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REVIEW

The evolutionary history of the hominin hand since the last common ancestor of *Pan* and *Homo*

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Abstract

Molecular evidence indicates that the last common ancestor of the genus *Pan* and the hominin clade existed between 8 and 4 million years ago (Ma). The current fossil record indicates the *Pan-Homo* last common ancestor existed at least 5 Ma and most likely between 6 and 7 Ma. Together, the molecular and fossil evidence has important consequences for interpreting the evolutionary history of the hand within the tribe Hominini (hominins). Firstly, parsimony supports the hypothesis that the hand of the last common ancestor most likely resembled that of an extant great ape overall (*Pan*, *Gorilla*, and *Pongo*), and that of an African ape in particular. Second, it provides a context for interpreting the derived changes to the hand that have evolved in various hominins. For example, the *Australopithecus afarensis* hand is likely derived in comparison with that of the *Pan–Homo* last common ancestor in having shorter fingers relative to thumb length and more proximo-distally oriented joints between its capitate, second metacarpal, and trapezium. This evidence suggests that these derived features evolved prior to the intensification of stone tool-related hominin behaviors beginning around 2.5 Ma. However, a majority of primitive features most likely present in the *Pan-Homo* last common ancestor are retained in the hands of *Australopithecus*, *Paranthropus*/early *Homo*, and *Homo floresiensis*. This evidence suggests that further derived changes to the hands of other hominins such as modern humans and Neandertals did not evolve until after 2.5 Ma and possibly even later than 1.5 Ma, which is currently the earliest evidence of Acheulian technology. The derived hands of modern humans and Neandertals may indicate a morphological commitment to tool-related manipulative behaviors beyond that observed in other hominins, including those (e.g. *H. floresiensis*) which may be descended from earlier tool-making species.

Key words carpals; comparative anatomy; hand muscles; manual phalanges; metacarpals.

Introduction

To study evolution is to study descent with modification (Darwin, 1859). To examine how morphology has become modified through descent over a particular interval of time, a collection of observable or reliably inferable information must first be assembled. These data are needed to either identify or infer what the morphological conditions were at the beginning of the time interval of interest. If such conditions can be directly identified or indirectly inferred, then there is a working hypothesis regarding the primitive (or ancestral) conditions within the evolutionary lineage under study. This working hypothesis is then used to evaluate the available fossil and comparative evidence in the context of when, where, and possibly why (i.e. selection vs. drift) certain modifications, or derived conditions, evolved.

The tribe Hominini includes all fossil species that are more closely related to modern humans than they are to extant species of the genus *Pan*, and species that belong to this tribe are collectively referred to as hominins (see Wood & Lonergan, 2008, this volume). In this paper, we are charged with reviewing the evolution of hominin hand morphology (the carpals, metacarpals, and phalanges as well as the associated soft-tissue anatomy). Hands account for roughly 25% of all the distinct bones in the adult hominin skeleton and include numerous soft tissue structures,

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making a review that aims to be both thorough and brief impossible. As such, we concentrate our review on a select group of osteological and myological features for which there is reasonably reliable evidence available from comparative and fossil sources.

Our goal is to coherently summarize the anatomy of select features of the hand in extant Hominidae and fossil hominins. This summary includes identifying when and in which hominins morphological changes have likely occurred. These morphological changes are identified by mapping the character evolution onto cladograms based on a phylogeny that incorporates the latest molecular and morphological evidence (Begun, 1992, 1994; Ruvolo, 1997; Gibbs et al. 2000, 2002; Page & Goodman, 2001; Lockwood et al. 2002, 2004; Wimmer et al. 2002; Salem et al. 2003; Eizirik et al. 2004; Uddin et al. 2004; Kumar et al. 2005; Steiper & Young, 2006). To accomplish our goal, we first tentatively infer the morphology most likely present in the last common ancestor (LCA) of the genus *Pan* and the hominin clade (hereafter referred to as the *Pan-Homo* LCA) using relevant comparative information from extant primates, particularly species of *Pongo*, *Gorilla*, *Pan*, and *Homo*. This task is complicated by uncertainties regarding the possible homologous, homoplastic, or homoiologic nature of hand features within the Hominidae, as well as uncertainties regarding the principal locomotor behavior of the *Pan-Homo* LCA. As such, we briefly discuss these uncertainties and the impact they have on the specific hand features which we infer were present in the *Pan-Homo* LCA. Next, we review the hand evidence for *Orrorin*, *Ardipithecus*, *Australopithecus*, *Paranthropus* and early *Homo* (treated here as Hominini gen. et sp. indet. [see Constantino & Wood, 2007]), *Homo floresiensis*, *Homo erectus sensu lato*, *Homo antecessor*, *Homo neanderthalensis*, and *Homo sapiens*. This includes identifying the conditions present in each taxon relative to the *Pan-Homo* LCA. We then combine the evidence from the hominin fossil record with the comparative evidence from modern humans and great apes to reassess our inferences regarding the hand of the *Pan-Homo* LCA. Finally, we conclude with a brief overview of what the current comparative and fossil evidence informs us about the evolutionary history of the hominin hand.

Reconstructing the hand of the *Pan-Homo* LCA

There is currently no fossil representative of the *Pan-Homo* LCA and it is reasonable to assume that one will never be conclusively identified. Thus, morphology of this LCA must be inferred using the principle of parsimony and a hypothesis about the phylogenetic relationships of living and extinct human and nonhuman primates (e.g. Wood Jones, 1916; Keith, 1923; Schultz, 1930; Le Gros Clark, 1940; Straus, 1949; Tuttle, 1974, 1975, 1981; Richmond et al. 2001). The inferential process is based on identifying the morphological conditions in out-groups of closely related species.

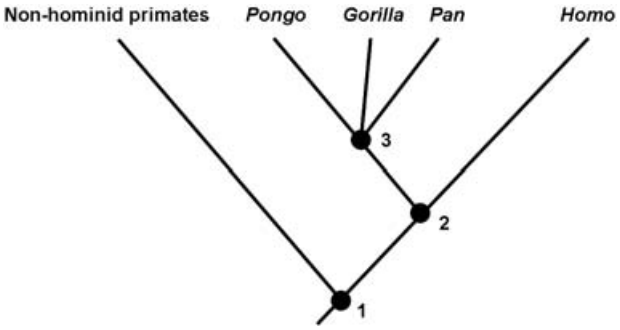

Fig. 1 Cladogram depicting the hominid evolution based on a pre-molecular phylogeny. The morphological conditions in the hypothetical ancestors at Nodes 1 and 2 are unresolved using parsimony (see text).

Prior to using molecular data to address the phylogenetic relationships of extant human and nonhuman primates, the general view was that the great apes formed one clade, Pongidae, and modern humans and their fossil relatives formed another, Hominidae, implying that the human lineage diverged prior to the LCA of the great apes (e.g. Tuttle, 1975). Although phrased here using modern cladistic terminology that was not necessarily formalized at the time, the underlying logic implicit in such a view involves interpreting morphological similarities among the great apes as synapomorphic (shared derived characters) rather than symplesiomorphic (shared primitive characters). A cladogram based on such a phylogenetic view is shown in Fig. 1. At first glance, the hands of the great apes appear more similar to one another than to those of modern humans. Using parsimony and a cladogram based on a pre-molecular phylogeny (Fig. 1), the shared characteristics of the great ape hand are inferred to be present at Node 3, which represents the LCA of the great ape clade. However, note that the most likely conditions present at Nodes 1 and 2 are thus unresolvable (Fig. 1). For example, the condition at Node 2 could be the same as is present in modern humans; it could be the same as is present in extant great apes or it could even be the same as is present in non-hominid primates. Therefore, directions of morphological change in fossil hominin hands are interpreted differently depending on the chosen hypothesis about the likely primitive condition (see Richmond et al. 2001). Using such a cladogram, it is reasonable to infer that modern human hand morphology predates the hypothetical split at Node 2 (e.g. Wood Jones, 1948; Napier, 1970), and explains why Napier (1970: p. 185) suggested 'that the ape hand has no bearing on the evolution of the human hand. The extreme specializations of the hands of the apes, such as the gorillas and chimpanzees, as far as we know took place *after* separation of the hominid and pongid stocks [emphasis Napier's]'.

Substantial evidence now indicates that such interpretations of hominid phylogeny are incorrect. The current

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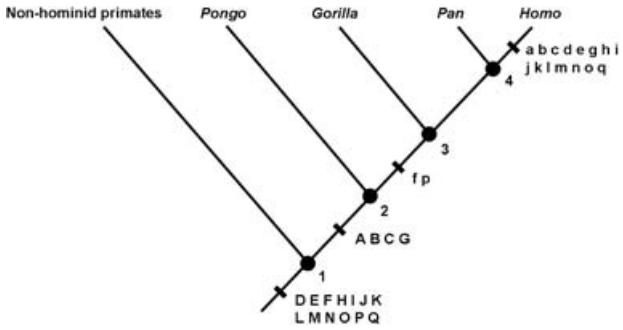

Fig. 2 Cladogram depicting hominid evolution based on a post-molecular phylogeny. The symplesiomorphic conditions present in the hands of the three extant great ape genera enable the morphological conditions in the hypothetical ancestors at Nodes 2, 3, and 4 to be inferred using parsimony (see text). Letters correspond to hypothesized character state changes of the features listed in Table 1.

consensus of molecular and morphological evidence suggests that *Pan* and *Homo* are more closely related to one another than either is to *Gorilla*, and *Homo*, *Pan*, and *Gorilla* are more closely related to each other than they are to *Pongo* (Begun, 1992, 1994; Ruvolo, 1997; Gibbs et al. 2000, 2002; Page & Goodman, 2001; Lockwood et al. 2002, 2004; Wimmer et al. 2002; Salem et al. 2003; Eizirik et al. 2004; Uddin et al. 2004; Kumar et al. 2005; Steiper & Young, 2006; see also Huxley, 1863; Gregory, 1927). This evidence also suggests that the LCA of the *Pan-Homo* clade existed between 8 and 4 Ma, the LCA of African apes and humans existed between 10 and 6 Ma, and the LCA of African apes, humans, and orangutans existed approximately 18 Ma. The cladogram shown in Fig. 2 is based on this current consensus of evidence.

Using the currently informed phylogeny of Hominidae, parsimony indicates that hand morphology shared by all of the extant great apes as well as non-hominid out-groups is almost certainly homologous; therefore, inferences that such morphology was also present in the hand of the *Pan-Homo* LCA (Fig. 2, Node 4) are the strongest. It is also highly probable that hand features shared by *Pongo* and the African apes but not with non-hominids were also present in the hands of the LCAs for Hominidae and Homininae as well as the *Pan-Homo* LCA (Fig. 2, Nodes 2–4). Admittedly, there is fossil evidence that suggests that some of the shared features of the great ape upper limb related to suspensory behaviors may be homoplastic (Pilbeam et al. 1990; Larson, 1998; Kappelman et al. 2003; Moyà-Solà et al. 2004, 2005; Almécija et al. 2007; but see Begun & Ward, 2005; Begun, 2007). If such features are homoplastic, then inferences regarding some of the hand features of the Hominidae LCA would require adjustment (Fig. 2, A, B, F). However, parsimony as well as many phenetic similarities between the hands of modern humans and African apes (rather than Asian apes) suggests it is more likely that the hand of the *Pan-Homo* LCA resembled that of an African ape (Corruccini, 1978; Begun, 1992, 2004; Richmond et al. 2001; Orr, 2005; Tocheri, 2007).

Locomotor behavior of the *Pan-Homo* LCA

Debate over the pre-bipedal locomotor mode for the hominin clade–specifically whether the *Pan-Homo* LCA was a terrestrially adapted knuckle-walker or a primarily arboreal climber/clamberer – may appear to obscure reconstruction of the hand morphology in the *Pan-Homo* LCA. However, this debate involves the functional interpretation of the reconstructed LCA morphology, which logically *follows* the establishment of the character states in question. Reconstructions of the hand morphology of the LCA should rely principally on comparative and fossil data that are independent of functional interpretations of that morphology. A model based on criteria external to the morphological data (e.g. analogies derived from biomechanical or behavioral studies of living primates) should not be adopted to infer the hand morphology of the *Pan-Homo* LCA. Although it might be biomechanically plausible for bipedality to have derived from a purely arboreal, orangutan-like climbing or clambering primate (e.g. Fleagle et al. 1981; Thorpe et al. 2007), this plausibility should not lead to inferences that the hand of the *Pan-Homo* LCA had close morphological affinities with the hands of orangutans. The highly suspensory Asian apes show many hand features that are likely uniquely derived yet independently acquired within the Pongidae and Hylobatidae and are probably directly related to their respective highly specialized locomotor repertoires. However, these features are shared neither with African apes and modern humans nor with non-hominoid primates (Sarmiento, 1988; Lewis, 1989). For example, Asian apes have highly mobile ball-and-socket midcarpal joints that appear to be poorly designed for weight-bearing (Jenkins & Fleagle, 1975; Sarmiento, 1988); orangutans show a radio-ulnarly expanded lunate, a reduced triquetrum, a distally projecting pisiform (Sarmiento, 1988; Lewis, 1989), a more palmarly expanded trapezium-2nd metacarpal joint (Tocheri, 2007), and an extreme degree of phalangeal curvature (Oxnard, 1973; Jungers et al. 1997); and hylobatids have a ball-and-socket-like first carpometacarpal joint (Lewis, 1989).

