full opposition of the thumb.

trapeziometacarpal joint) is a common and debilitating condition in many human populations, interfering with many activities of daily living. One contributing factor appears to be the restricted area of contact between the metacarpal and the convex trapezial surface when the thumb is drawn into full opposition to the fingers (Koebke, 1983; see Fig. 4), and Koebke found that degeneration of the cartilage begins in this region. Ateshian et al. (1992) and Xu et al. (1998) have shown that female humans (known to have a higher frequency of trapeziometacarpal osteoarthritis than males) have significantly greater reciprocal curvature of the trapezial and metacarpal surfaces than males, less congruence of the joint, smaller contact areas, and thus an increased likelihood of experiencing high contact stresses in small localised areas for activities with comparable amounts of joint loading. This finding suggests a possible explanation for the relatively flat joint in the Olduvai *H. habilis* and Neanderthals. Wide excursion of the thumb is required for opposing the thumb and 4th and 5th fingers in the manipulation of large stones during tool manufacture. This activity requires strong, repeated contraction of the thumb muscles, which would have loaded the areas of contact between the proximal anterior beak of the metacarpal and the surface of the trapezium at their position of full opposition. The more curved the trapezium and the more projecting the anterior beak of the metacarpal, the more restricted this contact area would have been, and thus the more vulnerable it would have been to degenerative disease. Thus the relatively flat joint is consistent with tool-making behaviour (Marzke, 1990, 1992). But if this is the case, why do modern humans have a more curved joint on the average than the earlier hominins?

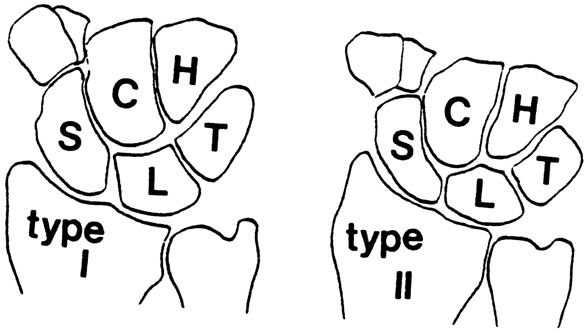

Fig. 5. Two midcarpal articular patterns. Left: type I, the hamate (H) does not meet the lunate (L). Right: type II, the hamate and lunate meet, creating a jog in the joint contour.

Another pathology involving the thumb emphasises the functional interrelationships that may explain the more curved trapeziometacarpal surfaces in modern humans. Frequently the thumb metacarpal slips dorsally and radially off the trapezium when objects are pinched between the thumb and index finger (Eaton & Dray, 1982). Mutually curved trapeziometacarpal surfaces have the advantage of stabilising the joint against this kind of subluxation, by locking of the anterior metacarpal beak (together with its extension, the anterior oblique ligament) against the convex surface of the trapezium. This stabilising morphology appears to be emphasised in chimpanzees and in *A. afarensis*, which, compared with modern humans, have a proportionately longer proximal anterior beak that restricts sliding and rotation of the metacarpal on the trapezium (Guthrie, 1991). Thus to some extent the requirements of human manipulative activities for both wide excursion and stability of the thumb metacarpal are contradictory. Comparative quantitative 3-D data on trapeziometacarpal joint surface curvature and congruence in humans and apes are needed to develop models for reconstructing the activities at joints involved in the manipulative behaviour of fossil species.

The high frequency of arthritis at the midcarpal joint (between the 1st and 2nd rows of carpals), and its link with variations in modern human articular patterns (Marzke et al. 1994) may also provide clues to the evolution of the human hand. Viegas et al. (1991) found that DJD at the proximal pole of the hamate bone in the wrist occurs only in individuals who have a blunt joint facet on this part of the hamate for a corresponding facet on the lunate bone, which lies proximal to it in the wrist. This pattern is present in most African apes and is consistent with the demands of their locomotor behaviour (Marzke et al. 1994; Fig. 5). This is the pattern seen in 65% of the

165 individuals in the Viegas et al. (1991) modern human cadaver sample. In the remaining 35%, the proximal hamate formed with the capitate a continuous curved surface for radioulnar deviation on the lunate and triquetrum, without creating a jog at the midcarpal joint. A functionally similar pattern is seen in Asiatic apes and is more compatible with repeated radioulnar movements of the wrist. The differential occurrence of cartilage damage in humans suggests an evolutionary explanation for midcarpal joint variability in humans. The pattern that appears in 65% of humans, in spite of its vulnerability to damage associated with activities requiring midcarpal radioulnar deviation, may be the remnant of an earlier adaptation for wrist stability, possibly relating to locomotor behaviour before the hand was used exclusively for the manipulation of tools and other objects. The relatively high frequency (35%) of the alternative pattern, which appears to be more compatible with human manipulative behaviour, may be the result of selection that occurred as the hand became used increasingly for manipulative activities requiring repetitive, forceful midcarpal radioulnar deviation.

It is too early to assess the effectiveness of localised pathology as a proxy for biomechanical studies, but the examination of fossil hominid hands for *combinations* of morphological features with known DJD correlates will throw interesting light on the sequence and possible causes of changes in joint morphology through time (Marzke et al. 1994).

OBSERVATIONS OF GRIPS AND THEIR RECRUITMENT DURING MANIPULATIVE BEHAVIOUR OF HUMANS, APES AND MONKEYS

A combination of Napier's observational and experimental approaches to the analysis of the functions of the hands of early fossil hominids is throwing new light on possible links between hand morphology and the manufacture and manipulation of tools. These studies address the broad question of how form and function relationships can be used to reconstruct the manipulative skills of humans, apes and monkeys. In our group we have investigated the following questions. (1) What grips are required to control tools, retrieve and process foods, groom other animals, and build nests? (2) What ranges and kinds of movement are associated with these manipulative grips and activities? (3) What regions of the hand are stressed by these grips and activities? By looking for behavioural and environmental correlates for between-species variation in hand morphology, and then investigating possible functional links between the morphological features, it should become possible to draw some reasonable inferences about manipulative and locomotor capabilities of the hand from fossil evidence.

