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Review

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Author for correspondence:

Tracy L. Kivell

e-mail: t.l.kivell@kent.ac.uk

Evidence in hand: recent discoveries and the early evolution of human manual manipulation

Tracy L. Kivell^{1,2}

¹Animal Postcranial Evolution (APE) Lab, Skeletal Biology Research Centre, School of Anthropology and Conservation, University of Kent, Marlowe Building, Canterbury, Kent CT2 7NR, UK

²Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, Leipzig 04103, Germany

For several decades, it was largely assumed that stone tool use and production were abilities limited to the genus *Homo*. However, growing palaeontological and archaeological evidence, comparative extant primate studies, as well as results from methodological advancements in biomechanics and morphological analyses, have been gradually accumulating and now provide strong support for more advanced manual manipulative abilities and tool-related behaviours in pre-*Homo* hominins than has been traditionally recognized. Here, I review the fossil evidence related to early hominin dexterity, including the recent discoveries of relatively complete early hominin hand skeletons, and new methodologies that are providing a more holistic interpretation of hand function, and insight into how our early ancestors may have balanced the functional requirements of both arboreal locomotion and tool-related behaviours.

1. Introduction

'Now it appears that man-apes—creatures able to run... and with brains no larger than those of apes now living—had already learned to make and to use tools'. Washburn ([1], pp. 63).

Washburn's ([1], see also [2]) declaration referred to the contemporary discoveries by the Leakey family [3,4] of the robust australopith skull of '*Zinjanthropus boisei*' in association with a living floor of Oldowan stone tools. Only a few months later the remains of *Homo habilis* Olduvai Hominid (OH) 7 were discovered [4–7] and quickly deemed the maker of these stone tools, while *Zinjanthropus* was considered likely to be the prey instead [7]. In the decades following, tool use and tool making were largely considered to be an ability limited to (and, indeed, used to define) the genus *Homo* (see [8] for a review). However, a growing wealth of palaeontological, archaeological and comparative primate evidence makes clear that Washburn's [1] assertion that pre-*Homo* 'ape-men' were making and using tools still holds true today. In particular, recent, relatively complete fossil hominin hand skeletons [9–11] and archaeological discoveries [12,13] have added greatly to the growing group of palaeoanthropologists and archaeologists open to the idea that enhanced manual dexterity and tool-related behaviours have been a part of our evolutionary history for much longer than traditionally believed ([14–22], see also [23,24]).

Inferences about manipulative ability and potential tool-related behaviours in the earliest hominins must rely largely on morphological fossil evidence. Comparative extant primate studies, showing a dominance of using organic plants as tools in New and Old World monkeys and hominoids, suggests that the modification of plants and tool use were behaviours probably present in the last common ancestor of humans and *Pan* (chimpanzees and bonobos) [24], and potentially evolved multiple times in extinct fossil primates and hominins [22]. However, evidence of the modification and use of organic materials as tools either does not preserve in the fossil record or is not recognizable as tools [17,22]. Thus, researchers are generally forced to focus their interpretation and understanding of the evolution of human manipulative behaviours on

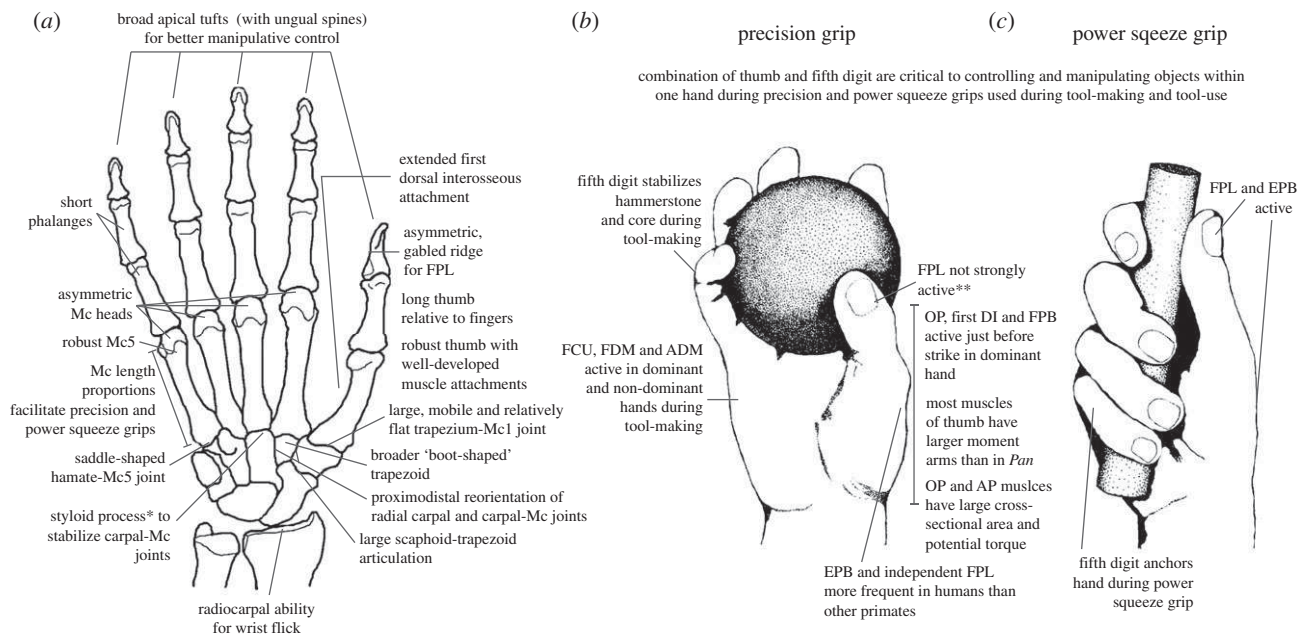


Figure 1. Bony and soft tissue morphology of the human hand considered advantageous for the manipulative precision and power squeeze grips used during stone tool use and production. (a) The suite of bony features typically considered distinct in the human hand (although some specific features are found in other primates, such as broad apical tufts in baboons) that reflect the ability to forcefully oppose the pads of the thumb and fingers, the well-developed musculature to the thumb and fifth digit, the high external loading of the thumb and distribution of that load across the wrist and palm, and the broad finger tips for control and manipulation of objects, especially within one hand. (b) Human precision grip (shown, a five-jaw chuck precision grip) in which the pads of the thumb and fingers grasp and manipulate the object and (c) a power squeeze grip, in which the fingers grasp the object diagonally and thumb is in line with the forearm. In stone tool behaviours, the thumb and fifth fingers are important for the manipulating and stabilizing objects in both the dominant and non-dominant hands. Muscles of the thumb and fifth digit that are strongly activated during use of these grips in tool making are noted [34]. FPL, flexor pollicis longus; FCU, flexor carpi ulnaris; FDM, flexor digiti minimi; ADM, abductor digiti minimi; OP, opponens pollicis; DI, dorsal interosseus; AP, oblique adductor pollicis; FPB, flexor pollicis brevis; EPB, extensor pollicis brevis; Mc, metacarpal. *The styloid process found at dorsoradial corner of the third metacarpal and thus cannot be seen in palmar view. **Marzke *et al.* [35] show that the FPL is not strongly active in either the dominant or non-dominant hand, particularly during precision pinch grips, in experienced knappers (but see [36]).

fossilized hand anatomy, especially in the earliest stages of human evolution (e.g. between approx. 7 and approx. 3.5 Ma; see below) and modified stone tools. Furthermore, the morphological evidence for the majority of our evolutionary history has been limited to isolated hand bones that are not directly associated with taxonomically identifying remains (i.e. craniodental material) or stone tool evidence. Thus, palaeoanthropologists have debated the taxonomic attribution and manipulative capabilities of many early fossil hominins for several decades [14,15,18,25–28]. However, recent palaeontological and archaeological discoveries, as well as advances in methods for analysing morphological remains, have shed new light on the manipulative abilities of early hominins.

There are several reviews of the morphological evidence for manipulative behaviours in human evolution [29–33]. Therefore, this paper focuses on the more recent fossil and archaeological evidence and the results of new methodologies that are helping to broaden our understanding of the evolution of the human hand and, in particular, the potential manipulative abilities of early hominins and how these might also have been balanced with requirements of arboreal locomotion.

2. What makes humans distinct? Manipulative abilities and morphological correlates

For the last few decades, research into the evolution of human manipulative abilities has focused—with good reason—on

identifying the manipulative behaviours that are unique to humans compared with other primates, and the morphological features of the human hand that might facilitate these abilities. This research is thoughtfully and thoroughly reviewed most recently by Markze [33] and others [29–32], and thus is briefly summarized below and in figure 1.