Hand features shared between modern humans and the African apes are most parsimoniously interpreted as homologies – otherwise they would have evolved independently three times. However, although the demonstration of homology for hand features in African apes and modern humans is a necessary condition for testing the hypothesis that the LCA was a knuckle-walker (Richmond & Strait, 2000; Richmond et al. 2001), it is not by itself a sufficient condition (Orr, 2005). The adaptive link between such features and knuckle-walking must be shown by (1) establishing that such features are derived relative to the morphology of appropriate non-knuckle-walking

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out-groups; (2) demonstrating through functional morphological studies that the features are biomechanically advantageous for the behavior of knuckle-walking relative to the inferred most recent primitive condition; and (3) where possible showing that comparable features evolved independently in animals that use similar locomotor hand postures (e.g. Richmond et al. 2001; Begun, 2004; Orr, 2005). The possibility remains that the hands of *Pan* and *Gorilla* are simply generalized enough to be reasonably exapted for knuckle-walking without having evolved specializations for the behavior (or at least osteological specializations that would be visible in the hominid fossil record). Either way, the hand morphology of the *Pan-Homo* LCA is most parsimoniously interpreted as being very similar to an African ape (Corruccini, 1978; Begun, 1992, 2004; Richmond et al. 2001; Orr, 2005; Tocheri, 2007) whether it was a terrestrial knuckle-walker or not.

The same inferential process holds for testing the suspensory or climbing model for the *Pan-Homo* LCA, but such models have additional challenges because of key similarities between modern human and African ape hand morphology (Corruccini, 1978; Begun, 1992, 2004; Richmond et al. 2001; Orr, 2005; Tocheri, 2007). Thus, based solely on morphological grounds it appears unlikely that the *Pan-Homo* LCA was as highly committed to a climbing and suspensory lifestyle as are extant orangutans and hylobatids. Arguments for such models are primarily based on studies of extant primate locomotor behavior that emphasize the biomechanical similarities of bipedality and certain orthograde suspensory behaviors such as climbing and clambering (e.g. Fleagle et al. 1981; Schmitt, 2003; Thorpe et al. 2007). While such suspensory behaviors may well have characterized the LCA of the Hominidae (Fig. 2, Node 2) (Begun & Ward, 2005; Begun, 2007; but see Moyà-Solà et al. 2004, 2005; Almécija et al. 2007), it is unclear whether they characterized the Homininae LCA as well (Fig. 2, Node 3). Given the many similarities of the African ape and modern human wrist (relative to Asian apes and non-hominoid primates), climbing and suspensory models must not only explain the independent evolution of knuckle-walking behavior in *Pan* and *Gorilla*, but also the evolution of any shared derived features of the African ape-human clade that are absent in closely related out-group taxa that have similar locomotor regimes to that hypothesized for the *Pan-Homo* LCA. For example, if the LCA is predicted to be a mostly arboreal orangutan-like suspensory ancestor (Thorpe et al. 2007), then it must be reasonably explained why modern humans and African apes share prenatal scaphoid-centrale fusion when orangutans and other arboreal suspensory non-hominid primates do not (Fig. 2, e) (Kivell & Begun, 2007).

It is not our specific charge to evaluate the models for the *Pan-Homo* LCA locomotor regime in detail or to review the literature on the functional morphology of the hominid hand in relation to locomotor forelimb postures (see Crompton et al. 2008, this volume; as well as Tuttle, 1967, 1969a,b; Jenkins & Fleagle, 1975; Richmond & Strait, 2000; Richmond et al. 2001; Begun, 2004; Orr, 2005). However, we have tried to consider the ramifications of the competing models in order to provide a reasonable interpretation of hominin hand evolution since the *Pan-Homo* LCA.

Seventeen osteological features most likely present in the hand of the *Pan-Homo* LCA

We have selected 17 osteological features that were most likely present in the hand of *Pan-Homo* LCA (Table 1). This initial reconstruction is based purely on extant comparative data. Many of the selected features are shared by out-groups to the hominins (the Asian apes and in some cases other non-hominid primates), and these features are strongly supported as homologies by parsimony (Fig. 2). Other selections assume that most features shared by *Gorilla* and *Pan* are probably homologous and thus would have appeared in the *Gorilla-Pan-Homo* LCA (Fig. 2, Node 3) and in the *Pan-Homo* LCA (Fig. 2, Node 4). It is possible that such features may be homoplastic in *Pan* and *Gorilla* if they are adaptively related to the shared behavior of knuckle-walking. However, the appearance of these features in the hominin clade would provide very strong evidence of their homology (Richmond & Strait, 2000; Richmond et al. 2001). We have left out several features (e.g. related to the ulnar portion of the wrist, metacarpophalangeal and interphalangeal joint morphology) that we think require more detailed, quantitative morphological assessments before reasonable inferences about their evolution can be made. In certain cases, we have also left out features that have been described as synapomorphies of the African apes such as the 'knuckle-walking ridges' on the metacarpal heads of *Pan* and *Gorilla* (Tuttle, 1967, 1969b). Such features are probably *homoiologies*. Homoiological features mimic potential homologies or homoplasies through phenotypic plasticity via common epigenetic factors such as a common developmental program coupled with a similar mechanical environment (Lycett & Collard, 2005; Collard & Wood, 2007). Finger bones are more likely to display homoiological features than are wrist bones because the behaviorally mediated mechanical environment during growth and development appears to have a significant effect on finger morphology (Richmond, 1998, 2007). Thus, the ridges on the dorsal aspects of the metacarpal heads in the knuckle-walking African apes may result primarily from their respective mechanical environments (Orr, 2005), a notion which is supported by allometric studies indicating that dorsal ridge expression varies with body size in *Pan* and *Gorilla* (Inouye, 1994). Wrist bones appear more constrained developmentally and phylogenetically in primates, which in general are born with cartilaginous wrist morphology that differs little in shape compared with the fully ossified version in the

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Table 1 Character state definitions for the 17 morphological features that are used to examine the evolution of hominin hand morphology. Upper and lowercase letters denote a primitive and derived state respectively within the Hominidae; asterisks (*) denote the inferred condition in the *Pan-Homo* LCA

Feature ID	Features of the thumb and fingers
A	fingers are long relative to length of thumb*
a	fingers are short relative to length of thumb
B	proximal phalanges are curved dorso-palmarly*
b	proximal phalanges are straight dorso-palmarly
C	proximal phalangeal shafts are robust with marked flexor sheaths*
c	proximal phalangeal shafts are gracile with weak flexor sheaths
D	distal phalanges have narrow apical tufts*
d	distal phalanges have broad apical tufts
E	first metacarpal is gracile*
e	first metacarpal is robust
	Features of the wrist and carpometacarpal joints
F	scaphoid and os centrale are two separate bones
f	scaphoid and os centrale form a single bone*
G	thumb is opposable with strongly curved first carpometacarpal joint surfaces*
g	thumb is opposable with less-curved first carpometacarpal joint surfaces
H	trapezium articular surface on the scaphoid does not extend onto scaphoid tubercle*
h	trapezium articular surface on the scaphoid extends onto scaphoid tubercle
I	joint between second metacarpal base and trapezium is oriented more radio-ulnarly*
i	joint between second metacarpal base and trapezium is oriented more proximo-distally
J	trapezoid is wedge-shaped*
j	trapezoid is boot-shaped
K	scaphoid articular surface on the trapezoid is relatively large and more triangular-shaped*
k	scaphoid articular surface on the trapezoid is relatively small and more rectangular-shaped
L	capitate-trapezoid articulation is relatively small and more dorsally placed*
l	capitate-trapezoid articulation is relatively large and more palmarly placed
M	capitate neck has a 'waisted' appearance, particularly on radial side*
m	capitate neck has an expanded appearance, particularly on radial side
N	joint between second metacarpal base and capitate is oriented more radio-ulnarly*
n	joint between second metacarpal base and capitate is oriented more proximo-distally
O	no styloid process at base of third metacarpal*
o	large styloid process at base of third metacarpal
P	relatively narrow midcarpal joint (capitate and hamate)
p	relatively broad midcarpal joint (capitate and hamate)*
Q	pisiform is relatively long and more rod-shaped*
q	pisiform is relatively short and more pea-shaped

adult (Čihák, 1972; Lewis, 1989; Stafford & Thorington 1998; Scheuer & Black, 2000; Kivell & Begun, 2007).

Throughout our review of the fossil hominin hand material, we map character state changes *vis-à-vis* the inferred primitive condition in the *Pan-Homo* LCA onto current cladistic hypotheses of hominin species relationships. In the discussion section, we then revisit our initial reconstruction of the hand in *Pan-Homo* LCA in light of the fossil evidence.

Eight myological features most likely present in the hand of the *Pan-Homo* LCA

We have selected eight muscular features of the hand that were most likely present in the *Pan-Homo* LCA (Table 2) using available information on the comparative myology of the hand in the great apes and modern humans. Inferences about the most likely condition of the hand musculature in the *Pan-Homo* LCA also represent the probable primitive condition for the hominin clade. Obviously, the fossil record cannot provide as much detailed information regarding soft-tissue structures as it does hard-tissue structures. As such, we postpone the discussion of these muscular features until after the fossil evidence has been reviewed. We then provide examples of how evolutionary modifications in hard-tissue features are possibly linked with modifications of the soft tissue, such that more specific muscle features and mechanics may be reasonably inferred in fossil hominin taxa.

The evolution of the hominin hand as evidenced by the fossil record

Using parsimony and a cladogram based on the current consensus hominid phylogeny, it is reasonable to infer

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Table 2 Muscular characters that were likely present in the hand of the *Pan-Homo* LCA in comparison with the derived condition present in modern humans

Muscle or myological character	Inferred condition of the *Pan-Homo* LCA	Derived condition in modern humans	What can be said from fossil evidence
Abductor pollicis longus	Inserts strongly into the base of the trapezium, trapezoid, and scaphoid and variably into the base of the first metacarpal. Its largest potential torque is probably in flexion (see **Discussion**).	Insertion is almost exclusively into the base of the pollical metacarpal and its largest potential torque is in extension (see **Discussion**).	Little can be inferred, but it may be possible to identify carpal insertion markings. Changes in the mechanics of the muscle mechanics may be identifiable based on carpal geometry.
Adductor pollicis (oblique and transverse heads)	Probably a relatively small PCSA* for the oblique head, but the dimensions of the muscle have not been measured in other apes. Both the transverse and oblique heads probably act as extensors and adductors of the trapeziometacarpal joint (see **Discussion**).	Relatively enlarged PCSA* for the oblique head. Both heads primarily act as flexors of the trapeziometacarpal joint (see **Discussion**).	The derived mechanics of this muscle may be identifiable based on carpal geometry, but more research is required (see **Discussion**).
Flexor pollicis brevis	Single superficial head that originates from the trapezium.	Expansion of superficial head origin to the flexor retinaculum; distinct deep head originates from the trapezoid, capitate and palmar ligaments.	Little can be inferred. It may be possible to identify carpal insertion markings for the derived deep head, but more likely such markings will be difficult to distinguish.
Flexor pollicis longus	Absent, degenerate or ligamentlike tendon slip with no separation of belly from the flexor digitorum profundus.	Distinct muscle belly and strong tendinous insertion into distal pollical phalanx.	Derived condition is probably difficult to determine from distal pollical phalanges (see **Discussion**).
Opponens pollicis	Probably a relatively small PCSA*, but the muscle's dimensions have not been measured in other apes.	Relatively enlarged (PCSA* approximately twice that of *Pan*).	Little can be inferred. The relationship between PCSA* and the muscle marking for the opponens pollicis on the lateral aspect of the pollical metacarpal shaft should be explored.
Forearm flexor mass relative to forearm extensor mass	Flexors > Extensors	Flexors = Extensors	Little can be inferred. With future work it may be possible to predict forearm muscle masses from bony markings. See **Discussion** regarding skeletal correlates of the flexor digitorum superficialis.
Dorsal interossei	First dorsal interosseus first metacarpal origin mostly restricted to proximal portion of pollical metacarpal shaft.	First dorsal interosseus has expanded distal origin along the pollical metacarpal shaft and covers a large area.	The derived condition can be identified in the fossil record (see **Discussion**).
Palmar interossei	First palmar interosseus absent	First palmar interosseus present	Little can be inferred. It may be difficult to distinguish palmar interosseus markings from those of the dorsal interosseus.