Experimental manufacture of prehistoric tools by humans

This approach is based on the hypothesis that hand morphology and prehistoric tool manufacture and use evolved concomitantly during the Plio-Pleistocene. Among activities that are likely to have required morphological adjustments would have been the use of unmodified stone, bone, horn and wood and the manufacture of tools based on these raw materials. Two experimental approaches have been used. First, to what extent are ape-like hands capable of making the earliest Oldowan stone tools? Secondly, at what stage in the archaeological record do we see tools that would have required the functional capabilities of a modern human hand for their manufacture and use?

Napier (1962, 1964) and Krantz (1960) used the first experimental approach when they attempted to replicate Oldowan tools by mimicking an ape-like power grip using the flexed fingers without opposition of the thumb. They concluded that human-like precision grips were not necessary for the manufacture of these artefacts (Napier, 1964), although Krantz (op. cit.) conceded that the lack of fine-tuned thumb/finger movements affected precision, as did the need to use large hammerstones. Marzke & Shackley (1986) used the second approach, when they examined the demands placed on modern human hands during the manufacture and use of prehistoric stone tools. They reasoned that if specific human grips and hand movements were consistently elicited by these activities, and if specific regions of the hand were consistently stressed by the activities, it is reasonable to assume that the complex of morphological features that enables these grips would be most likely to have evolved as adaptations to these tool-making and tool-using activities as hominins became increasingly dependent upon stone, wood and bone tools.

The initial findings using this approach, based upon a qualitative analysis of films of the activities (Marzke & Shackley, 1986), was that there is indeed a specific group of grips elicited by the tool-making and tool-using activities. During the use of hard hammer percussion for the removal of flakes from cores in the production of Oldowan-type tools, the core was

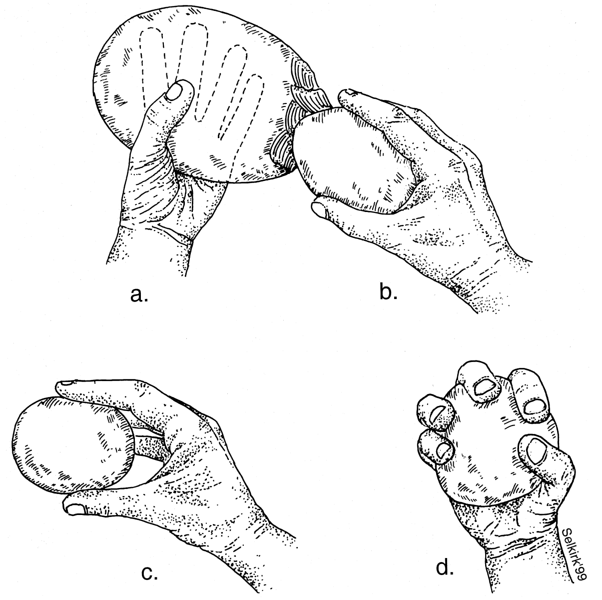

Fig. 6. Contrasts between: (*a*) a firm precision cradle grip of a stone core; (*b*) a 3-jaw chuck precision pinch grip of a hammerstone; (*c*) a delicate precision grip by the tips of the thumb and fingers and (*d*) a spherical power grip. The delicate precision grip would not resist displacement of the core by a hammerstone during the removal of flakes. The spherical power grip encloses the stone, exposing the fingers to damage by the hammerstone. The firm precision cradle and 3-jaw chuck grips resist displacement of the core, but allow exposure of the working edge of the core for safe flake removal.

generally held by a cradle grip (Fig. 6*a*), in which it is supported by the pads of the fingers, and secured by the opposing pressure of the thumb pad. A 3-jaw chuck (baseball) grip of the hammerstone, involving the thumb, index and third finger pads (Fig. 6*b*) was used exclusively. These 2 grips combine elements of the grip categories established by Napier (1956), precision (Fig. 6*c*) and power (Fig. 6*d*), and have been referred to as 'forceful precision grips' (Marzke & Wullstein, 1996). The element that forceful precision grips shares with the power grip is firmness, but their advantage is that by securing the grip with the thumb and finger pads (Fig. 6*a*, *b*) rather than against the palm in a power grip (Fig. 6*d*), the working surfaces of smaller stones can remain exposed for flaking, thus avoiding injury to the fingers. They share with precision grips the ability to make precise alterations to the orientation of the core and/or hammerstone for each strike by moving the thumb and finger joints. This important element of human manipulative behaviour was called 'precision handling' by Landsmeer (1962). Both these grips require convergence of the thumb and finger pads, and the large stresses generated by each hammerstone strike must be accommodated. It is hypothesised that these requirements are met by the distinctive combination of features in humans described above in the section on skeletal morphology, that facilitate cupping of the hand and the firm opposition of the thumb pad to the pads of all the fingers.