Comparative experimental studies of primate manual manipulation, including those on experienced human stone tool knappers, have revealed three manipulative abilities considered unique to the human hand [37–47]. The first is precision handling: the ability to rotate and manipulate objects within one hand using the thumb and finger tips [37,41]. Other primates typically need to use the palm as well [43] or their other hand, a foot or the mouth to manipulate an object into the desired position [39,41]. The second is forceful precision gripping, in which the pads of the thumb and one or more of the fingers are able to forcefully stabilize or manipulate an object, and at the same time withstand large external forces, such as when knapping a stone tool [29,41] (figure 1b). Other primates are capable of precision grips, typically tip-to-tip or pad-to-side grips between the thumb and index finger, but these are not generally done with strong force (i.e. precision holding; [38–40,45]). However, recent studies have revealed precision pinch grips in wild, habituated macaques [44] and chimpanzees [46,47] that may be forceful, requiring further investigation in whether forceful precision pinch grips are truly unique to humans.

The third uniquely human manipulative ability is power squeeze gripping of cylindrical objects in which the fingers

grip the object diagonally across the palm and the thumb is either wrapped around the object or is in line with the forearm, such as when using a hammer [48] (figure 1c). Other primates are capable of power grips (using the palm) or diagonal hook grips (fingers usually stabilized against the palm), but neither provide the same control that the power squeeze grip does in humans [48].

To potentially infer when these unique manipulative abilities may have evolved in the human lineage, many have tried to identify the distinctive features, or suites of features, in human bony and soft tissue anatomy that facilitate these gripping behaviours [29,30,32,49–51]. These anatomical features are summarized in figure 1. The most obvious and critical difference about the human hand compared with other primates is our robust and long thumb relative to the length of the fingers. Experimental studies have demonstrated that the thumb of the dominant hand [52,53] and, although much less so, the non-dominant hand [34], incur substantial external force during stone tool making and, particularly during tool use, such as when using a flake ([53,54], but see [52] and below). The bony morphology and musculature of the thumb reflect its importance in human manipulative behaviours. All but one of the muscles of the human thumb have a significantly larger moment arm (i.e. better mechanical advantage or leverage) than that of chimpanzees [35,55]. Two muscles in particular, the opponens pollicis and adductor pollicis muscles, also have larger cross-sectional area and potential torque that together provide better leverage and limit fatigue when opposing the thumb to the pads of the other fingers [55]. Larger muscle attachments on the first metacarpal (Mc1) for the opponens pollicis and first dorsal interosseous muscles also help to increase leverage and stabilize the joint at the base of the thumb during opposition [32,56]. Much attention has been paid to the independent and well-developed flexor pollicis longus (FPL) muscle of humans that helps to flex and stabilize the tip of the thumb [19,29,30,51,57]. Although this muscle is important for precision control and manipulation, it is particularly active during power squeeze grips ([35], but see [36]), rather than precision pinch grips, and other primates also have an independent FPL (e.g. hylobatids [51]) or a similar gabled-attachment on the pollical distal phalanx (e.g. orangutans [57]; figure 1a). Distinctive changes in carpal bone morphology, such a broader and flatter trapezium-Mc1 joint, the reorientation of the radial carpal (e.g. scaphoid-trapezoid) and carpometacarpal (e.g. capitate-Mc2) articulations, and the development of a styloid process on the base of the Mc3, together help to better distribute across the wrist and palm the large loads incurred by the thumb during tool-related behaviours [31,58–61].

The fifth digit is also particularly important during stone tool-related behaviours, but its morphology has been largely ignored in comparative and experimental studies [33,35,55]. The fifth digit stabilizes the dominant hand during power squeeze grips and precision grips (e.g. of the core during the strike of the hammerstone), as well as during precision grips of the non-dominant hand when manoeuvring an object within the hand to find the desired position [35]. In humans, the fifth metacarpal is the most robust of the digits 2–5 and has a unique saddle-shaped joint with the hamate that helps to rotate the fifth digit towards the thumb [31,35,50].

Several other distinctive features of the human bony and soft tissue hand anatomy have also been correlated with

forceful precision and power squeeze grips (figure 1), but the functional roles of the marginal aspects of the hand—the thumb and fifth digit—have been shown to be particularly important for the dexterity required to make and use stone tools [35,55]. Looking at the morphology of these two digits, and their associated wrist bones, in fossils hominins may be the most informative way of inferring the evolution of manipulative abilities and tool-related behaviours in human evolutionary history [33].

3. Manipulative abilities of the earliest fossil hominins

Functional interpretations of hand remains in the earliest fossil hominins have focused not only on their potential manipulative abilities, but also on how the morphological requirements for manipulation may have been balanced with those of arboreal locomotion. Perhaps the most critical aspect to the unique manipulative abilities of humans is our intrinsic hand proportions (relative length of the thumb and fingers). However, we are extremely limited in what we can say about hand proportions in the early hominins, because it requires the preservation of multiple bones from the same individual. The earliest relatively complete hand is that of *Ardipithecus ramidus* [62]. With hand proportions that are described as more Old World monkey-like than chimp-like (i.e. short metacarpals, long fingers, robust thumb), the authors describe the functional morphology only in relation to locomotion [62]. They do not discuss potential manipulative abilities, presumably because, at 4.4 Ma, *Ardipithecus* appears about a million years before the earliest evidence of stone tool use and tool making ([12,13,63], see below).

However, others have not been deterred from inferring human-like manipulative abilities in the absence of stone tool evidence, and from much less fossil evidence [19,21,64]. Among the two hand bones preserved from one of the earliest bipedal hominins, *Orrorin tugenensis* (ca 6 Ma), one is a distal pollical phalanx [65,66]. Its surprisingly human-like shape and FPL muscle attachment has led some to conclude that *Orrorin* possessed human-like precision grip abilities that evolved for the manipulation of organic objects, not stone tool making, with the relaxation of locomotor requirements on the forelimbs ([19], but see [66]).

Similar claims have been made for *Australopithecus afarensis* [18,28,50]. Though there is a wealth of hand fossils attributed to *Au. afarensis* [67–69], only a few metacarpals can be reliably associated with the same individual [50] (figure 2a). Hand proportions have been estimated in *Au. afarensis* by several researchers and range from potentially gorilla-like [27] to very similar [50], if not equal, to modern humans [18,28]. Functional interpretations based on these differences in reconstructed hand proportions, as well as other wrist and hand morphology, also vary: Rolian & Gordon [18] conclude that *Au. afarensis* could not have produced precision grips with the same efficiency as modern humans; Marzke [29,50] suggests *Au. afarensis* was capable of pad-to-side as well as three-jaw chuck precision grips, but likely had less effective precision handling and power squeeze grips; while Alba and co-workers [18,28] allow for the distinctly human-like pad-to-pad precision grips. Importantly, especially given the absence of evidence for stone tool behaviours prior to 2.6 Ma [63] until recently ([12,13]; see below), some researchers have