*PCSA, physiological cross-sectional area. This is an estimate of the number of muscle sarcomeres acting in parallel and is therefore directly proportional to the tension-production capability of a muscle (see Marzke et al. 1999).

many features that probably characterized the hand of the *Pan-Homo* LCA (Figs 2, 3; Tables 1, 2). Because there is sufficient fossil and comparative evidence for these 17 features, the likely conditions present at particular nodes within the hominin clade can also be reasonably resolved. The hand of the *Pan-Homo* LCA (Figs 2, 4, Node 4) most likely resembled that of an extant African ape overall, or at the very least it likely shared most, if not all, of the

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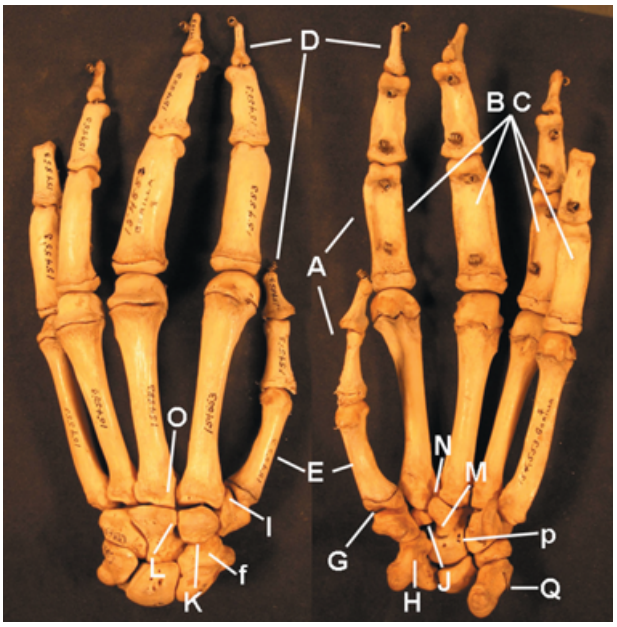

Fig. 3 Visual representation of the 17 inferred morphological features that were most likely present in the hand of the *Pan-Homo* LCA (the letters correspond with list in Table 1). The left hand of an adolescent *Gorilla gorilla* is shown in dorsal (at left) and palmar views (at right). Photograph by Matt Tocheri.

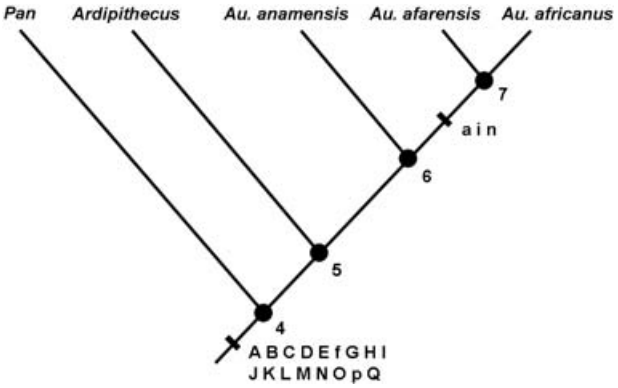

Fig. 4 Cladogram depicting the evolution of hand morphology in the earliest hominins. The hypothetical ancestor at Node 7 is likely derived in comparison with the hypothetical ancestor at Node 4 with respect to three synapomorphic features of *Au. afarensis* and *Au. africanus* (see text). This information suggests that 15 features are likely primitive in the hypothetical ancestors at Nodes 6 and 5 – the conditions of features a and i remain unresolved at these Nodes.

characteristics that are symplesiomorphic among the extant great apes (all except f because it is shared only among African apes and modern humans) (Fig. 3; Table 1). Thus, we have clearly stated our working hypothesis against which we now interpret the fossil evidence.

Ardipithecus, Orrorin, and *Sahelanthropus*

The earliest known fossil hominin genera currently include *Ardipithecus* (White et al. 1994; Haile-Selassie, 2001; Semaw et al. 2005), *Orrorin* (Senut et al. 2001; Pickford et al. 2002; Sawada et al. 2002), and *Sahelanthropus* (Brunet et al. 2002). Postcranial material has been recovered for *Orrorin* and *Ardipithecus*, both of which preserve some fossil evidence of manual phalangeal morphology (Haile-Selassie, 2001; Senut et al. 2001; Semaw et al. 2005; Gommery & Senut 2006). This evidence includes a fragmentary juvenile proximal phalanx (BAR 349'00) (Senut et al. 2001) and an adult distal thumb phalanx (BAR 1901'01) (Gommery & Senut, 2006) attributed to *Orrorin*. Material attributed to *Ardipithecus* includes the distal halves of an intermediate (ALA-VP-2/11) and proximal (DID-VP-1/80) phalanx (Haile-Selassie, 2001), as well as a nearly complete proximal phalanx (GWM-10/P1) and fragments of an intermediate (GWM-5SW/P58) and proximal (GWM-3/P2) phalanx (Semaw et al. 2005).

In comparison with the inferred morphology of the *Pan-Homo* LCA, all of the proximal phalanges attributed to these two hominin genera retain the primitive dorso-palmarly curved condition (Table 1, B). The *Ardipithecus* proximal phalanges are also described as having slightly less well-developed flexor ridges than *Australopithecus afarensis* (Haile-Selassie, 2001; Semaw et al. 2005), which would still correspond with the inferred condition in the *Pan-Homo* LCA (Table 1, C), and the intermediate phalanx also shows marked ridges (Haile-Selassie, 2001). Gommery & Senut (2006) suggest that the distal thumb phalanx of *Orrorin* has an expanded apical tuft (Table 1, d), which represents a derived condition relative to that inferred for the *Pan-Homo* LCA.

Australopithecus

Fossil hand remains have been attributed to *Australopithecus anamensis* (Leakey et al. 1998; Ward et al. 1999b), *Australopithecus afarensis* (Bush et al. 1982; Johanson et al. 1982; Ward et al. 1999a; Drapeau et al. 2005), and *Australopithecus africanus* (Broom & Schepers, 1946; Clarke, 1999). There are more hand fossils for *Au. afarensis* than for either of the other two taxa, but the hand fossils attributed to *Au. anamensis* and *Au. africanus* are broadly similar to *Au. afarensis*. In total, these fossils provide considerable information regarding hominin hand evolution during the first few million years of hominin evolution following the *Pan-Homo* split (Fig. 4).

In comparison with the inferred morphology of the *Pan-Homo* LCA, the *Australopithecus* hand exhibits derived features. Firstly, the fingers of *Au. afarensis* are short, relative to the length of the thumb (Marzke, 1983; Alba et al. 2003). A similar derived condition has also been shown to occur in *Au. africanus* (Green & Gordon, in press) and has been reported for the nearly complete hand of Stw 573, attributed to *Au. africanus* by Clarke (1999).

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Second, the capitates of both *Au. afarensis* (A.L. 288-1w, A.L. 333-40, KNM-WT 22944-H) and *Au. africanus* (TM 1526) no longer exhibit a radio-ulnarly oriented articulation for the base of the second metacarpal (Lewis, 1973; Marzke, 1983; McHenry, 1983; Ward et al. 1999a; Tocheri et al. 2007b). Instead, this articular surface is oriented more disto-laterally in these two species (Lewis, 1973; Marzke, 1983; McHenry, 1983; Ward et al. 1999a; Tocheri et al. 2007b). Although this is not strictly identical to the derived condition observed in modern humans (Table 1, n), for our purposes here it is simpler to group both derived states together. The second metacarpal bases (A.L. 333-15, A.L. 333-48, A.L. 333w-23, A.L. 438-1e, A.L. 438-1f, Stw 382) for these two taxa show reciprocal morphology for the articulation with the capitate (Marzke et al. 1992; Drapeau et al. 2005; Tocheri, 2007). The *Au. anamensis* capitate (KNM-KP 31724), however, retains the primitive condition seen in African apes (Leakey et al. 1998; Ward et al. 1999b), which is the condition inferred for the *Pan-Homo* LCA. Therefore, the current fossil evidence suggests that this particular modification of the capitate-second metacarpal joints in *Au. afarensis* and *Au. africanus* may have evolved between approximately 4.2 and 3.5 Ma, given the currently accepted East African dates for *Au. anamensis* and *Au. afarensis* (Leakey et al. 1998; Ward et al. 1999b).

Third, the joint between the second metacarpal base and the trapezium in *Au. afarensis* and *Au. africanus* no longer exhibits the primitive radio-ulnar orientation (Marzke, 1983, 1997; Tocheri et al. 2003; Drapeau et al. 2005; Tocheri, 2007). Instead, the joint is oriented more proximo-distally (Table 1, i); this derived condition is observed from a trapezium (A.L. 333-80) and the second metacarpal bases listed above (Marzke, 1983, 1997; Tocheri et al. 2003; Drapeau et al. 2005; Tocheri, 2007) and from a single second metacarpal base (Stw 382) attributed to *Au. africanus* (Tocheri, 2007; David Green, personal communication).

Finally, a distal pollical phalanx from Sterkfontein (Stw 294) displays a broad apical tuft (Table 1, d) (Ricklan, 1990), which differs from the narrow apical tufts of two *Au. afarensis* distal non-pollical phalanges (Table 1, D) (Bush et al. 1982). In this regard, Stw 294 may share some similarities to BAR 1901'01 (Gommery & Senut 2006) but more distal pollical phalanges from early hominins are necessary for more complete evaluation. However, setting aside the difficulties interpreting distal phalangeal morphology in primates (Mittra et al. 2007), the current fossil evidence for the genus *Australopithecus* suggests that the remaining 13 features of the hand are essentially unchanged from the inferred primitive conditions in the *Pan-Homo* LCA (Table 1; Fig. 3). *Australopithecus* shows curved proximal phalanges like those seen in *Orrorin* and *Ardipithecus* with marked flexor sheaths (Table 1, B, C) (Bush et al. 1982; Susman, 1988a,b; Haile-Selassie, 2001; Senut et al. 2001; Semaw et al. 2005), and gracile first metacarpals (Table 1, E) (Bush et al. 1982; Susman, 1994; Smith, 2000). Their first carpometacarpal joint surfaces are strongly curved (Table 1, G) (Tocheri, 2007), their capitate necks are 'waisted' on the radial side (Table 1, M) (Lewis, 1973; Bush et al. 1982; McHenry, 1983), their third metacarpals and capitates show no evidence of a styloid process (Table 1, O; Bush et al. 1982; Marzke, 1983; McHenry, 1983; Marzke & Marzke, 1987; Drapeau et al. 2005), and their pisiforms are long and rod-shaped (Table 1, Q; Bush et al. 1982). Although no scaphoids or trapezoids have been described for *Australopithecus*, the surrounding anatomy observed on the trapezium, second metacarpal bases, and capitates all suggest that features f, H, J, K, and L also remain primitive (Tocheri, 2007) – an indirect inference that is supported by direct evidence from OH 7 and *H. floresiensis* (Tocheri et al. 2007a,b), which are described below. Finally, the articulating capitates and hamates of A.L. 333 (-40, -50) and KNM-WT 22944 (-H, -I) each form a relatively broad midcarpal joint, which also corresponds to the primitive condition inferred for the *Pan-Homo* LCA (Table 1, p) (Richmond, 2006).

Therefore, in total the *Australopithecus* hand provides supportive evidence that the morphology for the *Pan-Homo* LCA inferred from extant comparative anatomy is probably correct. As additional hand fossils are recovered from other hominins that predate 2.5 Ma, they should also show the primitive conditions for these 13 features, unless they (or *Australopithecus*) have become uniquely derived (i.e. autapomorphic) at some point along their respective lineages.

Hominini gen. et sp. indet. (*Paranthropus* and early *Homo*)

Paranthropus and *Homo* appear in the fossil record at approximately the same time as the earliest archaeological evidence of stone tools (Semaw et al. 1997; de Heinzelin et al. 1999; Constantino & Wood, 2007). As such, *Paranthropus* and early species of *Homo* have played prominent roles in the debate over hand morphology, function, and behavior (Napier, 1962; Susman, 1988a,b, 1989, 1991, 1994, 1995, 1998; Marzke et al. 1992; Hamrick & Inouye, 1995; Ohman et al. 1995; Marzke, 1997; Panger et al. 2002).

There are over 20 hand fossils from Swartkrans (Susman, 1988b). Of these, two first metacarpals (SK 84 and SKX 5020), a distal pollical phalanx (SKX 5016), and a proximal phalanx (SKX 5018) have received the most attention (Napier, 1959; Rightmire, 1972; Susman, 1988a). From Olduvai, 13 hand fossils remain attributed to OH 7 of the original 21 fossils recovered (Day, 1976; Susman & Creel, 1979).

A critical point to emphasize is that, of all the hominin hand fossils that date between roughly 2.5 and 1.5 Ma, none is known with absolute certainty to belong to one hominin species rather than another (Wood & Collard, 1999; Constantino & Wood, 2007; see also Wood, 1974).

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Although Susman (1988a,b) argues that certain hand fossils from Swartkrans belong to *Paranthropus robustus*, these could also reasonably belong to *Homo* cf. *erectus* as both hominin genera are represented at this South African site (Trinkaus & Long, 1990). Similarly, the OH 7 hand fossils from Olduvai could reasonably belong to *Paranthropus boisei*, considering the OH 5 (*'Zinjanthropus'*) cranium was recovered within a few hundred meters along with other postcranial remains loosely attributed to *P. boisei* (Leakey et al. 1964; Leakey, 1971; Wood, 1974; Day, 1976; Constantino & Wood, 2007). Moreover, there is also the real possibility that other species of catarrhine or even hominid are also represented at these sites, and it is not always straightforward to differentiate isolated primate hand bones from one another, phalanges in particular (Begun, 1993).