The same experiments (Marzke & Shackley, 1986) demonstrated that prehistoric stone tool use required the same manipulative abilities and morphology as stone tool manufacture. When the flakes produced by the hard hammer technique were used for cutting and scraping, a firm pad-to-side precision grip made by the thumb and the side of the index finger was used. This requires a strong thumb and rotation of the index finger. The grasp of cylindrical objects (e.g. wood and bone clubs) consistently prompted the use of the squeeze form of power grip, in which the thenar and hypothenar regions of the palm, as well as the flexed fingers, squeeze the tool diagonally, so that it functions as an extension of the forearm as it is brought into contact with its target. The modern human ability to rotate the 5th metacarpal towards the opposed thumb metacarpal, to cup the palm, together with thumb/finger proportions that allow the thumb to stabilise objects at the level of the flexed fingers, are the cardinal elements of the ability to retain the core in the hand for one-handed clubbing and pounding (Marzke et al. 1992).

The tool replication experiments suggest a possible link between the evolution of human hand morphology and the evolution of tools, but how do we test the hypothesis that the human hand evolved in adaptation to these activities? How can we justify using the complex of morphological features outlined above as a model for inferring tool-making and tool-using capabilities from fossil hominid hands? Following the reasoning of Lauder (1995, 1996), an attempt can be made to explain a unique morphological pattern with experiments comparing performance capabilities for the hypothesised activities in other species with a different, but closely-related morphology. As Lauder has made clear, there are substantial weaknesses in this approach for predicting how structures might have been recruited for use in fossils, but he acknowledged that this biomechanical approach may allow researchers to 'define the realm of the possible' for fossils (Lauder, 1995).

In the next section we compare the abilities of modern humans with those of nonhuman primate species to maintain a grip on objects of varying shapes by each hand separately during activities similar to prehistoric human tool making and tool use. In these activities, it is imperative that the working edges of the manipulated objects remain exposed, and the complementary grips must be maintained against strong external forces.

Fig. 7. Chimpanzee using 2 hands and a foot to hold grapefruit during feeding.

Grips and hand movements of nonhuman primates in tool activities and feeding

The study of non-human primate manipulative capabilities most directly relevant to our question is one by Toth et al. (1993) of Oldowan-type stone tool manufacture and use by a *Pan paniscus* individual. These workers found that the subject (Kanzi) preferred to throw a stone core on the ground to remove flakes one-handed, rather than use 2 hands, controlling the hammerstone with one hand, and the core with the other. When the latter technique was used, many repetitive strikes of the hammerstone were required to dislodge a flake, indicating that the force applied was not large. The hammerstone was grasped by the fingers against the palm of the hand, and movement was generated primarily at the shoulder and elbow. Flake use elicited the same pad-to-side grip as in humans, but judging from the number of strokes required to cut a string with the flake to obtain a reward, there was relatively little force to the grip. The study showed that the modification of stone cores and the production of flakes similar to those found at Oldowan sites, is within the capabilities of *P. paniscus*. However, the experiment also emphasised the advantages to tool making and tool using that are conferred by the repertoire of firm precision grips used by modern humans.

Chimpanzee feeding activities resemble the hard hammer percussion manufacture of stone tools in that both require the maintenance of an exposed working surface, for the lips and teeth in the case of feeding. Chimpanzees observed by Marzke & Wullstein (1996) generally cup large fruits in the upturned palm with flexed fingers. When the fruit is raised to the teeth, the other hand is usually brought into play (and occasionally a foot as well) to maintain the flexed finger grip against the pull of the teeth (Fig. 7). Smaller pieces of fruit are held by the pad-to-side precision grip, but again, resistance against the pull of the teeth brings the other hand into play with the same pad-to-side grip. These behaviours suggest a limit to the strength of one-handed finger cup and pad-to-side grips, that is offset by the use of additional extremities. Marzke & Wullstein (1996) also found differences in manipulative performance capabilities for precision handling and for using cylindrical objects as extensions of the forearm. Chimpanzees reoriented objects by placing them in the mouth and retrieving them in a new orientation, rather than by translating and rotating them with the thumb and fingers. Cylindrical objects were held transversely instead of obliquely across the palm by the flexed fingers, and were therefore not held in line with the forearm. Similar deficiencies in the performance of precision gripping, precision handling and the 'squeeze' power grip are reported for capuchin monkeys by Westergaard & Suomi (1997), baboons (Guthrie, 1991; Jude, 1993), and orangutans (Marzke & Wullstein, 1996).

FUNCTIONAL LINKS BETWEEN HAND MORPHOLOGY AND MANIPULATIVE BEHAVIOUR: THE STRUCTURE AND USE OF THE HANDS OF PREHISTORIC TOOL MAKERS

Comparative studies of hand morphology and manipulative behaviour focused attention on an interesting pattern of capabilities and morphology that appears to distinguish modern human manipulative behaviour from that of other species. The distinctiveness is not confined to precision vs power grips, but is based on the emphasis of modern humans on forceful grips and precision handling, within the precision category, and on the squeeze grip within the power category. These grips, and related thumb/finger movements, allow for the one-handed control of stones, wood, bone and horn. Any models for modern human manipulation must overcome the weaknesses of earlier models that were based on isolated elements of an overall pattern (Marzke, 1997).

Susman (1998) recommends ignoring the diversity of grips within the precision and power categories in discussions of hominid evolution and prehistoric tool use and tool making. However, as Marzke & Shackley (1986), Marzke & Wullstein (1996), Marzke (1997) and Marzke et al. (1998) have shown, it is the discovery of this diversity in the course of our research that in fact has led to a much deeper understanding of morphological variations among living anthropoid primates than previously existed. Lewis (1989, pp. 114–115), concurred with the use of a more elaborate classificatory scheme in the evolutionary analysis of hominid morphology, noting that the power and precision grips (as defined by Napier 1956) both recruit features (in different combinations) that together he considered to be apomorphic in humans. A developing awareness of the behavioural and morphophysiological complexity of manipulation is indeed generating the interesting questions that will guide us in the development of more detailed models relevant to the functional analysis of fossil hominid hands in the future.