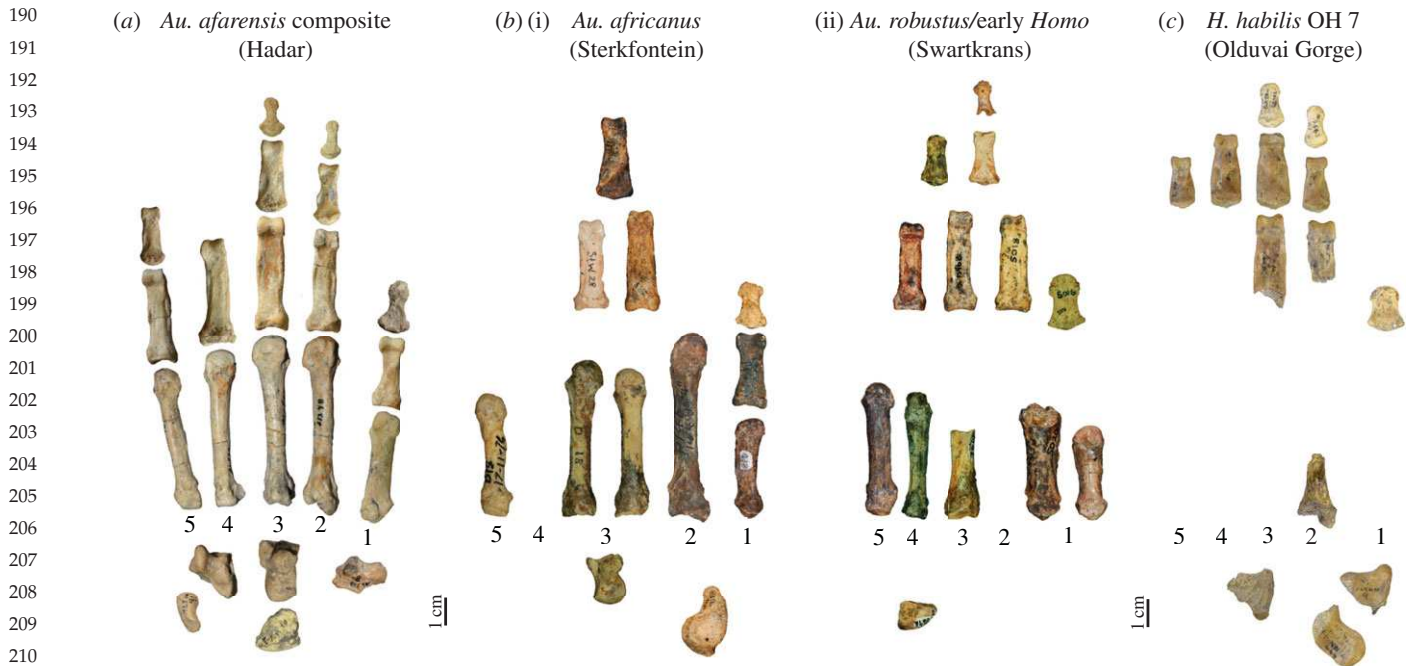


Figure 2. Fragmentary or unassociated early hominin hand remains. (a) The composite hand of *Au. afarensis* from various sites in Hadar, Ethiopia. Only metacarpals 2–5 articulate well together and are presumed to be from the same individual. (b) A sample of isolated hand bones from (i) Sterkfontein, generally attributed to *Au. africanus* and (ii) Swartkrans, associated with either *Au. robustus* or early *Homo*. None of the fossils can be associated with the same individual and several elements are not represented in the fossil record. (c) The associated juvenile hand fossils of *H. habilis* OH 7. Although the phalanges are well represented in the OH 7 hand, little of the thumb and palm is preserved making functional inferences challenging. All known wrist bones shown at bottom and numbers indicate digits 1–5. Note that the phalanges of rays 2–5 cannot be attributed to any particular ray with certainty. All bones are shown in palmar view (apart from the wrist bones) and to the same scale. (Online version in colour.)

supported the idea that the evolution of precision grip ability in *Au. afarensis* (and earlier hominins) should not be restricted to the context of stone tool behaviours, but may have initially evolved for non-lithic tool use or tool making, or any other complex manipulative behaviours that are required of extant non-human primates [14,17–20,24,28,29].

The inference of human-like manipulative ability in early hominins is generally inherently linked to the relaxation of selective pressures on the hands for locomotion. There has been decades of debate regarding the significance of arboreal locomotion in the early hominin locomotor repertoire and the functional importance of ‘arboreal’ features such as long and curved fingers (see review by Ward [70]). The most common evolutionary scenario is one in which, with the advent of bipedalism, long, curved fingers are needed less, or not at all, for grasping in trees, freeing the fingers to shorten in length (either via neutral or positive selection) and the thumb, somewhat by default, to become relatively long [18,71]. Alternatively, it has been suggested that human hand proportions may have been a pleiotropic by-product of reducing the length of our toes for bipedalism [18,72] or that they are actually symplesiomorphic, more similar to the Miocene apes, and that early hominins never had the long fingers typical of our living chimpanzee and bonobo cousins [28,73]. In all of these scenarios, human hand proportions can be viewed, at least partly, as an exaptation, rather than adaptation, for enhanced dexterity [18,28]. The key to choosing between these scenarios relies on being able to accurately reconstruct intrinsic hand (and potentially foot) proportions in early hominins, which is particularly challenging due to the poor preservation and lack of associated hand skeletons (see below). For example, the estimated human-like hand

proportions reconstructed for *Au. africanus* can only be estimated from unassociated metacarpals [74] (figure 2b). Hand proportions in *Paranthropus*/early *Homo* (e.g. Swartkrans specimens; figure 2c), the ‘handy-man’ *H. habilis* OH7 hand (*contra* [2]; figure 2d) and *Homo erectus* are completely unknown because there is simply not enough fossil evidence. The fossil hominin sites at Sierra de Atapuerca, Spain preserve numerous hand bones, ranging from a single early *Homo* phalanx from Sima del Elefante [75], to dozens of hand bones from Gran Dolina (*Homo antecessor*) [76] and Sima de los Huesos (*Homo heidelbergensis*), the latter of which remain unpublished [77]. All show morphology that can broadly be described as modern human-like, but they cannot be associated with any particular individual to directly quantify intrinsic hand proportions or provide an overall functional interpretation of the hand in these *Homo* species.

4. What can we learn from relatively complete hominin hand skeletons?

(a) Little foot

In addition to *Ar. ramidus*, there are only three relatively complete early hominin hands prior to Neandertals (figure 3). The first is the left hand of *Australopithecus prometheus* [78] StW 573 or ‘Little foot’, discovered in 1999 in the Silberberg Grotto of Sterkfontein, South Africa [9,78,79] and dated to as early as 3.7 Ma [80] or as late as 2.2 Ma [81] (figure 3a). It is associated with a relatively complete skeleton, allowing the rare opportunity to interpret the hand morphology within the context of the remainder of upper limb and postcranial skeleton, as well as

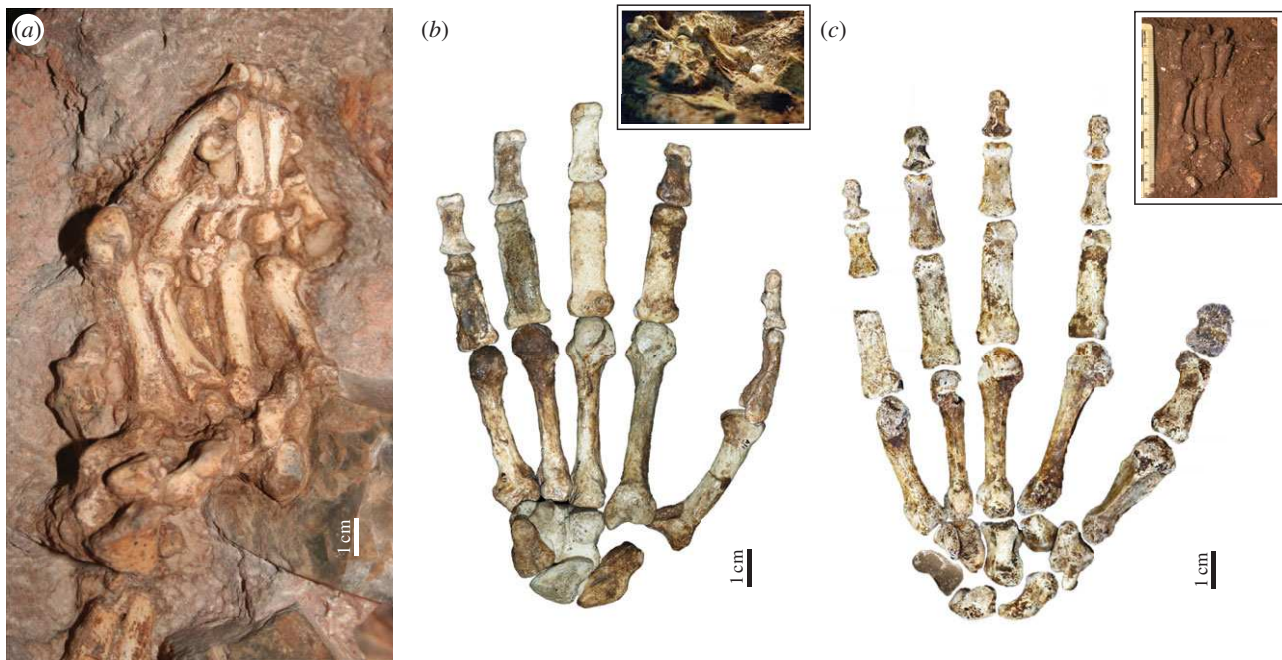


Figure 3. The associated hand remains of early hominins. (a) The left hand of *Au. prometheus* StW 573 [78] *in situ*; (b) the reconstructed right hand of MH2 (palmar view), with in set image of hand bones *in situ*; (c) the reconstructed right hand of Hand 1 *H. naledi* (palmar view) with in-set image of hand bones *in situ*. All hands are shown to the same scale. Photo credit: R. J. Clarke (a) and P. Schmid (b,c). (Online version in colour.)

taxonomically identifiable craniodental remains [9,78,79]. Preliminary observations of the hand morphology describe an unusual trapezium-Mc1 articulation that is unlike humans or chimpanzees, a robust, human-like thumb and proximal phalanges that are as curved as *Au. afarensis* [9]. No inferences about its manipulative capability have yet been made and we still await a full description and morphometric analysis of the left (and right; [79]) hand remains. However, curved phalanges suggest use of the hand for locomotor grasping and the current absence of stone tools in Member 2 at Sterkfontein [82] suggests that the evolution of any human-like manipulative capabilities in StW 573 may have been in response to non-lithic tool use.

(b) *Australopithecus sediba*

In 2010, a relatively complete right hand of the female adult *Australopithecus sediba* MH2 skeleton from Malapa, South Africa dated to 1.98 Ma was discovered [10,83] (figure 3b). Preserving 20 of the 27 bones in the human hand, MH2 offered the first (published) opportunity to make inferences about potential overall locomotor and manipulative hand function in an early hominin. Furthermore, the MH2 hand is found in association with a complete right arm [84] and much of the postcranial skeleton [83], and post-dates the appearance of stone tools in the archaeological record [13,63]. Although stone tools have not yet been found in direct association with *Au. sediba* [10], tool making (using stone and bone) has been documented at other local, contemporaneous sites, such as Sterkfontein [82] and Swartkrans [14,16].