The aforementioned issues notwithstanding, these fossils provide details about hominin hand morphology between approximately 2.0 and 1.5 Ma (Leakey et al. 1964; Leakey, 1971; Vrba, 1982). Assuming that the character states for the 17 features examined here that are present (or inferred) in *Au. afarensis* represent the primitive state for all later hominins, then we should expect to see a similar pattern of morphology in hominins from the Late Pliocene and Early Pleistocene, albeit with the possibility of exhibiting derived modifications in their hand structure. Notice that this is different than trying to find 'modern human-like' characteristics in these hominins (e.g. to infer manipulative capabilities). Instead, we work back to the closest node along the hominin lineage to determine whether a particular morphological feature is modified relative to its most likely primitive condition. In this case, the question is whether the fossil evidence differs from the primitive condition, which we infer to be the hand morphology seen in *Au. afarensis*, *Au. africanus*, and inferred in the LCA at Node 7 (Fig. 4).

Evaluating the fossil evidence in this way suggests that these particular hand fossils exhibit a combination of primitive and derived features. For example, the two distal phalanges of the thumb (SKX 5016 and OH 7-A) are similar to one another and both show broad apical tufts (Susman & Creel, 1979; Susman, 1988b; Smith, 2000). However, OH 7-A may belong to the foot (Susman & Creel, 1979). Other manual distal phalanges from both Swartkrans (SKX 8963, SKX 27504) and Olduvai (OH 7-B, C) also show broader apical tufts relative to the primitive condition (Susman & Creel, 1979; Susman, 1988b). In terms of phalangeal curvature, the included angle data for proximal phalanges suggest that while some specimens (SKX 5018, SKX 22741) are less curved than *Au. afarensis* proximal phalanges, others (SKX 27431, Stw 28) are within the range observed in *Au. afarensis* (Susman, 1988b). The proximal (OH 7-H, I) and middle phalanges (OH 7-D, E, F, G) of the Olduvai hand are also described as retaining primitive, African ape-like morphology (Susman & Creel, 1979).

Two first metacarpals and one third metacarpal provide additional information. The gracility (Table 1, E) (Napier, 1959; Rightmire, 1972) and strongly-curved trapezium articular surface (Table 1, G) (Tocheri, 2007) of SK 84 are primitive features. In contrast, SKX 5020 is robust (Table 1, e) (Susman, 1988a,b) and has a flatter trapezium joint surface relative to the primitive condition (Table 1, g) (Tocheri, 2007). The taxonomically unidentified third metacarpal base (SKX 3646) from Swartkrans Member 2 is described as displaying a 'faint styloid process' (Susman, 1988b: p. 162) and the accompanying published photographs suggest it probably retains morphology more similar to the primitive condition (Table 1, O).

With regard to wrist morphology, the fossil evidence for this time period includes a capitate (OH 7-R), scaphoid (OH 7-P), trapezium (OH 7-Q), and a triquetrum (SKX 3498). The triquetrum has been briefly described but more thorough comparative descriptions or analyses of hominid triquetrum morphology are needed to evaluate this specimen's morphological affinities (Susman, 1988b). The scaphoid exhibits primitive African ape-like morphology (e.g. the centrale is completely incorporated into the scaphoid proper [Table 1, F] and the articular surface for the trapezium does not extend onto the tubercle [Table 1, H] [Susman & Creel, 1979; Lewis, 1989; Tocheri, 2007; Tocheri et al. 2007b]). The trapezium exhibits an extremely flat first metacarpal articular surface (Table 1, g) (Trinkaus, 1989; Tocheri, 2007), which is derived in comparison with *Au. afarensis* and the *Pan-Homo* LCA, while the articular surface for the second metacarpal is oriented more radio-ulnarly (Table 1, I) (Napier, 1962; Lewis, 1989; Tocheri et al. 2003; Tocheri, 2007), which is the inferred primitive condition in the *Pan-Homo* LCA. Thus, this latter feature in OH 7 may represent (1) a reversal to the primitive state, (2) the presence of a fossil lineage that diverged prior to the split of *Australopithecus*, or (3) the condition in *Au. afarensis* and *Au. africanus* is not homologous with the condition observed in modern humans. The combination of primitive and derived morphology has previously prompted doubts as to whether the OH 7 trapezium actually belonged to a hominin (Tocheri et al. 2003; Tocheri, 2007). However, recent inspection of the original OH 7 hand fossils by one of us (MWT) suggests that the trapezium and scaphoid are most likely elements of the same hand (e.g. the articulating surfaces are extremely well-matched and both fossils show similar damage patterns to their dorsal non-articular surfaces suggesting the damage likely occurred while they were still articulated). The capitate from Olduvai is from a left hand (the trapezium and scaphoid are from a right hand) and is not well preserved (Napier, 1962; Susman & Creel, 1979). It appears comparatively proximo-distally short relative to the expected size as reflected by the trapezium and scaphoid and is most likely from a smaller individual than the trapezium and scaphoid. Although its poor preservation has precluded

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most investigators from making any firm assessments of its morphology, Lewis (1973) has argued that it appears most similar to that of an African ape.

The current fossil evidence available for Hominini gen. et sp. indet. suggests the following conclusions. The hands of these hominins are likely derived from the condition in the *Pan-Homo* LCA (and *Au. afarensis*) in features that relate to the distal phalanges of the thumb and fingers (i.e. they tend to have broader apical tufts in comparison with the primitive condition; however, recall the broad distal pollical phalanges described for *Orrorin* [Gommery & Senut, 2006] and *Au. africanus* [Ricklan, 1990]). SKX 5020, a robust first metacarpal with a flatter proximal articular surface relative to the primitive condition (Susman, 1988a,b; Tocheri, 2007), and the OH 7 trapezium, with its extremely flat first metacarpal surface (Trinkaus, 1989; Tocheri, 2007), together provide evidence that modifications have occurred to the more proximal portions of the thumb as well. However, several fossil elements (e.g. the OH 7 scaphoid, SK 84 first metacarpal) retain evidence of primitive features that are either observed or inferred in earlier hominins such as *Australopithecus* and the *Pan-Homo* LCA.

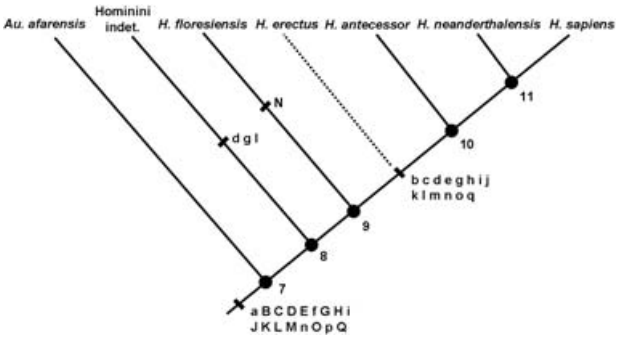

Fig. 5 Cladogram depicting the evolution of hand morphology in the genus *Homo*. The hypothetical ancestors at Nodes 10 and 11 are derived in comparison with the hypothetical ancestors at Nodes 7, 8, and 9 with respect to the majority of features examined. The conditions present in *H. erectus* remain unresolved (see text).

Homo floresiensis

The recent discovery of a hominin species on the Indonesian island of Flores adds significantly to our knowledge of early hominin wrist morphology despite the fact that this material dates to only 0.018 Ma (Brown et al. 2004; Morwood et al. 2004, 2005; Tocheri et al. 2007a,b). Although its relationships to other hominin taxa remain a topic of lively debate, there is little doubt that the morphology of its partially preserved wrist is remarkably primitive (Tocheri et al. 2007a,b). Two additional facts underscore the importance of the *H. floresiensis* partial wrist to our understanding of early hominin hand evolution. Firstly, with four articulating elements preserved, it is the most complete primitive hominin wrist recovered from a single individual (LB 1). Second, it was recovered in direct association with cranio-dental and additional postcranial material (Brown et al. 2004; Morwood et al. 2004, 2005; Tocheri et al. 2007b), an otherwise rare occurrence in the hominin fossil record.

The scaphoid (LB 1-44) has a congenitally fused centrale (Table 1, F) (Tocheri et al. 2007a,b), which is a synapomorphy of the *Gorilla-Pan-Homo* clade (Huxley, 1863; Begun, 1992; Richmond et al. 2001; Kivell & Begun, 2007). The articular surface for the trapezium on the scaphoid does not extend out onto the scaphoid tubercle (Table 1, H) (Tocheri et al. 2007a,b). No scaphoids have yet been described for any hominin dating to 2 Ma or older, but overall the LB 1 and OH 7 scaphoids are similar to those of African apes. This evidence suggests that all hominin species descended from the hypothetical ancestors present at Nodes 4 through 9 (Figs 4, 5) will also likely show similar scaphoid morphology, unless the scaphoid has become uniquely derived (autapomorphic) within a particular hominin lineage. The scaphoid articular facets on the trapezium and capitates of *Australopithecus*, which suggest a primitive scaphoid shape, are consistent with such an assessment.

The trapezoid (LB 1-47) is wedge-shaped (Table 1, J) and its articulation with the capitate (LB 1-45) is relatively small and more dorsally placed (Table 1, L) (Tocheri et al. 2007a,b). The radial side of the capitate neck is 'waisted' (Table 1, M) and the articular surface for the second metacarpal base is oriented more radio-ulnarly (Table 1, N) (Tocheri et al. 2007a,b). All of these features are remarkably similar to those of extant great apes in general, and African apes in particular (McHenry, 1983; Lewis, 1989; Tocheri et al. 2005, 2007). Again, this suggests that all hominin species descended from the hypothetical ancestors present at Nodes 4 through 9 (Figs 4, 5) will also likely show similarly primitive wrist morphology. The radio-ulnar orientation of the capitate-second metacarpal joint of LB 1 (Table 1, N), however, raises an important issue. This is the second fossil wrist bone (the other is the OH 7 trapezium) to exhibit a primitive joint configuration with the second metacarpal base. Recall that *Au. afarensis* and *Au. africanus* (but not *Au. anamensis*) show configurations that are derived relative to *Pan*, *Gorilla*, and the *Pan-Homo* LCA. These two derived features in *Australopithecus* have generally been considered synapomorphies with modern humans, but the OH 7 trapezium and the LB 1 capitate indicate that more fossil and comparative evidence is necessary to resolve the polarity of these particular characters as well as test whether they are in fact homologous in *Australopithecus* and modern humans.

Although descriptions of the incomplete hamate (LB 1-46) and metacarpal shaft (LB 1-59), as well as several hand phalanges (LB 1-40, -42, -48 , -49, -55), remain unpublished at present, these elements will likely shed further light not only on the hand of *H. floresiensis* but also

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inferentially regarding the hands of earlier hominin lineages.

In total, the relatively complete scaphoid, trapezoid, and capitate of *H. floresiensis* enable the resolution of several conditions present in the hand of the hypothetical ancestor at Node 8 (Fig. 5), which corresponds to the origin of the genus *Homo* (and perhaps *Paranthropus*) as presently defined (Wood & Collard, 1999; Wood & Richmond, 2000). These primitive hand features were also probably present in the hypothetical ancestors at Nodes 4 through 9 (Figs 4, 5), which include the *Pan-Homo* LCA.

Homo erectus sensu lato

The hand remains attributed to *H. erectus sensu lato* include two probable first metacarpals (KNM-WT 15000-BU and BV), a proximal pollical phalanx (KNM-WT 15000-BQ), a middle phalanx (KNM-WT 15000-BO), and a lunate (Weidenreich, 1941; Walker & Leakey, 1993). KNM-WT 15000 is a juvenile individual and each of its recovered hand elements is missing its proximal epiphysis (Walker & Leakey, 1993). Walker & Leakey (1993) are not certain that the first metacarpals actually belong to KNM-WT 15000, but they suggest these bones closely resemble juvenile modern human first metacarpals. At present, neither the proximal pollical phalanx (which may be from the foot [Brian Richmond, personal communication]) nor the lunate offers much information regarding the primitive or derived nature of their morphology because of the lack of comparative information on these elements. A similar conclusion applies to the first metacarpals given their lack of maturity and questionable taxonomic attribution. The shaft of the middle phalanx, however, is described as 'only very slightly curved', which implies a similar derived morphology as observed in some of the hominin hand material dated between roughly 2.0 and 1.5 Ma (Walker & Leakey, 1993: p. 138).

The limited fossil evidence for the hand of *H. erectus* and the questionable taxonomic and anatomical attribution of some of the elements results in a most unfortunate gap in our current knowledge of hominin hand evolution. This gap is emphasized because the hominin species that precede *H. erectus* generally exhibit an overall symplesiomorphic pattern of hand features, whereas the hominins that follow *H. erectus* exhibit a synapomorphic pattern (except *H. floresiensis*). For this reason, we cannot reasonably infer the hand morphology of this taxon; only further fossil discoveries can shed light on this likely important stage in the recent evolution of the hominin hand.