Models being developed require data on structure and functions that are only now becoming available. These include information about the patterns of muscle recruitment, and ranges of joint movement collected from living subjects during the manufacture and use of prehistoric tools, estimates of muscle torque potential estimated from muscle fibre length measurements and ranges of passive joint movement and tendon excursion in cadaver limb specimens, free body analysis of stresses associated with hard hammer percussion manufacture of stone tools, and 3-D imaging and measurement of joint surface areas and curvatures. In addition to these, comparative studies of bone density, trabecular patterns, cortical distribution, and area moments of inertia contribute important kinetic data for biomechanical models. Brief descriptions of the techniques used in these experiments, with consideration of their potential as well as their limitations for addressing our evolutionary questions, are given below.

It is important to keep in mind that models will be more effective at predicting the performance of fossil morphologies if they are based on activities that are generic to the living species under study. The musculoskeletal system and its neural control are very flexible, and can be recruited for a much wider range of activities than those for which they are regularly used. Thus modern humans can swing from bars by contracting their finger flexor muscles like apes, and apes can remove flakes from tools by holding large stones by the thumb and fingers like modern humans. Functional morphologists must therefore identify and focus upon the activities that elicit different musculoskeletal functional patterns, which in turn are facilitated by different patterns of associated morphologies.

EMG analysis of muscle recruitment during prehistoric tool making and tool use

In order to generate realistic models, we need to know, for a given bone-ligament-tendon system, which muscles are active during manipulation. One of the traditional approaches to these questions is the use of electromyography (EMG) to record the electrical signal produced by muscle contraction during prescribed activities. The approach is an important first stage in testing hypotheses about possible functional links between morphology and behaviours. It directs attention to the muscles that are most likely to have been consistently and strongly recruited in the behaviour of interest, and thus targets for further analysis skeletal regions that have the potential to reveal evidence about the musculoskeletal adaptations associated with the grips, ranges of motion and stresses relating to these behaviours.

In the past, inferences about hand use have been made from the size of muscle markings on fossil hominid hand bones. For example, well-developed attachments for flexor digitorum superificialis muscle on the middle phalanges of the Olduvai *H. habilis* hand have been interpreted as evidence for arboreal climbing (Susman & Creel, 1979); a large opponens pollicis insertion crest on a metacarpal from Swartkrans is interpreted as evidence for tool making (Napier, 1959); and a large excavation in the region of the flexor pollicis longus tendon has suggested human-like tool-making capabilities in the Olduvai *H. habilis* (Napier, 1962) and the Swartkrans early hominid (Susman, 1988). Forceful contraction, occurring repeatedly, does appear to cause some bone markings in modern humans at muscle attachments (Welton et al. 1994). However, it should be emphasised that at the present time there are no published data on the correlation between muscle force generated and the size of muscle markings, and it is not known whether it is the maximum strength of contraction, or the repetition of weaker contractions, or both, that generate the muscle markings on bone.

An EMG study was undertaken to test these inferences and to move beyond speculation to direct examination of the patterns of muscle recruitment associated with the manufacture and use of prehistoric tools. Modified stones are virtually the only direct evidence we have of early hominin tool making and tool use, but hominin hands were probably used in a much wider range of food-collecting and food-processing activities requiring forceful use of the hands alone for pulling and breaking fibrous materials, and the use of bones, horn and wood. The activities monitored in our experiments so far have therefore included: (1) the manufacture and use of stone tools, such as hard hammer percussion manufacture of Oldowan-type tools (Marzke et al. 1998), side scraping of hides with a stone flake (Reece et al.1997), end scraping, meat-cutting with flakes, bone-chopping with stones to acquire marrow, nut-pounding with stones, the manufacture of Acheulean hand axes, and pressure flaking; (2) stone-throwing; (3) digging with long sticks and with short bones and horns; and (4) clubbing with bones and small tree branches. The subjects were an archaeologist with extensive experience in the replication of prehistoric tools, and who makes them on a regular basis, a second archaeologist also with considerable experience in tool replication, and a physical anthropologist who had only recently begun experimenting with techniques to replicate and use prehistoric tools. A subsequent study (Marzke & He, unpublished) with 5 subjects incorporated a CyberGlove, which recorded thumb and finger positions simultaneously with muscle recruitment.

Fig. 8. Archaeologist (Dr N. Toth) replicating Oldowan tools, with EMG apparatus for monitoring the recruitment of his hand muscles. A microphone near his left hand registers each strike by the hammerstone on the core.

In the first study (Fig. 8), indwelling electrodes were used to monitor the activity of 10 muscles during each session. Seventeen muscles from both hands (including both extrinsic and intrinsic hand muscles and 1 wrist muscle, the flexor carpi ulnaris) were included in the study. A microphone recorded hammerstone strike and other sounds associated with the activities that served as reference points for analysis of the relative timing of muscle signals. Videotapes of the activities displayed simultaneously with the EMG signals provided a visual record for use in linking muscle activity with grips and hand movements. Results of the study have been published for the hard hammer percussion manufacture of Oldowan-type tools (Marzke et al. 1998) and for side scraping (Reece et al. 1997).