The MH2 hand bones present a unique mosaic of features. The proximal and intermediate phalanges are mildly curved, similar to those of *Au. africanus* and OH 7 [10,11], and display well-developed flexor sheath ridges indicating powerful flexion of the hand during grasping. The wrist bones also show more similarities to other australopiths than to *Homo* [11] and the metacarpal shafts, especially that of the Mc1, are remarkably gracile (although the Mc3 of the male juvenile

MH1 skeleton is more robust, suggesting a strong degree of sexual dimorphism in the hand morphology) [10,11]. However, the distal pollical phalanx is broad with a well-developed FPL attachment, the first metacarpal has a distally extended, human-like positioning of the dorsal interosseous tendon, and the robust base of the fifth metacarpal suggests that the extrinsic and intrinsic musculature to the fifth finger were well developed [10] (figures 1 and 3b). (However, it is important to note that recent evidence has not found a strong correlation between entheses shape and the size of the muscle [85,86].) Perhaps most importantly, the completeness of the *Au. sediba* MH2 hand offers the first accurate quantification of hand proportions in an early hominin, showing that the thumb is not only long relative to the fingers, but is actually relatively longer than that of modern humans (i.e. falling outside the range of human variation) [10]. Such a long thumb would have greatly facilitated pad-to-pad opposition of the thumb and fingers, and ultimately lead to greater control and manipulation of small objects in particular [29].

With the traditional view that the hand of the last common ancestor of *Pan* and humans was generally *Pan*-like (but see [62,87]) with long fingers, one can consider the long thumb of humans to be the result of reducing the length of the fingers, rather than increasing the length of the thumb *per se* [18]. Such a scenario is expected in a hand that is no longer significantly used for locomotion. However, if the hand were still under forelimb-dominated locomotor selective pressures, then lengthening the thumb would allow a hominin to retain long fingers needed for grasping branches but also a long thumb that is advantageous for pad-to-pad precision gripping [18]. Digit proportions in *Au. sediba* reveal that the length of the thumb, and particularly the Mc1, is unexpectedly long (relative to the length of the third ray and to hand size) [10,11,28], suggesting perhaps a selection for increased thumb length. However, the length of the proximal and intermediate phalanges (relative to metacarpal length) is similar to that of

modern humans, suggesting long fingers were not a functional requirement of its locomotor strategy. Within the context of the remainder of the MH2 skeleton, it may be that the functional requirements of locomotion were fulfilled by the long, ape-like upper limb [84] and mildly curved phalanges [10], while the hand proportions of *Au. sediba* reflect the requirements of enhanced dexterity.

(c) *Homo naledi*

The recent discovery of a complete right hand (missing only the pisiform) of *Homo naledi* offers unprecedented insight into how the hominin hand might balance the functional requirements of both locomotor grasping and manipulation [11,88] (figure 3c). The *H. naledi* right hand was found partially articulated in association with over 120 other isolated hand bones in the Dinaledi Chamber of the Rising Star cave system, South Africa [11,88]. The remains have yet to be dated but present yet another distinct mosaic of morphological features not yet known in any other hominin [11]. The wrist is remarkably derived, demonstrating most of the key features considered advantageous for coping with high external loading of the thumb during tool-related behaviours [27,32,33,59–61] (figure 1). The radial carpal and carpometacarpal joints show signs of reorientation to a more human-like proximodistal alignment, including a trapezoid that is palmarly expanded to have a human-like 'boot-shape'. However, the trapezium-Mc1 articulation is remarkably small and there is no styloid process on the Mc3 [11]. The thumb is long relative to the fingers; although not as long as *Au. sediba* MH2, *H. naledi* falls only within the variation of modern human males (and outside that of females) [11]. The thumb is robust with a human-like attachment for the FPL muscle and well-developed, flaring muscle attachments for the opponens pollicis and first dorsal interosseous muscles, while the hamate-Mc5 articulation is saddle-shaped like in humans. Together, this morphology suggests enhanced opposition of the thumb to the fingers, particularly while holding and manipulating large objects, as well as efficient precision and precision pinch grips [35]. The suite of features found in the *H. naledi* wrist and palm have only been found in committed stone tool makers like Neandertals and *H. sapiens*, strongly suggesting that *H. naledi* had enhanced manipulative abilities for tool-related behaviours. Like with *Au. sediba*, there are no stone tools yet found in association with the *H. naledi* remains and without knowing the geological age, *H. naledi* may have used stone and/or organic materials as tools.

In contrast to the derived morphology of the wrist and palm, however, the fingers of *H. naledi* are strongly curved; more curved than australopiths, including *Au. afarensis* [11]. Phalangeal curvature is one of the best indicators of function in the hand [89–92]. The degree of longitudinal curvature is strongly correlated with the degree arboreal locomotion across primates, with climbing and, especially, suspensory taxa showing much stronger curvature than terrestrial quadrupedal or bipedal taxa [89–91]. Phalangeal curvature is also known to be sensitive to changes in locomotion throughout ontogeny, such that more arboreal juveniles have more strongly curved phalanges than their more terrestrial adult counterparts [93]. The strong phalangeal curvature in both the proximal and intermediate phalanges of *H. naledi* is a clear functional indicator that this hominin still used its hands for locomotor grasping. The combination of such

curved phalanges with a largely late-*Homo*-like wrist and palm demonstrates that (i) locomotor grasping was a functionally significant behaviour [94], not just a primitive, non-adaptive retention that has yet to be lost (*contra* [95]) and (ii) this hominin was capable of using their hands for both enhanced manipulation and arboreal locomotion, such that one functional role did not necessarily need to be sacrificed for the other.

5. New insights from new discoveries and methodologies

Decades of research aiming to identify and test the potential morphological features of the human and hominin hand that are adaptive for stone tool behaviours were somewhat undermined by the discovery of the Late Pleistocene *Homo floresiensis* [96]. Hand bones dated to 17–19 000 BP [97,98] and belonging to at least two, small-bodied individuals (LB1 and LB6) are surprisingly primitive; more similar to extant apes and australopiths than to other *Homo* species, despite their remarkably young age [98–100]. For example, although *H. floresiensis* has a broad pollical distal phalanx with a human-like FPL attachment [98,100], the proximal phalanges are curved to a similar degree as in *Au. afarensis* [100] and the wrist lacks a Mc3 styloid process, a boot-shaped trapezoid, and a reorientation of the radial carpal and metacarpal joints that are found in later *Homo* (and *H. naledi*) [98,99]. However, there is a well-documented archaeological sequence at Flores clearly demonstrating that stone tool making and use were part of the behavioural repertoire of *H. floresiensis* from as early as 840 Ka [97,101]. Thus, the direct association between the largely primitive hand of *H. floresiensis* and stone tools (produced via a simple reduction sequence [97]) calls into question our traditional assumptions about the necessary morphological features and biomechanical consequences of stone tool production [98].

Furthermore, recent archaeological discoveries have changed the traditional perception that stone tool production is an ability limited to the genus *Homo* (see review in [8]). The first is that of stone cut marks on bone at Dikika, Ethiopia dated to 3.39 Ma and in deposits currently associated only with *Au. afarensis* [12,102]. The archaeological evidence demonstrates the use of sharp-edged stones to remove flesh and blunt stones to access marrow ([12], but see [103]). McPherron *et al.* [12,104] put forth the important message of changing the traditional archaeological paradigm that stone tool use could not have occurred prior to stone tool making, and the need to look for evidence of stone tool use in deposits that predate recognizable stone tools (and pre-date *Homo*).

McPherron *et al.* [12,104] somewhat controversial [103] claim of tool-use ability in pre-2.6 Ma-hominins is further substantiated by the recent discovery of pre-Oldowan stone tools, currently named Lomekwian, dated to 3.3 Ma from Lomekwi 3 in Kenya [13]. These tools are 700 000 years older than earliest Oldowan technology (2.6 Ma [63]) and over 500 000 years older than the earliest possible fossil evidence of *Homo* (2.8 Ma [105]). Their techno-morphology suggests they were made using arm and hand motions that are most similar to the hammer-on-anvil technique used by chimpanzees during nut-cracking (but likely requiring greater cognitive ability [106], see also [107]), rather than the free-hand knapping of the Oldowan [13]. The inferred knapping technique suggests a substantial

379 degree of hand motor control and forceful loading of the
 380 hands, but likely less dexterity than Oldowan-making homi-
 381 nins [13]. These tools are found in the same geographical
 382 and chronological context of *Kenyanthropus platyops*, but are
 383 also contemporaneous with *Au. afarensis* [13]. Importantly,
 384 both the Lomekwian and Dikika cut marks [12] are too old
 385 to be associated with currently known *Homo* fossils, and
 386 thus demonstrate a manipulative (and cognitive) ability of
 387 pre-*Homo* hominins that has not been traditionally recognized.