Modern humans, Neandertals, and *Homo antecessor*

In the hominin fossil record, the hand is well represented for Neandertals. Over 100 hand bones are preserved among the nine specimens from Shanidar Cave in Iraq, including an almost complete left hand belonging to Shanidar 4 (Trinkaus, 1983). The Kebara 2 specimen also preserves both hands and each is remarkably complete and well-preserved (Arensburg et al. 1985; Bar-Yosef et al. 1992). Previous studies have identified morphological differences between the hands of modern humans and Neandertals, mostly with regard to bone robusticity, carpometacarpal joint configurations, and the inferred mechanical advantages of certain muscles (Musgrave, 1971; Trinkaus, 1983; Trinkaus et al. 1991; Niewoehner et al. 1997; Niewoehner, 2000, 2001, 2005). More recently, Niewoehner (2006) compared Neandertal hand remains to those of modern humans and Late Pleistocene humans, including Early and Late Upper Paleolithic peoples as well as the Skhūl/Qafzeh sample. In these quantitative and qualitative comparisons, Niewoehner (2006) identifies a suite of morphological differences between modern human and Neandertal hands, most of which he summarizes into four carpometacarpal regions. These include (1) the first carpometacarpal joint, which appears dorso-palmarly flatter in Neandertals because of a lack of palmar beak development on the first metacarpal; (2) the second carpometacarpal joints, which in Neandertals include a more proximo-distally oriented joint between the trapezium and second metacarpal base, a flatter joint between the trapezoid and second metacarpal, and a joint between the capitate and second metacarpal that is oriented 'parasagittally in the coronal plane' (Niewoehner, 2006: p. 176); (3) a relatively larger joint between the capitate and third metacarpal in Neandertals with a smaller styloid process; and (4) a flatter and relatively smaller joint between the hamate and fifth metacarpal in Neandertals. However, Early and Late Upper Paleolithic human hands tend to fall in between modern human and Neandertal hands, although mostly they appear more similar to modern humans (Niewoehner, 2006). Therefore, we have no way of knowing which of these features were more likely present in the human-Neandertal LCA, an unfortunate fact which is confounded further due to the paucity of information about the hands of *H. erectus sensu lato* and other Middle Pleistocene hominins. However, all of the morphological differences noted by Niewoehner (2006) and others ultimately still suggest that modern human and Neandertal hands share an overall pattern of morphology that is derived in comparison with that of earlier hominins. Thus, here we focus primarily on identifying the pattern of derived features that modern human and Neandertal hands share relative to earlier hominins and the *Pan-Homo* LCA such that the morphology of their LCA can be reasonably inferred.

The hands of modern humans and Neandertals share several morphological features that are uniquely derived in comparison with earlier hominin species (Figs 5, 6) (Niewoehner, 2006; Tocheri, 2007; Tocheri et al. 2007a,b). Both of these species of *Homo* are derived in all of the

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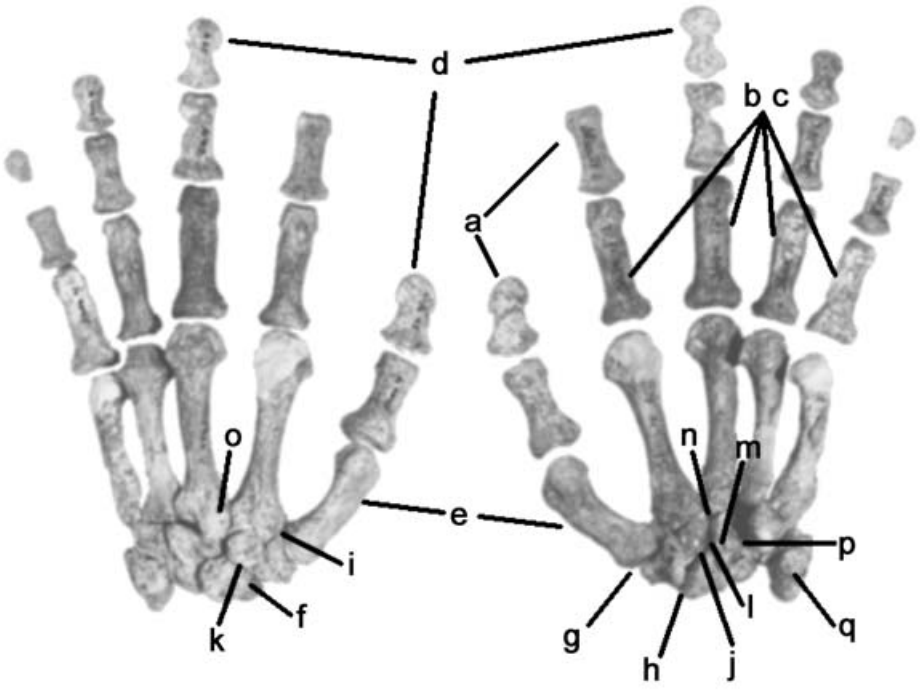

Fig. 6 Visual representation of the derived morphological features in the hands of modern humans and Neandertals (the lowercase letters correspond with list in Table 1). The left hand of Shanidar 4 (*H. neanderthalensis*) is shown in dorsal (at left) and palmar views (at right) (adapted from Trinkaus, 1983).

features listed in Table 1 (except f and p, for which they retain the condition that is inferred for the *Pan-Homo* LCA) in comparison with the *Pan-Homo* LCA. These shared derived features suggest it is reasonable to infer that they were inherited from the modern human-Neandertal LCA. The inference of common inheritance of these features is corroborated in part by fossil evidence from the Gran Dolina site at Sierra de Atapuerca (Lorenzo et al. 1999). The hand remains from this site, attributed to *H. antecessor*, were recovered from the Early Pleistocene level TD6, which dates to between 0.78 and 0.857 Ma (Falgueres et al. 1999). The recovered proximal phalanges are relatively straight (Lorenzo et al. 1999) representing direct evidence of this derived feature in hominins (Table 1, b), which as mentioned above may have appeared earlier in hominin evolution.

The capitate (ATD6-24) attributed to *H. antecessor* is described as closely resembling modern human and Neandertal capitates (Lorenzo et al. 1999). The angle between its second and third metacarpal joint surfaces is similar to that in modern humans and the trapezoid joint surface is enlarged and palmarly placed (Lorenzo et al. 1999), both of which are derived features shared among modern humans and Neandertals (Lewis, 1989; Tocheri, 2007; Tocheri et al. 2007a,b). The capitate lacks evidence of radial beveling on the dorso-distal border, suggesting that the third metacarpal styloid process was either small or non-existent (Lorenzo et al. 1999). Although it would be preferable to have corroborative evidence from a third metacarpal base, Lorenzo et al.'s (1999) description suggests that the styloid process seen in modern humans and Neandertals evolved either after the LCA shared with *H. antecessor*, or has evolved independently in both lineages. Lorenzo et al. (1999) noted that this capitate also displays a small, dorsally placed articulation for the trapezoid and concluded that 'ATD6-24 is the most ancient fossil with a morphology of the trapezoid facet transitional between *Australopithecus* and later *Homo*' (Lorenzo et al. 1999: p. 509). However, this facet pattern is well-documented in modern humans (Lewis, 1989: p. 81, Fig. 5.18B; Tocheri, 2007). The derived hominin condition is an enlarged, palmarly placed joint between the trapezoid and capitate regardless of whether an articular surface is retained dorsally (Table 1, l) (Lewis, 1989; Tocheri, 2007); this is, in part, due to the combined effects of the shape change of the trapezoid from a primitive pyramidal wedge-shape (which by definition cannot have an enlarged, palmarly placed articular surface) to a derived boot-shape. Unfortunately, we simply do not know whether the derived trapezoid shape evolved prior to the derived articular configuration or both features evolved together as a unit; hence, there is currently no way of predicting what the morphology of a 'transitional' hominin should look like.

In total, the morphological evidence from modern humans and Neandertals suggests that these two species

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of *Homo* share a suite of derived hand features. Current genetic evidence suggests that the modern human-Neandertal LCA existed between 0.5 and 1.0 Ma (Noonan et al. 2006), while fossil evidence for some of these derived features is also seen in *H. antecessor* (Lorenzo et al. 1999: p. 509). Together, this evidence suggests that most, if not all, of these derived features probably evolved at least as early as 0.8 Ma (Tocheri, 2007).

Derived myological features and mechanics of the hominin hand

Several aspects of the modern human hand musculature appear derived in relation to the inferred condition of the LCA with *Pan* (Table 2). In this section, we indicate the likelihood of fossils providing evidence about the evolution of muscle morphology in hominins. In some cases, features may reflect the presence, absence or relative size of a particular muscle, whereas in other cases, bone morphology may influence muscular mechanics by altering the direction or path of tendons relative to the inferred primitive condition.

Compared to the extant great apes, modern human extrinsic flexor and extensor muscles of the hand are more balanced in size (Tuttle, 1969a), and the long digital flexors of the second through fifth digits are relatively smaller (Tuttle, 1969a; Marzke, 1971). The *Pan-Homo* LCA probably had the primitive condition, with emphasis on the flexor muscles that facilitate strong power grips by the fingers.

Modern humans are also distinguished from the extant great apes in the differentiation of a distinct flexor pollicis longus (FPL) muscle belly and tendon in humans (Marzke, 1971; Susman, 1988a, 1994; Sarmiento, 1994; Hamrick et al. 1998). In particular, modern humans are unique among hominids in having a distinct muscle belly for the FPL that is separate from that of the flexor digitorum profundus (FDP). The FPL muscle belly is not separate in extant great apes, but a distinct tendon may run to the thumb from the belly of the FDP muscle for the index finger or from tenosynovium in the carpal region (Fig. 7A) (Marzke, 1971). In some individuals the tendon attaches to the distal pollical phalanx but reaches only to the distal end of the proximal phalanx, where it attaches and functions as a ligament, restricting extension of the pollical inter-phalangeal joint (Shrewsbury et al. 2003). Often the tendon is absent entirely (Howell & Straus, 1933; Straus, 1942; Marzke, 1971; Swindler & Wood, 1973). Interestingly, orangutans may show a tendon with a similar insertion and function as FPL, but with an origin from the adductor pollicis oblique head rather than from the extrinsic muscle mass passing through the carpal tunnel (Fig. 7B) (MCJ, personal observation).

Hylobatids and cercopithecids share with modern humans a FPL tendon to the distal pollical phalanx that

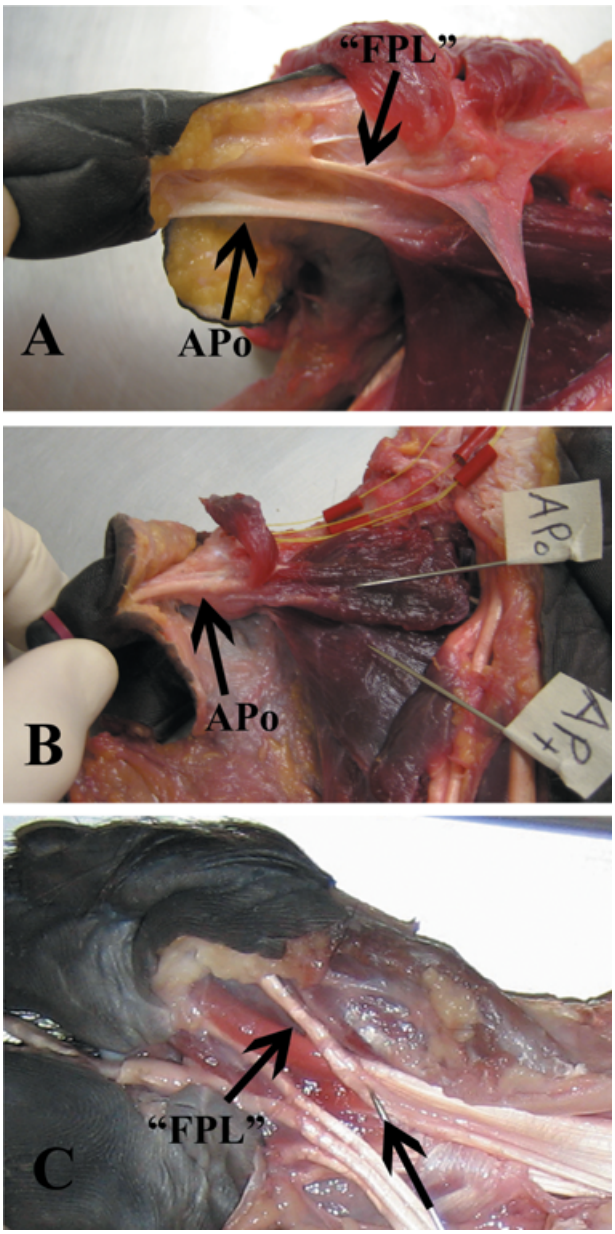

Fig. 7 Dissection photos of tendons that insert into the palmar portions of the thumb distal phalanx in nonhuman primates (radial is toward page top and distal is toward page left). (A) The right thumb of a chimpanzee showing a 'FPL' tendon that inserts into the distal phalanx but originates from tenosynovium (held with forceps) at the mid-shaft of the first metacarpal. The oblique head of adductor pollicis (APo) also showing a tendon to the distal phalanx along the ulnar margin that also functioned to flex the distal phalanx. (B) The right thumb of an orangutan showing a tendon that resembles 'FPL' in its insertion and function. However, the tendon originated from the adductor pollicis oblique head (APo), an intrinsic thenar muscle, and did not pass through the carpal tunnel to an extrinsic muscle mass. (C) The right thumb of a baboon showing a 'FPL' tendon bifurcating within the carpal tunnel from the ulnar side of the FDP tendon for the middle finger (other arrow) and crossing radially over the FDP tendon to the index finger as it exited the carpal tunnel distally. In baboons, the FDP tendon is not well differentiated by digit when it enters the proximal carpal tunnel.