There are 3 findings from the tool-making experiment of particular significance for the functional analysis of early hominid hand bones. First, there is a substantial contribution by muscles attached to the 5th finger and adjacent wrist bones to grips by both the right and left hands during this activity, with interesting recruitment patterns (Marzke et al. 1998;

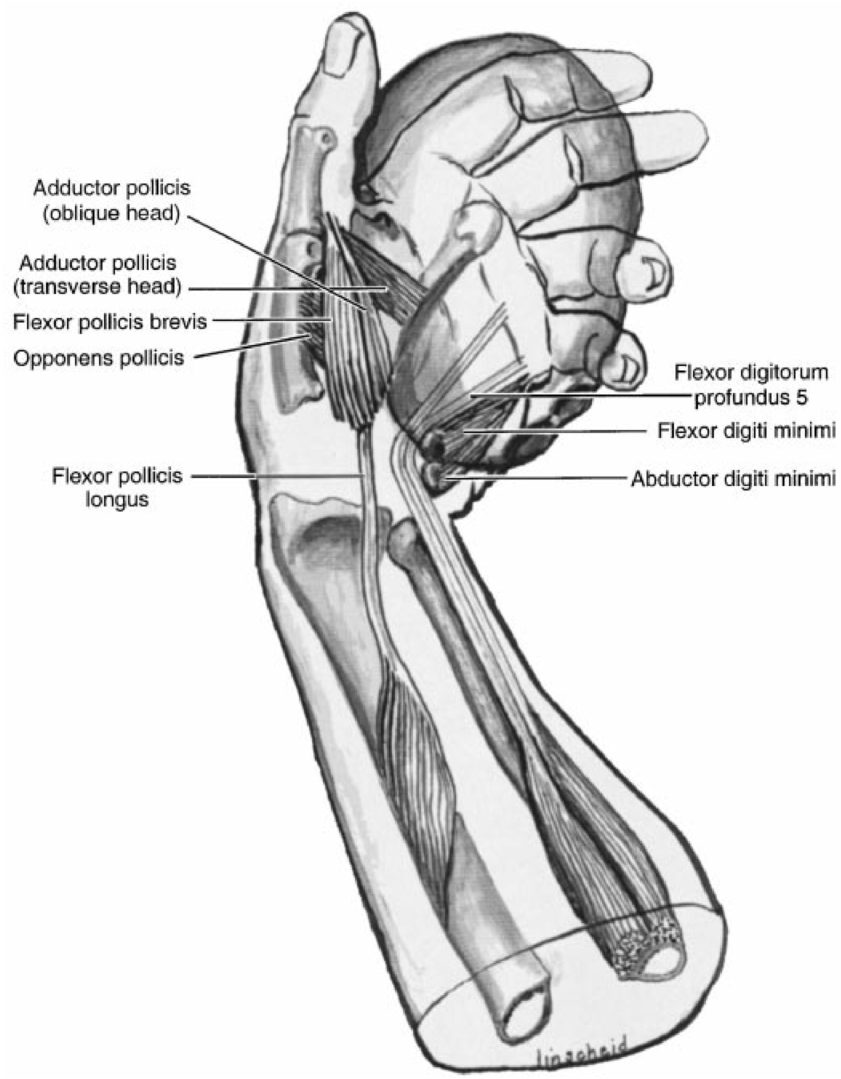

Fig. 9. Muscles strongly recruited during hard hammer percussion manufacture of Oldowan-type tools.

Fig. 9). Until now, paleoanthropologists have focused almost entirely on the thumb in their search for evidence in fossil hominids of tool-making capabilities, but 5th finger skeletal morphology may contain important signatures of bone and joint loading patterns associated with the forceful precision grips used today by modern humans during the manufacture and use of tools.

The second significant finding was the strong contribution to the hammerstone grip of a pair of intrinsic muscles that act on the thumb: flexor pollicis brevis, which originates on the trapezium and adjacent tissues and inserts distal to the first metacarpophalangeal joint on the radial side of the proximal phalanx (Figs 2, 9), and the 1st dorsal interosseous muscle, which originates on the 1st and 2nd metacarpals and inserts in the region of the index finger metacarpophalangeal joint (Fig. 2). The 2 muscles are associated functionally in manipulation; the 1st dorsal interosseus is in a position to stabilise the base of the thumb on its ulnar side while the short flexor contracts strongly on its other aspect (Brand & Hollister, 1993).

Thirdly, results of the EMG experiments for flexor pollicis longus indicate that it may not have been as strong a contributor to tool-making activities involving precision grips as has been assumed in the past. However, our data show that it clearly contributes substantially to the squeeze grip of cylindrical objects such as branches or long bones, when they are used for clubbing and pounding, as Ohman et al. (1995) predicted. Hamrick et al. (1998), in an EMG experiment directed exclusively to recording the activity of flexor pollicis longus, also observed heavy use of the muscle for the squeeze grip.

Electromyographic studies such as these are a first step in attempts to demonstrate functional links between morphology and behaviour in living species. The studies are particularly valuable when they are followed by biomechanical studies on cadaver hands, described in the next section, which measure the cross sectional areas and tendon moment arms of the muscles whose functions are found to play an important role in hypothesised prehistoric behaviours. However, there are limitations to the kinds of information that can be acquired with EMG. A few cautionary comments are given below, along with a discussion of what can be learned from these studies that is relevant to functional analyses of fossil hominid hand structure.

Size of electromyographic signals. It is well-known that there is not a precise relationship between the amount of muscle tension and the magnitude of the voltage electrical signal recorded by an electrode. Reasons for difficulties in finding the relationship, and a discussion of approaches to investigating it may be found in Herzog et al. (1994). The size of a signal also does not reflect the relative importance of a muscle in an activity. Muscles have multiple roles in joint movements as prime movers (causing motion in the desired direction), synergists (augmenting the movement and stabilising joints against unwanted ancillary movements) and agonists (helping to control motion in the desired direction). The relative amount of contraction will thus vary with any change in the role of a muscle. It also will be affected by the length of its moment arm, which affects its leverage. A muscle with a long moment arm could make the same contribution to torque at a joint as another muscle with more fibres, but with a shorter moment arm.