388 Biomechanical studies of tool use and tool making have
 389 helped to clarify how fossil hominin hands may have been
 390 loaded during stone tool-use and tool-making activities
 391 [34,52–54]. Rolian *et al.* [52] created artificial ‘stone tools’
 392 instrumented with force plates to examine how the external
 393 forces and joint stress were distributed across the thumb
 394 and index finger. They found that the thumb experienced
 395 higher external loads and joint stress during tool making
 396 than during flake use (but see [53,54] and below). They also
 397 found that individuals with longer digits required relatively
 398 less muscle force to stabilize the digit joints and experienced
 399 relatively less joint stress during stone tool behaviours,
 400 because their digits and joints were relatively more robust.
 401 The implications of their results, they suggest, are that the
 402 gracile pollical metacarpals of chimpanzees and early austra-
 403 lopiths could not produce or withstand the high forces that
 404 occur during stone tool making [52].

405 Others [34,53,54] have also investigated external loading of
 406 the radial digits during Oldowan stone tool making, but by
 407 using pressure strips along the digits, such that force was
 408 measured directly on the hand rather than by the tool (as in
 409 [52]). In contrast to Rolian *et al.* [52], Williams *et al.* [53] found
 410 that the loading experienced by the thumb during tool
 411 making was actually lower (not higher) than that of the index
 412 and middle finger. In other words, the human thumb is
 413 ‘over-built’ for Oldowan stone tool making, but appears well
 414 adapted for the much higher external forces experienced
 415 during flake use [54]. Key & Dunmore [34] further suggest
 416 that the robust thumb of humans and other hominins was
 417 selected for, at least in part, the loads experienced in the non-
 418 dominant hand during stone tool making (although these
 419 loads are much lower than those experienced by the thumb
 420 of the dominant hand). This variation in experimental results
 421 at least partly reflects differences in methodology (portable
 422 force plates [52] *versus* pressure strips [34,53,54], and novice
 423 [52] *versus* expert [34,53,54] knappers), but also demonstrates
 424 the challenges of trying to simulate and quantify the biomechan-
 425 ics of tool-related manipulative behaviours in fossil hominins
 426 using modern humans (and modern human hand anatomy).

427 Kinematic modelling of the primate hand also has
 428 the potential to make more informed inferences of the manip-
 429 ulative abilities in early hominins. Feix *et al.* [108] created a
 430 kinematic model of thumb and index finger precision grip
 431 and manipulative movement based on bony hand morphology
 432 in a broad sample of extant primates and fossil hominins. They
 433 found that joint mobility and (scaled) digit proportions are
 434 critical for determining precision grip and manipulation
 435 potential (figure 1), but having a relatively long thumb or
 436 high joint mobility alone do not necessarily result in greater
 437 dexterity [108]. Despite (potential) differences in digit pro-
 438 portions and joint mobility in australopiths, *Au. afarensis* and
 439 *Au. sediba* show a manipulation workspace that is similar to
 440 that of modern humans [1088], supporting previous inter-
 441 pretations of increased dexterity in these taxa [10,18,29] and

archaeological evidence of tool-related behaviours in
 pre-*Homo* hominins [12,13].

Finally, greater access to three-dimensional scanning
 techniques, including surface scanning [34–36,53–61,98,99]
 and microtomography [109,110], has allowed for more com-
 prehensive functional analyses of both the external and
 internal morphology of hand bones. In particular, analyses
 of the internal trabecular morphology of hand bones has pro-
 vided new insights into how early hominins may have
actually, rather than *potentially*, used their hands [110]. Trabe-
 cular bone remodels throughout an individual’s life in
 response to mechanical loading; a concept known as bone
 functional adaptation [111]. Several experimental studies
 have shown that changes in loading direction or magnitude
 can be associated with corresponding changes in the orien-
 tation of trabeculae struts or relative volume of trabecular
 bone (e.g. [112,113]). Previous comparative studies show
 that variation in trabecular structure in extant hominoid
 (including humans) hand bones correlates well with differ-
 ences in inferred joint posture and loading during
 locomotion and manipulation [110]. Within this context,
 Skinner *et al.* [21] recently analysed the trabecular structure
 in several fossil hominin hand bones, and found that Nean-
 dertals, early *Homo sapiens* and modern humans share a
 distinct asymmetrical pattern in the distribution of trabecular
 bone in the metacarpals consistent with forceful opposition of
 the thumb and fingers that is not found in other extant apes
 (including nut-cracking Tai chimpanzees). Interestingly,
Au. africanus also shows the Neandertal- and human-like pat-
 tern of trabecular bone, suggesting that this early hominin
 was also habitually using forceful human-like opposition of
 the thumb and fingers, such as in the precision and power
 squeeze grips that are used during tool use and tool making
 [21]. Although many have proposed that *Au. africanus* [64]
 and earlier hominins [18–20,28,29] were potentially capable
 of human-like precision grips, the trabecular structure provides
 more direct evidence that *Au. africanus* was *actually* loading
 its hand in a human-like way, despite not having a fully
 human-like external hand morphology [21,114]. These results
 provide morphological evidence of enhanced manipula-
 tive ability in an australopith and additional support for
 archaeological evidence of tool use [12] and tool making [13]
 in pre-*Homo* hominins.

6. Conclusion

Darwin [115] first proposed that the advent of bipedalism
 was directly linked tool use as it freed the hands from the
 constraints of locomotion. This view was maintained with
 the earliest discoveries of stone tools and fossil hominin
 remains in the 1950s and 1960s [1,116]. However, there was
 a paradigm shift in the 1970s with the discovery of the
 small-brained, bipedal *Au. afarensis* 1.5 Myr earlier than the
 appearance of stone tools [8]. Further discoveries of earlier
 bipedal hominins dating back to at least approximately
 6 Ma [65] only increased the gap between bipedalism and
 stone tools [8]. Thus, tool-related behaviours have generally
 no longer been thought to have a cause–effect relationship
 with the origin of hominin bipedalism [50,117,118]. However,
 it may be worthwhile to revisit Darwin’s original hypothesis.
 On the one hand, recent discoveries are closing chronological
 gap between the origin of bipedalism and evidence for

442 tool-related behaviours. Morphological evidence (albeit lim-
 443 ited) suggests the potential for human-like precision grip
 444 ability in some of the earliest hominins (*Orrorin*; [19]). Fur-
 445 thermore, comparative extant primate evidence [22–24] and
 446 the recognition of the enhanced manipulative and cognitive
 447 abilities required for the production of Oldowan
 448 [106,107,119] and, less so, Lomekwian stone tools [13],
 449 together suggest that there was likely a long history of exper-
 450 imental tool use and improvements to manual dexterity prior
 451 to the first recognizable stone tool behaviours in the archaeo-
 452 logical record [17,22]. On the other hand, morphological
 453 evidence from relatively complete hand skeletons [9–11]
 454 indicates that fossil hominins did not necessarily need to
 455 ‘free’ their hands from the functional requirements of loco-
 456 motion to increase their dexterity. Together recent evidence
 457 suggests that pre-*Homo* hominins were more dextrous than
 458 has been traditionally assumed, that tool-related behaviours
 459 have played a chronologically deeper and more prominent
 460 role in our evolutionary history than previously considered,
 461 and that the hands of these early hominins were capable of

combining the functional requirements of both arboreal
 locomotion and enhanced manipulation.

Competing interests. I have no competing interests.