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arises from the extrinsic hand musculature (Fig. 7C). In most hylobatids, the FPL tendon arises from a muscle belly that is separate from the FDP muscle to the fingers (Marzke, 1971), but in baboons it bifurcates within the carpal tunnel from the ulnar side of the FDP tendon for the middle finger and crosses radially over the FDP tendon to the index finger as it exits the carpal tunnel distally (Fig. 7C). Because the FDP muscle is not well differentiated in baboons, independent digital control of distal phalangeal flexion is unlikely. Similarly, the FPL tendon cannot function to flex the thumb independently of the other digits. Overall, it is clear that more comparative work in nonhuman primates is necessary to resolve the polarity of these FPL tendon and muscle belly characters as well as test whether they are in fact homologous in particular groups of primates.

It has also been suggested that the modern human FPL inserts into a fossa on the proximovolar aspect of the distal pollical phalanx and this insertion site has been subsequently used as a proxy for FPL attachment location and size in fossil hominins (Napier, 1962; Trinkaus, 1983; Susman, 1988a,b, 1994). For example, prominent volar fossae of the distal phalanx of the thumb have been described for fossil specimens such as Stw 294 from Sterkfontein attributed to *Au. africanus* (Ricklan, 1987), SKX 5016 from Swartkrans attributed to *P. robustus* (Susman, 1988a,b, 1998), OH 7-A attributed to *H. habilis* (Napier, 1962), and in Neandertal material from Shanidar (Trinkaus, 1983). However, detailed dissection of the distal pollical phalanx in modern humans and other primates indicates that the FPL tendon does not insert directly into the fossa – which instead lies proximal to the tendon insertion and is filled with areolar connective tissue – and that there is no correlation between the size of the tendon and the size of the fossa across taxa (Wilkinson, 1953; Shrewsbury et al. 2003). Thus, it may be premature to infer a tendinous attachment from the presence of a pit or ridge on the distal pollical phalanx. Even when a tendon inserts into the distal phalanx, we cannot be certain from which muscle belly (if any) it originates (Fig. 7A,B). However, a volar fossa might be a useful taxonomic marker for recognizing hominin distal pollical phalanges regardless of its relationship to the FPL tendon if it is indeed heritable.

Attempts have been made to infer muscle size in fossil taxa from the size of fossae and ridges on the phalanges of digits 2–5. For example, it has been suggested that fossae on either side of the middle phalanges of *Au. afarensis*, *Au. africanus*, and *H. habilis* reflect powerful digital flexors (Susman & Creel, 1979; Stern & Susman, 1983; Ricklan, 1987). However, recent comparative work has shown that the flexor digitorum superficialis (FDS) does not insert exclusively, entirely, or in some cases at all, into these fossae, and that there is no correlation between the cross-sectional area of the FDS tendon and the size of the fossae (Marzke et al. 2007). Rather than being the exclusive site of muscle insertion, these phalangeal fossae are simply the depressed areas along the sides of a longitudinal palmar median bar. This palmar reinforcement may play a structural role in increasing the dorsovolar strength of each phalanx during strong recruitment of the FDS (Marzke et al. 2007). Middle phalangeal specimens attributed to *Au. afarensis* (Bush et al. 1982), *Paranthropus* (Susman, 1989), *H. habilis* (Napier, 1962; Susman & Creel, 1979), *H. erectus/ergaster* (Walker & Leakey, 1993), and *H. antecessor* (Lorenzo et al. 1999) all show evidence of such a palmar median bar. A tendency toward gracilization of the phalanges may be a more recent autapomorphy of modern humans, but more study is needed.

The pollical attachment of the first dorsal interosseous muscle (DI1) may provide a less ambiguous skeletal character (Jacofsky, 2003). In nonhuman primates, the attachment on the pollex for the DI1 is typically restricted to the proximo-medial aspect of the pollical metacarpal shaft (Fig. 8) (Swindler & Wood, 1973; Jacofsky, 2003). In contrast, the attachment in modern humans typically extends further distally to incorporate approximately half of the metacarpal length and it is associated with a marked area of rugosity on the shaft (Fig. 8) (Jacofsky, 2003). This configuration provides the human DI1 with a

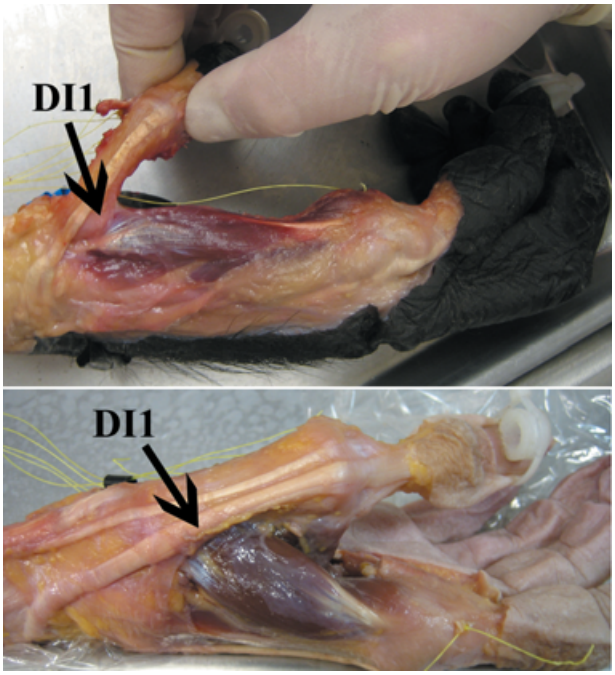

Fig. 8 In chimpanzees (top), the DI1 pollical insertion is localized to the proximo-medial base of the first metacarpal and the dorso-medial aspect of the trapezium. In modern humans (bottom), the DI1 pollical insertion is more extensive along the medial aspect of the first metacarpal shaft that often leaves a clear muscle-marking on the bone.

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longer moment arm for adduction of the thumb than seen in the great apes and other primates, and this modification may be an important factor in various grips employed during human tool-use (Marzke et al. 1998).

The derived modern human DI1 pollical morphology is not shared with *Au. afarensis* (A.L. 333w-39), which exhibits the primitive *Pan*-like insertion marking that is proximally restricted and only slightly raised with respect to the surrounding bone (Jacofsky, 2003). However, both metacarpals from Swartkrans (SK 84 and SKX 5020) show DI1 muscle markings that extend distally along the length of the pollical metacarpal shaft (Jacofsky, 2003). Markings on Neandertal first metacarpals indicate that they also share DI1 pollical morphology with modern humans (Musgrave, 1971). Despite the controversy over the taxonomic attribution of the Swartkrans specimens, they both suggest that the derived condition of the DI1 had evolved in the hominin clade by at least 1.5 Ma – with the hypothetical ancestor (Fig. 5, Node 8) most likely exhibiting a robust, distally extending DI1 insertion on the pollical metacarpal.

Marzke et al. (1999) demonstrated that modern humans are derived in having significantly longer muscle moment arms (around at least one of the anatomical axes of rotation) for several of the muscles of the hand including opponens pollicis, adductor pollicis (oblique and transverse heads), flexor pollicis brevis (superficial head), abductor pollicis longus, abductor pollicis brevis, and extensor pollicis longus. Furthermore, some of the functional roles of these muscles at the first carpometacarpal joint are reversed compared with the homologous muscles in *Pan*. The flexor pollicis brevis (superficial head) and opponens pollicis abduct rather than adduct the thumb and the extensor pollicis longus adducts rather than abducts the thumb. The adductor pollicis transverse and oblique heads flex rather than extend the thumb and the abductor pollicis longus metacarpal head extends rather than flexes the thumb. These differences in modern humans may be due to the supinated position of the trapezium within the modern human wrist, which is a consequence of the palmar expansion of the trapezoid (Table 1, j) and is further recognized by the extension of the trapezium joint surface onto the scaphoid tubercle (Table 1, h) (Lewis, 1989; Tocheri, 2007). The relationship between the skeletal geometry of the wrist and the moment arms of the hand musculature is not well understood, but future work examining the three-dimensional relationships of bones and muscle tendon paths may allow the mechanics of these muscles to be reasonably reconstructed from fossil material. The necessity of such research is underscored by the mesenchymal formation of the osteological and myological structures of the hand during embryogenesis (Čihák, 1972). This would enable inferences about how the mechanics of particular muscles have become derived compared with their function in the *Pan-Homo* LCA. However, studies of muscular mechanics in the other great apes are also needed to verify that they share the pattern of mechanics observed in *Pan*.

Discussion

There is no question that additional fossil and comparative evidence is needed to more fully reconstruct the evolutionary history of the hominin hand. The current fossil evidence does, however, provide some interesting clues as to when and where particular changes in hominin hand morphology may have occurred. What is most clear is that the hands of modern humans and Neandertals show more shared derived features relative to the *Pan-Homo* LCA than any other hominin taxa. The presence of some derived characteristics in earlier hominins suggests that the evolution of the hominin hand, from the origin of the hominin clade to the present, has probably proceeded in a mosaic fashion. The first clearly visible changes are present in *Au. afarensis*, at approximately 3.0 Ma, and involve shortening of the fingers relative to the thumb as well as modifications to the joints between the index finger and the trapezium and capitate. The second visible changes involve modifications to the distal phalanges, thumb robusticity, and the first carpometacarpal joint; these are first observed in specimens attributed to either *Paranthropus* or early *Homo* that date to between 2.0 and 1.5 Ma. The third visible changes involve a structural reorganization of the radial side of the wrist. This reorganization is best seen in modern humans and Neandertals, but there is also evidence of it in the *H. antecessor* capitate. The observed timing of these three changes (ca. 3.0 Ma, 2.0–1.5 Ma, and 0.8 Ma) is of course unlikely to have been the true origin of these features in the hominin fossil record; the 'real' origins may well be earlier.

The fossilized remains of *Au. afarensis* provide an indication of the structure of the hominin hand approximately 0.5 Ma prior to the earliest direct evidence of stone tool use or manufacture (Bush et al. 1982; Semaw et al. 1997; de Heinzelin et al. 1999; Drapeau et al. 2005). Stone tools have yet to be recovered in association with *Au. afarensis*; however, the hand of *Au. afarensis* is likely a reasonable model for the hand structure of the hominin species responsible for the stone tools present at around 2.5–2.6 Ma (Semaw et al. 1997; de Heinzelin et al. 1999). Panger et al. (2002) remind us that 2.5–2.6 Ma is the earliest that stone tools are visible as an archaeological record of behavior; stone tools may well have been made prior to 2.5–2.6 Ma, but the intensity with which they were made and used may not have been sufficient to leave an archaeological signal (Potts, 1991; Panger et al. 2002). The recent discoveries of *H. floresiensis*, with associated dates of between 0.095 and 0.012 Ma and its remarkably primitive wrist (Brown et al. 2004; Morwood et al. 2004, 2005; Tocheri et al. 2007a,b), are an additional reminder that more than one type of hominin hand is

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found in direct association with stone tools in the fossil record (Napier, 1962; Susman, 1988a,b, 1994; Tocheri, 2007).

In their overview of hominin evolution, Wood & Richmond (2000; p. 51) suggest that 'we can no longer be sure that stone tool manufacture was a behavior exclusive to members of the genus *Homo*' (see also Susman, 1988a,b, 1994; Wood & Collard, 1999). Although we recognize that this statement is undoubtedly true, the evidence reviewed in this paper suggests that currently only three species of the genus *Homo* (*H. sapiens*, *H. neanderthalensis*, and *H. antecessor*) display derived hand morphology that is noticeably absent elsewhere in the hominin lineage (Tocheri, 2007), including *H. floresiensis* (Tocheri et al. 2007a,b). At present, this evidence suggests that these features are probably synapomorphies, which may have originated sometime between approximately 1.8 and 0.8 Ma, a temporal span that encompasses the origin and initial spread of Acheulian technology (~1.5–0.2 Ma). This does not imply that the derived features of the radial wrist are necessary to make or use Acheulian tools, only that the current evidence suggests that these features probably originated within a temporal and behavioral context characterized by Acheulian technology (Tocheri, 2007). The important and interesting questions that remain to be answered are whether the complete suite of derived characteristics present in the hands of modern humans and Neandertals originated earlier with *H. erectus sensu lato* or possibly with another closely related hominin species, and whether the derived changes are functionally advantageous for manipulative behaviors involving stone tool use and manufacture.

We may never be absolutely certain how the observed mosaic combinations of primitive and derived features in fossil hominin hands functioned within their respective locomotor and manipulative behavioral repertoires. However, we can be certain that our species, *H. sapiens*, is the only living descendant of the tribe Hominini, and that our hand is different than it was in the *Pan-Homo* LCA and elsewhere in the hominin clade. As such, the evolutionary history of the hand within the hominin clade will remain a prime example for studying descent with modification for many years to come.

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References

Alba DM, Moyà-Solà S, Köhler M (2003) Morphological affinities of the *Australopithecus* hand on the basis of manual proportions and relative thumb length. *J Hum Evol* **44**, 225–254.

Almécija S, Alba DM, Moyà-Solà S, Köhler M (2007) Orang-like manual adaptations in the fossil hominoid *Hispanopithecus laietanus*: first steps towards great ape suspensory behaviours. *Proc R Soc B* **274**, 2375–2384.