Cross talk. Neighbouring muscles may convey similar signals because of 'cross talk', in which an electrode picks up a signal from a muscle nearby. We address this potential for error by looking for evidence of identity between muscle signals during the experiment, and change the combinations of muscles monitored if there is evidence for cross talk. The use of indwelling rather than surface electrodes reduces these artifacts, as well as those associated with intervening tissues between surface electrodes and the muscles they monitor.

Relative amounts of activity of a given muscle during different behaviours. Two kinds of information may be gleaned from the EMG that are relevant to functional morphological studies. One is the relative amounts of activity of a given muscle during different behaviours. The other is the temporal pattern of recruitment for the full set of muscles during each behaviour.

Since subjects vary in the total amount of force that can be applied to functions such as gripping, their signals must be compared using relative rather than absolute scales. A standard baseline may be established either by: (1) having a subject generate maximum possible signals for each action, such as each grip in the experiment described above, and calculating a percentage level of each action during the experimental sessions relative to the baseline; or (2) using as a baseline the largest signal generated by the action during the full experimental session. Consistency among individuals in high recruitment level for a given muscle in a specific action is the most suggestive evidence we can obtain of a behaviour that might explain a muscle attachment marking in a fossil. High recruitment levels of functional muscle groups in an activity are especially informative about the kind of activity indicated by large muscle markings for these groups.

Temporal pattern of muscle recruitment. Observing the temporal pattern of muscle recruitment relative to stages in an activity cycle can help to explain patterns of markings on bone for muscles that do not necessarily cocontract. For example, the use of hammerstones elicits signals in the intrinsic thumb muscles prior to strike and in the 5th finger muscles after strike. Thus a single activity might explain the presence of marks for both sets of muscles in a fossil hand.

Hand muscle force potential, moment arms and torque potential

Having targeted with EMG studies regions of the hand whose skeletal morphology is most likely to reflect torque capabilities of muscles important in tool making and tool using, our research group proceeded to a full comparative kinematic study of these regions in a cadaver sample of hominoid hands. This work expanded upon the classic study of hominoid hand musculature by Tuttle (1967, 1969), who compared genera in dry muscle weights. These weights are proportional to the work potential of a muscle (force × distance through which the muscle contracts). Our study (Marzke et al. 1999) took muscle cross-sectional area and tendon moment arms into account in comparing apes and humans in potential muscle torque (i.e., in the ability of each muscle to rotate a bone at a joint). The cross-sectional area is proportional to the force a muscle can generate and the moment arm lengths affect the leverage of a muscle. For a muscle of a given force potential, its potential torque increases in proportion to the length of its moment arm. Marzke et al. (1999) estimated muscle potential force using the approach of Brand et al. (1981), in which the muscle fibre length is measured with digital calipers, muscle volume is determined by

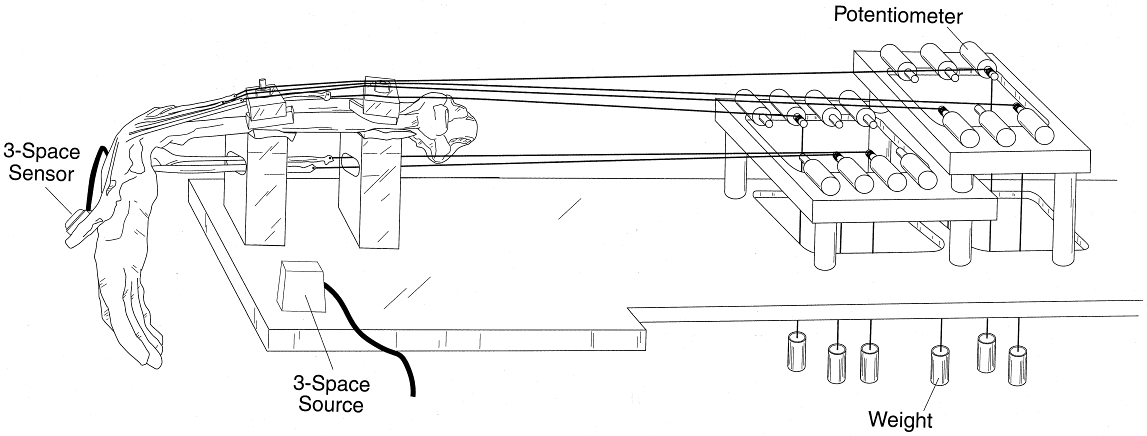

Fig. 10. Chimpanzee hand mounted in a vice for measurements of tendon excursion and joint angle changes during passive movement.

water displacement and the volume is divided by mean fibre length to obtain physiological cross-sectional area (PCSA). The PCSA is proportional to the number of fibres and therefore to the potential force of the muscle.

The cadaver forelimbs are then placed in a plastic vice (Fig. 10). Long sutures, tied to the tendons during the dissection after removal of the muscle fibres, are run along the wrist and forearm according to the lines of action of their muscles and are wound around drums of an electric potentiometer. When the hand is moved passively, pulling the tendons, the pull of the attached sutures rotates the potentiometer drums, which record the tendon excursion distance. Sensors from a 3-space magnetic tracking device (3Space Tracker System, Polhemus Navigation Sciences Division, McDonnell Douglas Corp., Colchester, Vermont) are placed in positions on the hand and wrist to record changes in a joint angle during passive movement of each joint. Thus during the passive movement both the distance of tendon excursion and the change in joint angle are measured simultaneously.