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References

1. Washburn SL. 1960 Tools and human evolution. *Sci. Am.* **203**, 62–75. (doi:10.1038/scientificamerican.0960-62)
2. Napier JR. 1962 The evolution of the hand. *Sci. Am.* **207**, 56–62. (doi:10.1038/scientificamerican.1262-56)
3. Leakey LSB. 1959 A new fossil skull from Olduvai. *Nature* **184**, 491–493. (doi:10.1038/184491a0)
4. Leakey LSB. 1960 Recent discoveries at Olduvai Gorge. *Nature* **188**, 1050–1052. (doi:10.1038/1881050a0)
5. Leakey LSB. 1961 New finds at Olduvai Gorge. *Nature* **189**, 649–650. (doi:10.1038/189649a0)
6. Napier JR. 1962 Fossil hand bones from Olduvai Gorge. *Nature* **196**, 409–411. (doi:10.1038/196409a0)
7. Leakey LSB, Tobias PV, Napier JR. 1964 A new species of the genus *Homo* from Olduvai Gorge. *Nature* **202**, 7–9. (doi:10.1038/202007a0)
8. de la Torre I. 2011 The origins of stone tool technology in Africa: a historical perspective. *Phil. Trans. R. Soc. B* **366**, 1028–1037. (doi:10.1098/rstb.2010.0350)
9. 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.
10. Kivell TL, Kibii JM, Churchill SE, Schmid P, Berger LR. 2011 *Australopithecus sediba* hand demonstrates mosaic evolution of locomotor and manipulative abilities. *Science* **333**, 1411–1417. (doi:10.1126/science.1202625)
11. Kivell TL, Deane AS, Tocheri MW, Orr CM, Schmid P, Hawks J, Berger LR, Churchill SE. 2015 The hand of *Homo naledi*. *Nat. Comm.*
12. McPherron SP, Alemseged Z, Marean CW, Wynn JG, Reed D, Geraads D, Bobe R, Bérart HA. 2010 Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature* **466**, 857–860. (doi:10.1038/nature09248)
13. Harmand S *et al.* 2015 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. *Nature* **521**, 311–315. (doi:10.1038/nature14464)
14. Susman RL. 1988 Hand of *Paranthropus robustus* from Member 1, Swartkrans: fossil evidence for tool behaviour. *Science* **240**, 781–784. (doi:10.1126/science.3129783)
15. Susman RL. 1994 Fossil evidence for early hominid tool use. *Science* **265**, 1570–1573. (doi:10.1126/science.8079169)
16. Backwell LR, d’Errico F. 2001 Evidence of termite foraging by Swartkrans early hominids. *Proc. Natl Acad. Sci. USA* **98**, 1358–1363. (doi:10.1073/pnas.98.4.1358)
17. 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. (doi:10.1002/evan.10094)
18. Alba DM, Moyà-Solà S, Köhler M. 2003 Morphological affinities of the *Australopithecus afarensis* hand on the basis of manual proportions and relative thumb length. *J. Hum. Evol.* **44**, 225–254. (doi:10.1016/S0047-2484(02)00207-5)
19. Almécija S, Moyà-Solà S, Alba DM. 2010 Early origin for human-like precision grasping: a comparative study of pollical distal phalanges in fossil hominins. *PLoS ONE* **5**, e11727. (doi:10.1371/journal.pone.0011727)
20. Almécija S, Wallace IJ, Judex S, Albar DM, Moyà-Solà S. 2015 Comment on ‘Human-liked hand use in *Australopithecus africanus*. *Science*.
21. Skinner MM, Stephens NB, Tsegai ZI, Foote AC, Nguyen NH, Gross T, Pahr DH, Hublin J-J, Kivell TL. 2015 Human-like hand use in *Australopithecus africanus*. *Science* **347**, 395–399. (doi:10.1126/science.1261735)
22. Haslam M *et al.* 2009 Primate archaeology. *Nature* **460**, 339–344. (doi:10.1038/nature08188)
23. Luncz LV, Wittig RM, Boesch C. 2015 Primate archaeology reveals cultural transmission in wild chimpanzees (*Pan troglodytes verus*). *Phil. Trans. R. Soc. B* **370**, 20140348. (doi:10.1098/rstb.2014.0348)
24. Whiten A. 2015 Experimental studies illuminate the cultural transmission of percussive technologies in *Homo* and *Pan*. *Phil. Trans. R. Soc. B* **370**, 20140359. (doi:10.1098/rstb.2014.0359)
25. 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. (doi:10.1002/ajpa.1330830403)
26. Hamrick MW, Inouye SE. 1995 Thumbs, tools and early humans. *Science* **268**, 586–587. (doi:10.1126/science.7725112)
27. Rolian C, Gordon AD. 2013 Reassessing manual proportions in *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* **152**, 393–406. (doi:10.1002/ajpa.22365)
28. Almécija S, Alba DM. 2014 On manual proportions and pad-to-pad precision grasping in *Australopithecus afarensis*. *J. Hum. Evol.* **73**, 88–92. (doi:10.1016/j.jhev.2014.02.006)
29. Marzke MW. 1997 Precision grips, hand morphology, and tools. *Am. J. Phys. Anthropol.* **102**, 91–110. (doi:10.1002/(SICI)1096-8644(199701)102:1<91::AID-AJPA8>3.0.CO;2-G)
30. Susman RL. 1998 Hand function and tool behaviour in early hominids. *J. Hum. Evol.* **35**, 23–46. (doi:10.1006/jhev.1998.0220)
31. Marzke MW, Marzke RF. 2000 Evolution of the human hand: approaches to acquiring, analysing and interpreting the anatomical evidence. *J. Anat.*

- 505 **197**, 121–140. (doi:10.1046/j.1469-7580.2000.
506 19710121.x)
- 507 32. Tocheri MW, Orr CM, Jacofsky MC, Marzke MW. 2008
508 The evolutionary history of the hominin hand since
509 the last common ancestor of *Pan* and *Homo*.
510 *J. Anat.* **212**, 544–562. (doi:10.1111/j.1469-7580.
511 2008.00865.x)
- 512 33. Marzke MW. 2013 Tool making, hand morphology
513 and fossil hominins. *Phil. Trans. R. Soc. B* **368**,
514 20120414. (doi:10.1098/rstb.2012.0414)
- 515 34. Key AJ, Dunmore CJ. 2015 The evolution of the
516 hominin thumb and the influence exerted by the
517 non-dominant hand during stone tool production.
518 *J. Hum. Evol.* **78**, 60–69. (doi:10.1016/j.jhevol.
519 2014.08.006)
- 520 **Q1** 35. Marzke MW, Toth N, Schick K, Reece S, Steinberg B,
521 Hunt K, Linscheid RL, An, K-N. 1998 EMG study of
522 hand muscle recruitment during hard hammer
523 percussion manufacture of Oldowan tools.
524 *Am. J. Phys. Anthropol.* **105**, 315–332. (doi:10.
525 1002/(SICI)1096-8644(199803)105:3<315::AID-
526 AJPA3>3.0.CO;2-Q)
- 527 36. Hamrick MW, Churchill SE, Schmitt D, Hylander WL.
528 1998 EMG of the human flexor pollicis longus
529 muscle: implications for the evolution of hominid
530 tool use. *J. Hum. Evol.* **34**, 123–136. (doi:10.1006/
531 jhev.1997.0177)
- 532 37. Marzke MW, Shackley MS. 1986 Hominid hand use
533 in the Pliocene and Pleistocene: evidence from
534 experimental archaeology and comparative
535 morphology. *J. Hum. Evol.* **15**, 439–460. (doi:10.
536 1016/S0047-2484(86)80027-6)
- 537 38. Boesch C, Boesch H. 1993 Different hand postures
538 for pounding nuts with natural hammers by
539 wild chimpanzees. In *Hands of primates* (eds
540 H Preuschoft, D Chiver), pp. 31–43. New York, NY:
541 Springer.
- 542 39. Christel MI. 1993 Grasping techniques and hand
543 preferences in Hominoidea. In *Hands of primates*
544 (eds H Preuschoft, D Chiver), pp. 91–108.
545 New York, NY: Springer.
- 546 40. Jones-Engel LE, Bard KA. 1996 Precision grips in
547 young chimpanzees. *Am. J. Primatol.* **39**, 1–15.
548 (doi:10.1002/(SICI)1098-2345(1996)39:1<1::AID-
549 AJP1>3.0.CO;2-2)
- 550 41. Marzke MW, Wullstein KL. 1996 Chimpanzee and
551 human grips: a new classification with a focus
552 on evolutionary morphology. *Int. J. Primatol.* **17**,
553 117–139. (doi:10.1007/BF02696162)
- 554 42. Christel MI, Fragaszy D. 2000 Manual function
555 in *Cebus apella*: digital mobility, reshaping,
556 and endurance in repetitive grasping.
557 *Int. J. Primatol.* **21**, 697–719. (doi:10.1023/
558 A:1005521522418)
- 559 43. Crast J, Fragaszy D, Hayashi M, Matsuzawa T.
560 2009 Dynamic in-hand movements in adult and
561 young juvenile chimpanzees (*Pan troglodytes*).
562 *Am. J. Phys. Anthropol.* **138**, 274–285. (doi:10.
563 1002/ajpa.20925)
- 564 44. Gumert MD, Kluck M, Malaivijitnond S. 2009 The
565 physical characteristics and usage patterns of stone
566 axe and pounding hammers used by long-tailed
567 macaques in the Andaman Sea region of Thailand.
Am. J. Primatol. **71**, 594–608. (doi:10.1002/
ajp.20694)
45. Pouydebat E, Reghem E, Borel A, Gorce P. 2011
Diversity of grip in adults and young humans
and chimpanzees (*Pan troglodytes*). *Behav.*
Brain Res. **218**, 21–28. (doi:10.1016/j.bbr.2010.
11.021)
46. Marzke MW, Marchant LF, McGrew WC, Reece SP.
2014 Grips and hand movements of chimpanzees
during feeding in Mahale Mountains National Park,
Tanzania. *Am. J. Phys. Anthropol.* **156**, 317–326.
(doi:10.1002/ajpa.22651)
47. Neufuss J, Humle T, Deschner T, Robbins MM,
Siriani G, Boesch C, Kivell TL. 2015 Diversity of
hand grips and laterality in wild African apes. *Folia*
Primatol.
48. 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. (doi:10.1002/ajpa.
1330890303)
49. Landsmeer JMF, Long C. 1965 The mechanism of
finger control, based on electromyograms and
location analysis. *Cells Tissues Organs* **60**, 330–347.
(doi:10.1159/000142668)
50. Marzke MW. 1983 Joint functions and grips of the
Australopithecus afarensis hand, with special
reference to the region of the capitate. *J. Hum. Evol.*
12, 197–211. (doi:10.1016/S0047-2484(83)
80025-6)
51. Diogo R, Richmond BG, Wood B. 2012 Evolution and
homologies of primate and modern human hand
and forearm muscles with notes on thumb
movements and tool use. *J. Hum. Evol.* **63**, 64–78.
(doi:10.1016/j.jhevol.2012.04.001)
52. Rolian C, Lieberman DE, Zermeno JP. 2011 Hand
biomechanics during simulated stone tool use.
J. Hum. Evol. **61**, 26–41. (doi:10.1016/j.jhevol.
2011.01.008)
53. Williams EM, Gordon AD, Richmond BG. 2012 Hand
pressure distribution during Oldowan stone tool
production. *J. Hum. Evol.* **62**, 520–532. (doi:10.
1016/j.jhevol.2012.02.005)
54. Williams EM, Richmond BG. 2012 Manual pressure
distribution during stone tool use. *Am. J. Phys.*
Anthropol. **147**(Suppl. 54), 303.
55. Marzke MW, Marzke RF, Linscheid RL, Smutz P,
Steinberg B, Reece S, An K-N. 1999 Chimpanzee
thumb muscle cross sections, moment arms and
potential torques, and comparisons with humans.
Am. J. Phys. Anthropol. **110**, 163–178. (doi:10.
1002/(SICI)1096-8644(199910)110:2<163::AID-
AJPA4>3.0.CO;2-A)
56. Maki J, Trinkaus E. 2011 Opponens pollicis
mechanical effectiveness in Neandertals and early
modern humans. *PaleoAnthropology* **2011**, 62–71.
(doi:10.4207/PA.2011.ART43)
57. Shrewsbury MM, Marzke MW, Linscheid RL, Reece
SP. 2003 Comparative morphology of the pollical
distal phalanx. *Am. J. Phys. Anthropol.* **121**, 30–47.
(doi:10/1002/ajpa.10192)
58. Marzke MW, Marzke RF. 1987 The third metacarpal
styloid process in humans: origin and functions.
Am. J. Phys. Anthropol. **73**, 415–431. (doi:10.1002/
ajpa.1330730403)
59. 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.
Dissertation, Arizona State University, Tempe,
AZ, USA.
60. Tocheri MW, Marzke MW, Liu D, Bae M, Jones GP,
Williams RC, Razdan A. 2003 Functional capabilities
of modern and fossil hominid hands: three-
dimensional analysis of trapezia. *Am. J. Phys.*
Anthropol. **122**, 101–112. (doi:10.1002/ajpa.10235)
61. 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. (doi:10.1016/j.jhevol.
2005.06.005)
62. Lovejoy CO, Simpson SW, White TD, Asfaw B, Suwa
G. 2009 Careful climbing in the Miocene: the
forelimbs of *Ardipithecus ramidus* and humans are
primitive. *Science* **326**, 70, 70e1–70e8. (doi:10.
1126/science.1175827)
63. Semaw S *et al.* 2003 2.6-Million-year-old stone
tools and associated bones from OGS-6 and OGS-7,
Gona, Afar, Ethiopia. *J. Hum. Evol.* **45**, 169–177.
(doi:10.1016/S0047-2484(03)00093-9)
64. 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*
(eds GH Sperber), pp. 171–183. New York, NY:
Wiley-Liss.
65. 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.: Series*
IIA-Earth Planetary Sci. **332**, 137–144. (doi:10.
1016/S1251-8050(01)01529-4)
66. Gommery D, Senut B. 2006 La phalange distale du
pouce d'*Orrorin tugenensis* (Miocene supérieur du
Kenya). *Geobios* **39**, 372–384. (doi:10.1016/j.
geobios.2005.03.002)
67. 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.
(doi:10.1002/ajpa.1330570410)
68. 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. (doi:10.1016/j.
jhevol.2005.02.005)
69. Ward CV, Kimbel WH, Harmon EH, Johanson DC.
2012 New postcranial fossils of *Australopithecus*
afarensis from Hadar, Ethiopia (1990–2007).
J. Hum. Evol. **63**, 1–51. (doi:10.1016/j.jhevol.
2011.11.012)
70. Ward CV. 2002 Interpreting the posture and
locomotion of *Australopithecus afarensis*: where do
we stand? *Am. J. Phys. Anthropol.* **119**(Suppl. 35),
185–215. (doi:10.1002/ajpa.10185)