Arensburg B, Bar-Yosef O, Chech M, et al. (1985) Une sépulture néanderthalien dans la grotto de Kebara (Israel). *C R Acad Sci Paris, Série II* **300**, 227–230.

Bar-Yosef O, Vandermeersch B, Arensburg B, et al. (1992) The excavations in Kebara cave, Mt. Carmel. *Curr Anthropol* **33**, 497–450.

Begun DR (1992) Miocene fossil hominids and the chimp-human clade. *Science* **257**, 1929–1933.

Begun DR (1993) New catarrhine phalanges from Rudabánya (Northeastern Hungary) and the problem of parallelism and convergence in hominoid postcranial morphology. *J Hum Evol* **24**, 373–402.

Begun DR (1994) Relations among the great apes and humans: New interpretations based on the fossil great ape *Dryopithecus*. *Yrbk Phys Anthropol* **37**, 11–63.

Begun DR (2004) Knuckle-walking and the origin of human bipedalism. In *From Biped to Strider: The Emergence of Modern Human Walking, Running, and Resource Transport* (eds Meldrum DJ, Hilton CE), pp. 9–33. New York: Kluwer Academic/Plenum Publishers.

Begun DR (2007) How to identify (as opposed to define) a homoplasy: examples from fossil and living great apes. *J Hum Evol* **52**, 559–572.

Begun DR, Ward CV (2005) Comment on '*Pierolapithecus catalaunicus*, a new Middle Miocene great ape from Spain'. *Science* **308**, 203c.

Broom R, Schepers GWH (1946) The South African ape-men: the Australopithecinae. *Trans Mus Mem* **2**, 1–272.

Brown P, Sutikna T, Morwood MJ, et al. (2004) A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature* **431**, 1055–1061.

Brunet M, Guy F, Pilbeam D, et al. (2002) A new hominid from the Upper Miocene of Chad, Central Africa. *Nature* **418**, 145–151.

Bush ME, Lovejoy CO, Johanson DC, Coppens Y (1982) Hominid carpal, metacarpal, and phalangeal bones recovered from the Hadar Formation: 1974–1977 collections. *Am J Phys Anthropol* **57**, 651–677.

Čihák R (1972) Ontogenesis of the skeleton and intrinsic muscles of the human hand and foot. *Ergeb Anat Entwicklungsgesch* **46**, 1–194.

Clarke RJ (1999) Discovery of complete arm and hand of the 3.3 million-year-old *Australopithecus* skeleton from Sterkfontein. *S Afr J Sci* **95**, 477–480.

Collard M, Wood B (2007) Hominid homoiology: an assessment of the impact of phenotypic plasticity on phylogenetic analyses of humans and their fossil relatives. *J Hum Evol* **52**, 573–584.

Constantino P, Wood B (2007) The evolution of *Zinjanthropus boisei*. *Evol Anthropol* **16**, 49–62.

Corruccini RS (1978) Comparative osteometrics of the hominoid wrist joint, with special reference to knuckle-walking. *J Hum Evol* **7**, 307–321.

Crompton RH, Vereecke EE, Thorpe SKS (2008) Locomotion and posture from the common hominoid ancestor to fully modern hominins, with special reference to the common panin/hominin ancestor. *J Anat* **12**, 501–543.

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Darwin C (1859) *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. London: John Murray.

Day M (1976) Hominid postcranial material from Bed I, Olduvai Gorge. In *Human Origins: Louis Leakey and the East African Evidence* (eds Isaac GL, McKown ER), pp. 363–374. Menlo Park, CA: W.A. Benjamin, Inc.

Drapeau MSM, Ward CV, Kimbel WH, Johanson DC, Rak Y (2005) Associated cranial and forelimb remains attributed to *Australopithecus afarensis* from Hadar, Ethiopia. *J Hum Evol* **48**, 593–642.

Eizirik E, Murphy WJ, Spinger MS, O'Brien SJ (2004) Molecular phylogeny and dating of early primate divergences. In *Anthropoid Origins: New Visions* (eds Ross CF, Kay RF), pp. 45–64. New York: Kluwer Academic/Plenum Publishers.

Falgueres C, Bahain JJ, Yokoyama Y, et al. (1999) Earliest humans in Europe: the age of TD6 Gran Dolina, Atupuerca, Spain. *J Hum Evol* **37**, 343–352.

Fleagle JG, Stern JT, Jungers WL, Susman RL, Vangor AK, Wells JP (1981) Climbing: a biomechanical link with brachiation and with bipedalism. *Symp Zool Soc Lond* **48**, 359–375.

Gibbs S, Collard M, Wood B (2000) Soft-tissue characters in higher primate phylogenetics. *Proc Natl Acad Sci USA* **97**, 11130–11132.

Gibbs S, Collard M, Wood B (2002) Soft-tissue anatomy of the extant hominoids: a review and phylogenetic analysis. *J Anat* **200**, 3–49.

Gommery D, Senut B (2006) The terminal thumb phalanx of *Orrorin tugenensis* (Upper Miocene of Kenya). *Geobios* **39**, 372–384.

Green DJ, Gordon AD (2008) Metacarpal proportions in *Australopithecus africanus*. *J Hum Evol* (in press).

Gregory WK (1927) Two views of the origin of man. *Science* **65**, 601–605.

Haile-Selassie Y (2001) Late Miocene hominids from the Middle Awash, Ethiopia. *Nature* **412**, 178–181.

Hamrick MW, Churchill SE, Schmitt D, Hylander WL (1998) EMG of human flexor pollicis longus muscle: implications for evolution of hominid tool use. *J Hum Evol* **34**, 123–136.

Hamrick MW, Inouye SE (1995) Thumbs, tools and early humans. *Science* **268**, 587.

de Heinzelin J, Clark JD, White T, et al. (1999) Environment and behavior of 2.5-million-year-old Bouri hominids. *Science* **284**, 625–629.

Howell AB, Straus WL (1933) The muscular system. In *The Anatomy of the Rhesus Monkey* (ed. Hartman CG), pp. 89–175. New York: Hafner Publishing Co., Inc.

Huxley TH (1863) *Evidence as to Man's Place in Nature*. London: Williams and Norgate.

Inouye S (1994) Ontogeny of knuckle-walking hand postures in African apes. *J Hum Evol* **26**, 459–485.

Jacofsky MC (2003) Variation in morphology and musculoskeletal stress marker expression of the first dorsal interosseous muscle in catarrhines. *Am J Phys Anthropol* **36**, 122 (Suppl).

Jenkins FA, Fleagle JG (1975) Knuckle-walking and the functional anatomy of the wrists in living apes. In *Primate Functional Morphology and Evolution* (ed. Tuttle RH), pp. 213–228. The Hague: Mouton.

Johanson DC, Lovejoy CO, Kimbel WH, et al. (1982) Morphology of the Pliocene partial hominid skeleton (A.L. 288-1) from the Hadar Formation, Ethiopia. *Am J Phys Anthropol* **57**, 403–451.

Jungers WL, Godfrey LR, Simons EL, Chatrath PS (1997) Phalangeal curvature and positional behavior in extinct sloth lemurs (Primates, Palaeopropithecidae). *Proc Natl Acad Sci USA* **94**, 11998–12001.

Kappelman J, Richmond BG, Seiffert ER, Maga AM, Ryan TM (2003) Hominoidea (Primates). In *Geology and Paleontology of the Miocene Sinap Formation, Turkey* (eds Fortelius M, Kappelman J, Sen S, Bernor RL), pp. 90–124. New York: Columbia University Press.

Keith A (1923) Man's posture: its evolution and disorders. *Br Med J* **1**, 451–454, 499–502, 545–548, 587–590, 624–626, 669–672.

Kivell TL, Begun DR (2007) Frequency and timing of scaphoid-centrale fusion in hominoids. *J Hum Evol* **52**, 321–340.

Kumar S, Filipski A, Swarna V, Walker A, Hedges SB (2005) Placing confidence limits on the molecular age of the human-chimpanzee divergence. *Proc Natl Acad Sci USA* **102**, 18842–18847.

Larson SG (1998) Parallel evolution in the hominoid trunk and forelimb. *Evol Anthropol* **6**, 87–99.

Le Gros Clark WE (1940) Palaeontological evidence bearing on human evolution. *Biol Rev* **15**, 202–230.

Leakey LSB, Tobias PV, Napier JR (1964) A new species of the genus *Homo* from Olduvai Gorge. *Nature* **202**, 7–9.

Leakey MD (1971) *Olduvai Gorge*. Volume III. *Excavations in Beds I and II, 1960–1963*. Cambridge: The University Press.

Leakey MG, Feibel CS, McDougall I, Ward C, Walker A (1998) New specimens and confirmation of an early age for *Australopithecus anamensis*. *Nature* **393**, 62–66.

Lewis OJ (1973) The hominoid os capitatum, with special reference to the fossil bones from Sterkfontein and Olduvai Gorge. *J Hum Evol* **2**, 1–11.

Lewis OJ (1989) *Functional Morphology of the Evolving Hand and Foot*. Oxford: Clarendon Press.

Lockwood CA, Lynch JM, Kimbel WH (2002) Quantifying temporal bone morphology of great apes and humans: an approach using geometric morphometrics. *J Anat* **201**, 447–464.

Lockwood CA, Kimbel WH, Lynch JM (2004) Morphometrics and hominoid phylogeny: Support for a chimpanzee–human clade and differentiation among great ape subspecies. *Proc Natl Acad Sci USA* **101**, 4356–4360.

Lorenzo C, Arsuaga JL, Carretero JM (1999) Hand and foot remains from the Gran Dolina Early Pleistocene site (Sierra de Atapuerca, Spain). *J Hum Evol* **37**, 501–522.

Lycett SJ, Collard M (2005) Do homoiologies impede phylogenetic analyses of the fossil hominids? An assessment based on extant papionin craniodental morphology. *J Hum Evol* **49**, 618–642.

Marzke MW (1971) Origin of the human hand. *Am J Phys Anthropol* **34**, 61–84.

Marzke MW (1983) Joint function and grips of the *Australopithecus afarensis* hand, with special reference to the region of the capitate. *J Hum Evol* **12**, 197–211.

Marzke MW (1997) Precision grips, hand morphology, and tools. *Am J Phys Anthropol* **102**, 91–110.

Marzke MW, Marzke RF (1987) The 3rd metacarpal styloid process in humans – origin and functions. *Am J Phys Anthropol* **73**, 415–431.

Marzke MW, Wullstein KL, Viegas SF (1992) Evolution of the power ('squeeze') grip and its morphological correlates in hominids. *Am J Phys Anthropol* **89**, 283–298.

Marzke MW, Toth N, Schick K, Reece S, Steinberg B, Hunt K (1998) EMG study of hand muscle recruitment during hard hammer percussion manufacture of Oldowan tools. *Am J Phys Anthropol* **105**, 315–332.

Marzke MW, Marzke RF, Linscheid RL, et al. (1999) Chimpanzee thumb muscle cross sections, moment arms and potential torques, and comparisons with humans. *Am J Phys Anthropol* **110**, 163–178.

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Marzke MW, Shrewsbury MM, Horner KE (2007) Middle phalanx skeletal morphology in the hand: can it predict flexor tendon size and attachments? *Am J Phys Anthropol* **134**, 141–151.

McHenry HM (1983) The capitate of *Australopithecus afarensis* and *A. africanus*. *Am J Phys Anthropol* **62**, 187–198.

Mittra ES, Smith HF, Lemelin P, Jungers WL (2007) Comparative morphometrics of the primate apical tuft. *Am J Phys Anthropol* **134**, 449–459.

Morwood MJ, Soejono RP, Roberts RG, et al. (2004) Archaeology and age of a new hominin from Flores in eastern Indonesia. *Nature* **431**, 1087–1091.

Morwood MJ, Brown P, Jatmiko, et al. (2005) Further evidence for small-bodied hominins from the Late Pleistocene of Flores, Indonesia. *Nature* **437**, 1012–1017.

Moyà-Solà S, Köhler M, Alba DM, Casanovas-Vilar I, Galindo J (2004) *Pierolapithecus catalaunicus*, a new Middle Miocene great ape from Spain. *Science* **306**, 1339–1344.

Moyà-Solà S, Köhler M, Alba DM, Casanovas-Vilar I, Galindo J (2005) Response to comment on '*Pierolapithecus catalaunicus*, a new Middle Miocene great ape from Spain'. *Science* **308**, 203d.

Musgrave JH (1971) How dextrous was Neanderthal man? *Nature* **233**, 538–541.

Napier JR (1959) *Fossil Metacarpals from Swartkrans. Fossil Mammals of Africa No. 17*. London: British Museum of Natural History.

Napier JR (1962) Fossil hand bones from Olduvai Gorge. *Nature* **196**, 409–411.

Napier JR (1970) *The Roots of Mankind*. New York: Harper & Row.

Niewoehner WA (2000) *The Functional Anatomy of Late Pleistocene and Recent Human Carpometacarpal and Metacarpophalangeal Articulations*. Ph.D. Dissertation, University of New Mexico, Albuquerque, NM.