When the tendon excursion is plotted against joint angle over the joint's range of motion, an approximately linear relationship between these 2 quantities is seen. The slope of this plot has a simple interpretation, according to a model of joint rotation about a single axis produced by tendon excursion (Model I originally proposed by Landsmeer, 1961). The slope of the plot is directly the moment arm of the force exerted via the tendon about the axis. The moment arm of each muscle is thus the derivative of the tendon excursion vs joint angle plot, suitably averaged over the range of motion. The tendon moment arm is multiplied by the PCSA of its muscle to obtain the estimate of potential torque, since torque is the product of force and the lever arm of the force.

Marzke et al. (1999) found that the moment arms contribute more to significant differences between humans and chimpanzees in potential torque of the thumb muscles than the physiological cross-sectional areas. This finding is important because it suggests a new, quantifiable source of clues in fossils to possible skeletal adaptations in the hand to the ranges of activities that recruit the muscles and stress the joints in living species. Three-dimensional modelling and measurement of these regions in modern anthropoid hands should allow us to identify and measure features relating to tendon moment arms that differ significantly among living anthropoids and thus may serve as guides to joint functional capabilities in fossil species.

Two thumb muscles that were found in the EMG experiments to play an important role in Oldowan-type tool making (flexor pollicis brevis and first dorsal interosseus) proved in the cadaver study to have interesting morphological correlates. The short flexor muscle has a significantly larger tendon moment arm in humans and the origin of the interosseus muscle extends well beyond the base of the 1st metacarpal to about half the length of the bone in modern humans, whereas the 1st metacarpal origin of the 1st dorsal interosseous muscle in a sample of 10 chimpanzees was restricted to the base of the bone. The twin findings of: (1) a functional relationship between the 2 muscles involved in a grip modern humans use in tool making; and (2) possibly derived human morphology relating to activity of both muscles suggest 2 new regions to examine in fossil hominid hand bones for evidence that the bones were stressed in a way characteristic of modern human manipulative behaviour. Finding an indication of both elements in this complex would be more compelling evidence for a given range of hand functions and associated behaviours than finding an indication of one. In fact, there is a potential third element in this behavioural/morphological pattern, the oblique portion of adductor pollicis, which originates in the region of the base of the 2nd metacarpal and inserts distal to the ulnar side of the 1st metacarpophalangeal joint. Both the physiological cross-sectional area and the moment arm of this muscle for flexion of the trapeziometacarpal joint were significantly larger in humans compared with chimpanzees. This muscle functions with the short flexor in stabilising the joint during firm grips (Brand & Hollister, 1993). The moment arms of both muscles would be affected by the orientation of the thumb relative to the metacarpals, by the degree of palmar projection of the metacarpal head and/or by the size of the sesamoid bones, which tend to occur in the joint capsule.

Modelling bone and joint surfaces

Stereophotogrammetry. In recent years several techniques have become available for 3-D modelling of bone and joint surfaces, thus enabling quantitative comparisons of the joint surface of individuals, sexes and species. This will enable the quantification of skeletal contours that affect joint movement, load transfer and tendon moment arms. The hypotheses that the joint regions of modern human hands are unique, based upon the qualitative observations and simple measurements described at the beginning of this review, can therefore be tested quantitatively. Two techniques for obtaining 3-D images are stereophotogrammetry and laser scanning. Stereophotogrammetry involves photography of a surface from 2 or 3 directions. The bone is mounted in a calibrated frame and a grid is projected onto the joint surface by a projector, providing intersection points for subsequent digitising. Borders of joint surfaces and other skeletal features can be easily marked for identification in the photographic images. Initially precision format cameras were used (Ateshian et al. 1992), but more recently digital cameras have been used to feed the images directly into the computer for digitising and subsequent analysis (Marzke et al. unpublished observations). Resolution up to approximately 60 μm is possible, allowing for comparison of small joint surfaces, for example in the wrist and ankle. By digitising the images it is possible to reconstruct 3-D models of joint surfaces in the computer, which can then be compared among individuals, sexes, populations or species in area and curvatures as Ateshian et al. (1992) have done for the trapeziometacarpal joint. This technique has the advantage of portability to museums and laboratories for use in obtaining images of large samples of joint surfaces from skeletons of contemporary species and from fossil bones. All that is required are a digital camera and tripod, laptop computer, and a slide with the grid. Projectors are usually available at the museum or laboratory site. A disadvantage of the technique is that it currently requires hand digitising of the images. This drawback should be overcome in the near future with software that can reference data points from the multiple images.

Laser scanning and digitising. Laser scanning systems (e.g. Cyberware Inc.) have the advantage of both capturing images and digitising them with currently available software. Scanners of varying sizes are available for obtaining images of whole living bodies or small joint surfaces with up to 200 μm resolution. The current drawback of the technique is that the margins of joint surfaces may not be clearly recognisable in the images and may therefore need to be defined prior to imaging with markers if comparative measurements are to be made (Aiello et al. 1998). Systems are near the limit for portability, which is also constrained by the expense of having more than one system to allow for data capture and analysis at the home institution while the other is away from the laboratory. Kappelman (1998) provided an excellent review of the state of the art for this technique, addressing some of the current problems in its application to research in functional morphology and paleoanthropology.

Software for measuring and comparing in detail the 3-D topography of joint surfaces imaged by the 2 techniques is not widely available at present, but has been written for specific applications (e.g. Ateshian, 1993; Steinberg, 1999) and is becoming available to the public. Aiello et al. (1998) devised a technique for limited comparison of sections through the joint surfaces in a study of joint congruency.