- 568 71. Wood Jones F. 1916 *Arboreal man*. London, UK:
569 Arnold.
- 570 72. Rolian C, Lieberman DE, Hallgrímsson B. 2010 The
571 coevolution of human hands and feet. *Evolution* **64**,
572 1558–1568. (doi:10.1111/j.1558-5646.2009.
573 00944.x)
- 574 73. Almécija S, Shrewsbury M, Rook L, Moyà-Solà S.
575 2014 The morphology of *Oreopithecus bambolii*
576 pollical distal phalanx. *Am. J. Phys. Anthropol.* **153**,
577 582–597. (doi:10.1002/ajpa.22458)
- 578 74. Green DJ, Gordon AD. 2008 Metacarpal proportions
579 in *Australopithecus africanus*. *J. Hum. Evol.* **54**,
580 705–719. (doi:10.1016/j.jhevol.2007.10.007)
- 581 75. Lorenzo C, Pablos A, Carretero JM, Huguet R,
582 Valverdú J, Martínón-Torres M, Arsuaga JL,
583 Carbonell E, Bermúdez de Castro JM. 2015 Early
584 Pleistocene human hand phalanx from the Sima del
585 Elefante (TE) cave site in Sierra de Atapuerca
586 (Spain). *J. Hum. Evol.* **78**, 114–121. (doi:10.1016/j.
587 jhevol.2014.08.007)
- 588 76. Lorenzo C, Arsuaga JL, Carretero JM. 1999 Hand and
589 foot remains from the Gran Dolina Early Pleistocene
590 site (Sierra de Atapuerca, Spain). *J. Hum. Evol.* **37**,
591 501–522. (doi:10.1006/jhev.1999.0341)
- 592 77. Arsuaga JL, Martínez I, García A, Carretero JM,
593 Lorenzo C, García N, Ortega AI. 1997 Sima de los
594 Huesos (Sierra de Atapuerca, Spain). The site.
595 *J. Hum. Evol.* **33**, 109–127. (doi:10.1006/jhev.
596 1997.0132)
- 597 78. Clarke RJ. 2013 *Australopithecus* from Sterkfontein
598 Caves, South Africa. In *The paleobiology of*
599 *Australopithecus* (eds KE Reed, JG Fleagle, RE
600 Leakey), pp. 105–123. Dordrecht, The Netherlands:
601 Springer.
- 602 79. Clarke RJ. 2008 Latest information on Sterkfontein's
603 *Australopithecus* skeleton and a new look at
604 *Australopithecus*. *S. Afr. J. Sci.* **104**, 443–449.
605 (doi:10.1590/S0038-23532008000600015)
- 606 80. Granger DE, Gibbon RJ, Kuman K, Clarke RJ,
607 Bruxelles L, Caffee MW. 2015 New cosmogenic
608 burial ages for Sterkfontein Member 2
609 *Australopithecus* and Member 5 Oldowan. *Nature*
610 **522**, 85–88. (doi:10.1038/nature14268)
- 611 81. Pickering R, Kramers JD. 2010 Re-appraisal of the
612 stratigraphy and determination of new U-Pb dates
613 for the Sterkfontein hominin site, South Africa.
614 *J. Hum. Evol.* **59**, 70–86. (doi:10.1016/j.jhevol.
615 2010.03.014)
- 616 82. Kuman K, Clarke RJ. 2000 Stratigraphy, artefact
617 industries and hominid associations for Sterkfontein,
618 Member 5. *J. Hum. Evol.* **38**, 827–847. (doi:10.
619 1006/jhev.1999.0392)
- 620 83. Berger LR, de Ruiter DJ, Churchill SE, Schmid P,
621 Carlson KJ, Dirks PH, Kibii JM. 2010 *Australopithecus*
622 *sediba*: A new species of *Homo*-like australopith
623 from South Africa. *Science* **328**, 195–204. (doi:10.
624 1126/science.1184944)
- 625 84. Churchill SE *et al.* 2013 The upper limb of
626 *Australopithecus sediba*. *Science* **340**, 1233477.
627 (doi:10.1126/science.1233477)
- 628 85. Rabey K, Green DJ, Taylor AB, Begun DR, Richmond
629 BG, McFarlin SC. 2015 Locomotor activity influences
630 muscle architecture and bone growth but not
muscle attachment site morphology. *J. Hum. Evol.*
78, 91–102. (doi:10.1016/j.jhevol.2014.10.010)
86. Williams-Hatala EM, Hiles S, Hatala KG, Rabey K.
2015 Relationships between muscle architectural
anatomy and the morphology of entheses in the
thenar and hypothenar regions of modern humans.
Am. J. Phys. Anthropol. **156**(Suppl. 60), 326.
87. Drapeau MS, Ward CV. 2007 Forelimb segment
length proportions in extant hominoids and
Australopithecus afarensis. *Am. J. Phys. Anthropol.*
132, 327–343. (doi:10.1002/ajpa.20533)
88. Berger LR *et al.* 2015 A new species of the Genus
Homo from the Dinaledi Chamber, South Africa.
Nature.
89. Jungers WL, Godfrey LR, Simons EL, Chatrath PS.
1997 Phalangeal curvature and positional
behaviour in extinct sloth lemurs (Primates,
Palaeopithecidae). *Proc. Natl Acad. Sci. USA* **94**,
11 998–12 001. (doi:10.1073/pnas.94.22.11998)
90. Richmond BG. 2007 Biomechanics of phalangeal
curvature. *J. Hum. Evol.* **53**, 678–690. (doi:10.1016/
j.jhevol.2007.05.011)
91. Deane AS, Begun DR. 2008 Broken fingers: retesting
locomotor hypotheses for fossil hominoids using
fragmentary proximal phalanges and high-
resolution polynomial curve fitting (HR-PCF).
J. Hum. Evol. **55**, 691–701. (doi:10.1016/j.jhevol.
2008.05.005)
92. Nguyen NH, Pahr DH, Gross T, Skinner MM, Kivell
TL. 2014 Micro-finite element (μ FE) modeling of
the siamang (*Symphalangus syndactylus*) third
proximal phalanx: the functional role of curvature
and the flexor sheath ridge. *J. Hum. Evol.* **67**,
60–75. (doi:10.1016/j.jhevol.2013.12.008)
93. Richmond BG. 1998 Ontogeny and biomechanics of
phalangeal form in primates. Dissertation, State
University of New York at Stony Brook, NY, USA.
94. Stern Jr JT, Susman RL. 1983 The locomotor
anatomy of *Australopithecus afarensis*. *Am. J. Phys.
Anthropol.* **60**, 279–317. (doi:10.1002/ajpa.
1330600302)
95. Latimer B. 1991 Locomotor adaptations in
Australopithecus afarensis: the issue of arboreality.
In *Origine (s) de la Bipédie chez les Hominidés* (eds
B Senut, Y Coppens), pp. 169–176. Paris: CNRS.
96. Brown P, Sutikna T, Morwood MJ, Soejono RP,
Jatmiko, Wayhu Saptomo E, Awe Due R. 2004
A new small-bodied hominin from the Late
Pleistocene of Flores, Indonesia. *Nature* **431**,
1055–1061. (doi:10.1038/nature02999)
97. Moore MW, Sutikna T, Morwood MJ, Brumm A.
2009 Continuities in stone flaking technology at
Liang Bua, Flores, Indonesia. *J. Hum. Evol.* **57**,
503–526. (doi:10.1016/j.jhevol.2008.10.006)
98. Orr CM, Tocheri MW, Burnett SE, Awe Due R, Wahyu
Saptomo E, Sutikna T, Wasisto S, Morwood MJ,
Jungers WL. 2013 New wrist bones of *Homo*
floresiensis from Liang Bua (Flores, Indonesia).
J. Hum. Evol. **64**, 109–129. (doi:10.1016/j.jhevol.
2012.10.003)
99. Tocheri MW, Orr CM, Larson SG, Sutikna T, Wahyu
Saptomo E, Awe Due R, Djubiantono T, Morwood
MJ, Jungers WL. 2007 The primitive wrist of *Homo*
floresiensis and its implications for hominin
evolution. *Science* **317**, 1743–1745. (doi:10.1126/
science.1147143)
100. Larson SG, Jungers WL, Tocheri MW, Orr CM,
Morwood MJ, Sutikna T, Awe Due R, Djubiantono T.
2009 Descriptions of the upper limb skeleton of
Homo floresiensis. *J. Hum. Evol.* **57**, 555–570.
(doi:10.1016/j.jhevol.2008.06.007)
101. Brumm A, Aziz F, van den Bergh GD, Morwood MJ,
Moore MW, Kurniawan I, Hobbs DR, Fullagar R.
2006 Early stone technology on Flores and its
implications for *Homo floresiensis*. *Nature* **441**,
624–628. (doi:10.1038/nature04618)
102. Alemseged Z, Spoor F, Kimbel WH, Bobe R, Geraads
D, Reed D, Wynn JG. 2006 A juvenile early hominin
skeleton from Dikika, Ethiopia. *Nature* **443**,
296–301. (doi:10.1038/nature05047)
103. Dominguez-Rodrigo M, Pickering TP, Bunn HT. 2011
Reply to McPherron *et al.*: Doubting Dikika is about
data, not paradigms. *Proc. Natl Acad. Sci. USA* **108**,
e117. (doi:10.1073/pnas.1104647108)
104. McPherron SP, Alemseged Z, Marean CW, Wynn JG,
Reed D, Geraads D, Bobe R, Béarat HA. 2011 Tool-
marked bones from before the Oldowan change the
paradigm. *Proc. Natl Acad. Sci. USA* **108**, e116.
(doi:10.1073/pnas.1101298108)
105. Villmoare B, Kimbel WH, Seyoum C, Campisano CJ,
DiMaggio EN, Rowan J, Braun DR, Arrowsmith JR,
Reed KE. 2015 Early *Homo* at 2.8 Ma from Ledi-
Geraru, Afar, Ethiopia. *Science* **347**, 1352–1355.
(doi:10.1126/science.aaa1343)
106. de la Torre I. 2010 Insights on the technical
competence of the early Oldowan. In *Stone tools*
and the evolution of human cognition (eds A Nowell,
I Davidson), pp. 45–65. Boulder, CO: University
Press of Colorado.
107. Brill B, Parry R, Dietrich G. 2015 How similar are
nut-cracking and stone-flaking? A functional
approach to percussive technology. *Phil.
Trans. R. Soc. B* **370**, 20140355. (doi:10.1098/rstb.
2014.0355)
108. Feix T, Kivell TL, Pouydebat E, Dollar AM. 2015
Estimating thumb-index finger precision grip and
manipulation potential in extant and fossil
primates. *J. R. Soc. Interface* **12**, 20150176. (doi:10.
1098/rsif.2015.0176)
109. Kivell TL, Skinner MM, Lazenby R, Hublin J-J. 2011
Methodological considerations for analyzing
trabecular architecture: an example from the
primate hand. *J. Anat.* **218**, 209–225. (doi:10.
1111/j.1469-7580.2010.01314.x)
110. Tsegai ZI, Kivell TL, Gross T, Nguyen NH, Pahr DH,
Smaers JB, Skinner MM. 2013 Trabecular bone
structure correlates with hand posture and use in
hominoids. *PLoS ONE* **8**, e78781. (doi:10.1371/
journal.pone.0078781)
111. Ruff C, Holt B, Trinkaus E. 2006 Who's afraid of the
big bad Wolff?: 'Wolff's law' and bone functional
adaptation. *Am. J. Phys. Anthropol.* **129**, 484–498.
(doi:10.1002/ajpa.20371)
112. Biewener AA, Fazzalari NL, Konieczynski DD,
Baudinette RV. 1996 Adaptive changes in trabecular
architecture in relation to functional strain patterns