Niewoehner WA (2001) Behavioral inferences from the Skhul/Qafzeh early modern human hand remains. *Proc Natl Acad Sci USA* **98**, 2979–2984.

Niewoehner WA (2005) A geometric morphometric analysis of Late Pleistocene human metacarpal I base shape. In *Modern Morphometrics in Physical Anthropology* (ed. Slice D), pp. 285–298. Amsterdam: Kluwer Academic Publishers.

Niewoehner WA (2006) Neanderthal hands in their proper perspective. In *Neanderthals Revisited: New Approaches and Perspectives* (eds Harvati K, Harrison T), pp. 157–190. Dordrecht, The Netherlands: Springer.

Niewoehner WA, Weaver AH, Trinkaus E (1997) Neandertal capitate-metacarpal articular morphology. *Am J Phys Anthropol* **103**, 219–233.

Noonan JP, Coop G, Kudaravallis S, et al. (2006) Sequencing and analysis of Neanderthal genomic DNA. *Science* **314**, 1113–1118.

Ohman JC, Slanina M, Baker G, Mensforth RP (1995) Thumbs, tools and early humans. *Science* **268**, 587–589.

Orr CM (2005) The knuckle-walking anteater: a convergence test of adaptation for purported knuckle-walking features of African Hominidae. *Am J Phys Anthropol* **128**, 639–658.

Oxnard CE (1973) *Form and Pattern in Human Evolution: Some Mathematical, Physical, and Engineering Approaches*. Chicago: University Chicago Press.

Page SL, Goodman M (2001) Catarrhine phylogeny: Noncoding DNA evidence for a diphyletic origin of the mangabeys and for a human-chimpanzee clade. *Mol Phylogenet Evol* **18**, 14–25.

Panger MA, Brooks AS, Richmond BG, Wood B (2002) Older than the Oldowan? Rethinking the emergence of hominin tool use. *Evol Anthropol* **11**, 235–245.

Pickford M, Senut B, Gommery D, Treil J (2002) Bipedalism in *Orrorin tugenensis* revealed by its femora. *C R Palevol* **1**, 191–203.

Pilbeam D, Rose MD, Barry JC, Shah SMI (1990) New *Sivapithecus* humeri from Pakistan and the relationship of *Sivapithecus* and *Pongo*. *Nature* **348**, 237–239.

Potts R (1991) Why the Oldowan? Plio-Pleistocene tool-making and the transport of resources. *J Anthropol Res* **47**, 153–176.

Richmond BG (1998) Ontogeny and biomechanics of phalangeal form in primates. Ph.D. Dissertation, State University of New York at Stony Brook, Stony Brook.

Richmond BG (2006) Functional morphology of the midcarpal joint in knuckle-walkers and terrestrial quadrupeds. In *Human Origins and Environmental Backgrounds* (eds Ishida H, Tuttle R, Pickford M, Ogihara N, Nakatsukasa M), pp. 105–122. USA: Springer.

Richmond BG (2007) Biomechanics of phalangeal curvature. *J Hum Evol* **53**, 678–690.

Richmond BG, Strait DS (2000) Evidence that humans evolved from a knuckle-walking ancestor. *Nature* **404**, 382–385.

Richmond BG, Begun DR, Strait DS (2001) Origin of human bipedalism: The knuckle-walking hypothesis revisited. *Yrbk Phys Anthropol* **44**, 70–105.

Ricklan DE (1987) Functional anatomy of the hand of *Australopithecus africanus*. *J Hum Evol* **16**, 643–664.

Ricklan DE (1990) The precision grip in *Australopithecus africanus*: anatomical and behavioral correlates. In *From Apes to Angels:Essays in Anthropology in Honor of Phillip V. Tobias* (ed. Sperber GH), pp. 171–183. New York: Wiley-Liss.

Rightmire GP (1972) Multivariate analysis of an early hominid metacarpal from Swartkrans. *Science* **176**, 159–161.

Ruvolo M (1997) Molecular phylogeny of the hominoids: Inferences from multiple independent DNA sequence data sets. *Mol Biol Evol* **14**, 248–265.

Salem AH, Ray DA, Xing J, et al. (2003) Alu elements and hominid phylogenetics. *Proc Natl Acad Sci USA* **100**, 12787–12791.

Sarmiento EE (1988) Anatomy of the hominoid wrist joints, its evolutionary and functional implications. *Int J Primatol* **9**, 281–345.

Sarmiento EE (1994) Terrestrial traits in the hands and feet of gorillas. *Am Mus Nov* **3091**, 1–56.

Sawada Y, Pickford M, Senut B, et al. (2002) The age of *Orrorin tugenensis*, an early hominid from the Tugen Hills, Kenya. *C R Palevol* **1**, 293–303.

Scheuer L, Black S (2000) *Developmental Juvenile Osteology*. London: Academic Press.

Schmitt D (2003) Insights into the evolution of human bipedalism from experimental studies of humans and other primates. *J Exp Biol* **206**, 1437–1448.

Schultz AH (1930) The skeleton of the trunk and limbs of higher primates. *Hum Biol* **2**, 303–438.

Semaw S, Renne P, Harris JWK, et al. (1997) 2.5-million-year-old stone tools from Gona, Ethiopia. *Nature* **385**, 333–336.

Semaw S, Simpson SW, Quade J, et al. (2005) Early Pliocene hominids from Gona, Ethiopia. *Nature* **433**, 301–305.

Senut B, Pickford M, Gommery D, Mein P, Cheboi K, Coppens Y (2001) First hominid from the Miocene (Lukeino Formation, Kenya). *C R Acad Sci Paris* **332**, 137–144.

Shrewsbury MM, Marzke MW, Linscheid RL, Reece SP (2003) Comparative morphology of the pollical distal phalanx. *Am J Phys Anthropol* **121**, 30–47.

Smith SL (2000) Shape variation of the human pollical distal phalanx and metacarpal. *Am J Phys Anthropol* **113**, 329–348.

Stafford BJ, Thorington RW (1998) Carpal development and morphology in Archontan mammals. *J Morpol* **235**, 135–155.

Steiper ME, Young NM (2006) Primate molecular divergence dates. *Mol Phylogenet Evol* **41**, 384–394.

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Stern JT, Susman RL (1983) The locomotor anatomy of *Australopithecus afarensis*. *Am J Phys Anthropol* **60**, 279–317.

Straus WL (1942) Rudimentary digits in primates. *Q Rev Biol* **17**, 228–243.

Straus WL (1949) The riddle of man's ancestry. *Q Rev Biol* **24**, 200–223.

Susman RL (1988a) Hand of *Paranthropus robustus* from Member 1, Swartkrans: fossil evidence for tool behavior. *Science* **240**, 781–784.

Susman RL (1988b) New postcranial remains from the Swartkrans and their bearing on the functional morphology and behavior of *Paranthropus robustus*. In *Evolutionary History of the 'Robust' Australopithecines* (ed. Grine FE), pp. 149–172. New York: Aldine de Gruyter.

Susman RL (1989) New hominid fossils from the Swartkrans Formation (1979–1986 excavations): postcranial specimens. *Am J Phys Anthropol* **79**, 451–474.

Susman RL (1991) Who made the Oldowan tools? Fossil evidence for tool behavior in Plio-Pleistocene hominids. *J Anthropol Res* **47**, 129–149.

Susman RL (1994) Fossil evidence for early hominid tool use. *Science* **265**, 1570–1573.

Susman RL (1995) Thumbs, tools and early humans. *Science* **268**, 589.

Susman RL (1998) Hand function and tool behavior in early hominids. *J Hum Evol* **35**, 23–46.

Susman RL, Creel N (1979) Functional and morphological affinities of the subadult hand (OH 7) from Olduvai Gorge. *Am J Phys Anthropol* **51**, 311–331.

Swindler DR, Wood CD (1973) *Atlas of Primate Gross Anatomy*. Seattle: University of Washington Press.

Thorpe SKS, Holder RL, Crompton RH (2007) Origin of human bipedalism as an adaptation for locomotion on flexible branches. *Science* **316**, 1328–1331.

Tocheri MW (2007) Three-dimensional riddles of the radial wrist: Derived carpal and carpometacarpal joint morphology in the genus Homo and the implications for understanding the evolution of stone tool-related behaviors in hominins. Ph.D. Dissertation, Arizona State University, Tempe, Arizona.

Tocheri MW, Marzke MW, Liu D, et al. (2003) Functional capabilities of modern and fossil hominid hands: Three-dimensional analysis of trapezia. *Am J Phys Anthropol* **122**, 101–112.

Tocheri MW, Razdan A, Williams RC, Marzke MW (2005) A 3D quantitative comparison of trapezium and trapezoid relative articular and nonarticular surface areas in modern humans and great apes. *J Hum Evol* **49**, 570–586.

Tocheri MW, Jungers WL, Larson SG, et al. (2007a) Morphological affinities of the wrist of *Homo floresiensis*. Paper presented at the annual meeting of the Paleoanthropology Society, Philadelphia, PA.

Tocheri MW, Orr CM, Larson SG, et al. (2007b) The primitive wrist of *Homo floresiensis* and its implications for hominin evolution. *Science* **317**, 1743–1745.

Trinkaus E (1983) *The Shanidar Neandertals*. London: Academic Press.

Trinkaus E (1989) Olduvai Hominid 7 trapezial metacarpal 1 articular morphology: Contrasts with recent humans. *Am J Phys Anthropol* **80**, 411–416.

Trinkaus E, Long JC (1990) Species attribution of the Swartkrans Member 1 first metacarpals: SK 84 and SKX 5020. *Am J Phys Anthropol* **83**, 419–424.

Trinkaus E, Churchill SE, Villemeur I, Riley KG, Heller JA, Ruff CB (1991) Robusticity versus shape: The functional interpretation of Neandertal appendicular morphology. *J Anthropol Soc Nippon* **99**, 257–278.

Tuttle RH (1967) Knuckle-walking and the evolution of hominoid hands. *Am J Phys Anthropol* **26**, 171–206.

Tuttle RH (1969a) Quantitative and functional studies on the hands of the anthropoidea: I. The Hominoidea. *J Morphol* **128**, 309–363.

Tuttle RH (1969b) Knuckle-walking and the problem of human origins. *Science* **166**, 953–961.

Tuttle RH (1974) Darwin's apes, dental apes, and the descent of man: normal science in evolutionary anthropology. *Curr Anthropol* **15**, 389–398.

Tuttle RH (1975) Parallelism, brachiation, and hominoid phylogeny. In *Phylogeny of the Primates: A Multidisciplinary Approach* (eds Luckett WP, Szalay FS), pp. 447–480. New York: Plenum Press.

Tuttle RH (1981) Evolution of hominid bipedalism and prehensile capabilities. *Phil Trans R Soc Lond [Biol]* **292**, 89–94.

Uddin M, Wildman DE, Liu G, et al. (2004) Sister grouping of chimpanzees and humans as revealed by genome-wide phylogenetic analysis of brain gene expression profiles. *Proc Natl Acad Sci USA* **101**, 2957–2962.

Vrba ES (1982) Biostratigraphy and chronology, based particularly on Bovidae, of southern hominid-asociated assemblages: Makapansgat, Sterkfontein, Taung, Kromdraai, Swartkrans; and also Elandsfontein (Saldanha), Broken Hill (now Kabwe) and Cave of Hearths. In *L'*Homo erectus *et la Place de L'homme de Tautavel parmi les Hominidés Fossils*. Prétirage du 1er Congrès International Paléontologie Humaine. Volume 2. (eds DeLumley F, DeLumley MA), pp. 707–752. Nice: Louis-Jean.

Walker A, Leakey R (1993) The postcranial bones. In *The Nariokotome* Homo erectus *Skeleton* (eds Walker A, Leakey R), pp. 95–160. Cambridge, MA: Harvard University Press.

Ward CV, Leakey MG, Brown B, Brown F, Harris J, Walker A (1999a) South Turkwel: a new Pliocene hominid site in Kenya. *J Hum Evol* **36**, 69–95.

Ward CV, Leakey MG, Walker A (1999b) The new hominid species *Australopithecus anamensis*. *Evol Anthropol* **7**, 197–205.

Weidenreich F (1941) The extremity bones of *Sinanthropus pekinensis*. *Paleontol Sinica New Series D* **5**, 1–150.

White TD, Suwa G, Asfaw B (1994) *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature* **371**, 306–312.

Wilkinson JL (1953) The insertion of the flexores pollicis longus et digitorium profundus. *J Anat* **87**, 75–91.

Wimmer R, Kirsch S, Rappold GA, Schempp W (2002) Direct evidence for the *Homo-Pan* clade. *Chromosome Res* **10**, 55–61.

Wood BA (1974) Olduvai Bed I post-cranial fossils: a reassessment. *J Hum Evol* **3**, 373–378.

Wood B, Collard MC (1999) The human genus. *Science* **284**, 65–71.

Wood B, Richmond BG (2000) Human evolution: taxonomy and paleobiology. *J Anat* **197**, 19–60.

Wood B, Lonergan N (2008) The hominin fossil record: taxa, grades and clades. *J Anat* **12**, 354–376.

Wood Jones F (1916) *Arboreal Man*. London: Edward Arnold.

Wood Jones F (1948) *Hallmarks of Mankind*. London: Ballière, Tindall and Cox.

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