Application of cross-sectional, radiographic, computerised tomographic (CT) and magnetic resonance imaging (MRI) techniques to modelling of hand biomechanics

Metacarpal shape and bone mass distribution measured on metacarpal sections and biplanar radiographs. Data from scans of metacarpal cross-sections from a large modern human skeletal sample have been used by Lazenby (1998) to model metacarpal shape and bone mass distribution. His results point to differences between right and left hands, and between sexes and age groups, suggesting that there are likely to be patterns of variation between groups of individuals associated with occupations that differentially recruit the hands. Any such patterns might serve as models for the interpretation of fossil hominid metacarpal shape and bone mass distribution. Coffing's (1998) finding of differences between *A. afarensis* and modern humans in metacarpal cortical mass thickness and distribution, using biplanar radiographs, has raised interesting questions about the nature of habitual hand recruitment patterns in this fossil species.

Angles between joint axes measured on CT images. There are additional features of the hand whose measurement and comparison may further illuminate the morphological basis of the human facility for cupping objects in the hand and maintaining control of them against strong resistance. One of these is the relative orientations of 2 sets of joint axes: (1) the radioulnar (flexion/extension) axes of the distal carpal bones relative to one another; and (2) the relative orientations of the proximal and distal radioulnar (flexion/extension) joint axes of each metacarpal. Napier (1961), Day & Napier (1963), and later Lewis (1989) and Sarmiento (1994) have noted an apparently more marked angle between the trapeziometacarpal joint axis and the axes of the joints at the bases of the finger metacarpals in African apes compared with humans. If this difference does indeed exist, it may help to explain differences between chimpanzees and humans in functions of the thumb muscles found by Marzke et al. (1999), and thus the angle might serve as a guide to possible muscle functions in fossil hands.

Peters & Koebke (1990) have developed a technique for examining torsion of the finger metacarpals, using CT images of human hands to locate the radioulnar axes of the proximal and distal joint surfaces. They found an interesting pattern of metacarpal torsion that contributes to different orientations of metacarpal heads for the 2nd and 3rd fingers compared with the 4th and 5th fingers. These differences affect the orientations of the fingers when they are flexed, and in turn affect the potential functions of these fingers in power and precision grips. Comparable images from nonhuman anthropoid species are currently being analysed (Marzke et al. unpublished observations), to determine whether there are differences among them and from humans that might be applied to the functional interpretation of metacarpal morphology in fossil hands.

Force generation capability measured with MRI and force transducer. An innovative approach to estimating functional capabilities from fossil hominid hand bones was devised by Bimson et al. (1997) who used magnetic resonance imaging together with a force transducer to test a common assumption that the dimensions of the human distal pollical phalanx reflect relative force generation capability. High resolution magnetic resonance images of the thumb were obtained on a sample of living human subjects, and measurements were made on the images of distal pollical phalangeal length, breadth, tuft breadth and joint depth. A force transducer measured peak interphalangeal thumb joint flexion in the same subjects. Multiple linear regression analysis showed correlation coefficients of 0.73 and 0.67 for 2 different combinations of dimension measurements vs force capability. Formulae for force capability derived from the study of the living sample were used to predict potential distal pollical flexion force in several fossil hominid hands. It was found that the force estimates for earlier hominids were at the low end of the modern human range, while Neanderthal force estimates were higher than those found for modern humans. The authors tested for potential error in measuring bone dimensions on MR images and found no more than 5% error in a test using MRI and direct measurements of chicken bones, indicating that this is a reasonable approach to obtaining bone dimensions in living subjects. However, the correlation coefficients are low, and as the authors note, additional factors of bone shape differences and body size differences among these closely related hominids cannot be considered in the model.

FOSSIL EVIDENCE FOR EVOLUTION OF THE HUMAN HAND

After all of these morphological and biomechanical investigations, are we any closer to an answer to Napier's question about the Olduvai hand? Was it capable of making the tools found at the same level at Olduvai Gorge? The relatively flat metacarpal surface on the trapezium would have allowed full opposition of the thumb to the 4th and 5th fingers, which our experiments indicate is essential for stabilising large cores against the blows of hammerstones in Oldowan-type tool manufacture. Control of the stones by strong pinch and precision handling would have been enhanced by the broad distal phalangeal pads. Clear evidence of a sesamoid bone at the distal interphalangeal joint of the thumb indicates good leverage for the flexor pollicis longus muscle, which appears to be essential for the use of cylindrical tools in activities such as clubbing (but note the caveat of Susman &

Creel, 1979, that this may be the distal phalanx of the hallux).

Reviews by Marzke et al. (1992) and Marzke (1997) of existing evidence for morphological correlates to prehistoric tool-making and tool-using activities led to the disappointing conclusion that we currently did not have enough regions of the hand from any fossil species contemporary with manufactured stone tools to be able to confidently determine whether any, or all of them, were the makers of the tools and capable of all modern human grips. Morphological patterns were identified that are consistent with the human squeeze form of power grip (Marzke et al. 1992) and with human forceful precision grips and precision handling (Marzke, 1997), but only isolated elements of the patterns occur in the parts of the hand skeleton that are preserved from hands discovered at Olduvai, Sterkfontein, and Swartkrans, and these elements occur in different combinations, rendering comparisons among the fossils difficult. Their occurrence might cause us to surmise that the other complementary and necessary elements of the pattern were also present, but without direct evidence for this the possibility remains that the human-like elements were part of other overall patterns.

However, we are now at a crossroad in the functional interpretation of early hominid hand morphology. The comparative studies of manipulative behaviours, together with data on the relevant muscle mechanics and associated skeletal topography, are pointing to the existence of a distinctively modern human pattern of features whose presence in fossil hands will be compelling evidence for an ability to effectively manufacture and use stone, wood, bone and horn tools. Models of hands in living species generated by these studies will provide us with an increasingly extensive set of clues throughout the hand skeleton to potential manipulative functions in fossil species. With the wealth of new techniques available to us for capturing and analysing data on hand biomechanics, it should be possible to substantially improve our ability to predict these capabilities from the hominin fossil record in the future.

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