- 631 and disuse. *Bone* **19**, 1–8. (doi:10.1016/8756-
632 3282(96)00116-0)
- 633 113. Barak MM, Lieberman DE, Hublin J-J. 2011 A Wolff
634 in sheep's clothing: trabecular bone adaptation in
635 response to changes in joint loading orientation.
636 *Bone* **49**, 1141–1151. (doi:10.1016/j.bone.2011.
637 08.020)
- 638 114. Skinner MM, Stephens NB, Tsegai ZJ, Foote AC,
639 Nguyen NH, Gross T, Pahr DH, Hublin J-J, Kivell TL.
640
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642
643
644
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684
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686
687
688
689
690
691
692
693
- 2015 Response to comment on 'Human-like hand
use in *Australopithecus africanus*'. *Science*.
115. Darwin CR. 1871 *The descent of man, and
selection in relation to sex*. London, UK: John
Murray.
116. Washburn SL. 1967 Behavior and the origin of man.
Proc. Royal Anthropol. Inst. **1967**, 21–27.
117. Richmond BG, Begun DR, Strait DS. 2001 Origin of
human bipedalism: the knuckle-walking hypothesis
revisited. *Amer. J. Phys. Anthropol.* **116**, 70–105.
(doi:10.1002/ajpa.10019)
118. Lovejoy CO. 2009 Reexamining human origins
in light of *Ardipithecus ramidus*. *Science* **326**,
74e1–74e8.
119. Stout D. 2011 Stone tool-making and the
evolution of human culture and cognition. *Phil.
Trans. R. Soc. B* **336**, 1050–1059. (doi:10.1098/rstb.
2010.0369)