

Chapter 18

Evolution of the Early Hominin Hand

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1 Introduction

The hand is among the most primitive anatomical regions in the human body. The basic five-digit pattern of our manus, including the number of bones in each ray and the retention of many extrinsic and intrinsic muscles (see Chap. 7), is likely retained from the ancestral condition for all mammals. While primate hands are generally characterized by two major novelties, namely, nails instead of claws and enhanced thumb divergence and opposability during grasping, human hands are not particularly derived compared with our primate relatives. The fact that our hands are so little modified from those of early mammals is a testament to the astonishing versatility of the hand as a functional organ (e.g., Wood Jones 1916, 1920; Napier 1993).

What makes the primitive gestalt of the human hand surprising is that it has been the object of major changes in function. Since the Devonian, when our ancient sarcopterygian ancestors made the transition from swimming to weight support on land some 390 million years (Ma) or so ago (Niedźwiedzki et al. 2010), hands have functioned as organs of weight support. Since then, our ancestors went through a variety of locomotor transitions involving weight support on land and in trees, including

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using hands in arboreal settings in a variety of ways (Chaps. 14, 16, and 17). However, after the earliest hominins split from our last common ancestor with bonobos and chimpanzees, two fundamental changes in function occurred. First, bipedality and reduced arboreality removed the need for weight support through the forelimb during locomotion. Second, intensification of hand function in manipulation, tool use, and tool making in hominins required more precise and powerful fine motor actions. These functional changes did not necessarily take place at the same time or in the same context. Indeed, the timing and context of these two major changes in function are the subject of active debate and fertile ground for new research.

This chapter explores the evolution of early hominin hand anatomy, from the *Pan-Homo* last common ancestor (LCA) through *Homo erectus*, in the context of these two major changes in function. For clarity, we treat early hominins here as three discrete groups: basal hominins, australopiths, and early *Homo*. The term “basal hominins” is used to describe *Sahelanthropus*, *Orrorin*, and *Ardipithecus* (Fig. 18.1), with the caveat that the systematics of some of these taxa are uncertain due to the limited anatomical evidence. “Australopith” is used to describe species in *Australopithecus* and *Paranthropus*, and “early *Homo*” refers to members of the genus *Homo* that are more primitive than, and sister taxa to, *H. erectus* (Fig. 18.1).

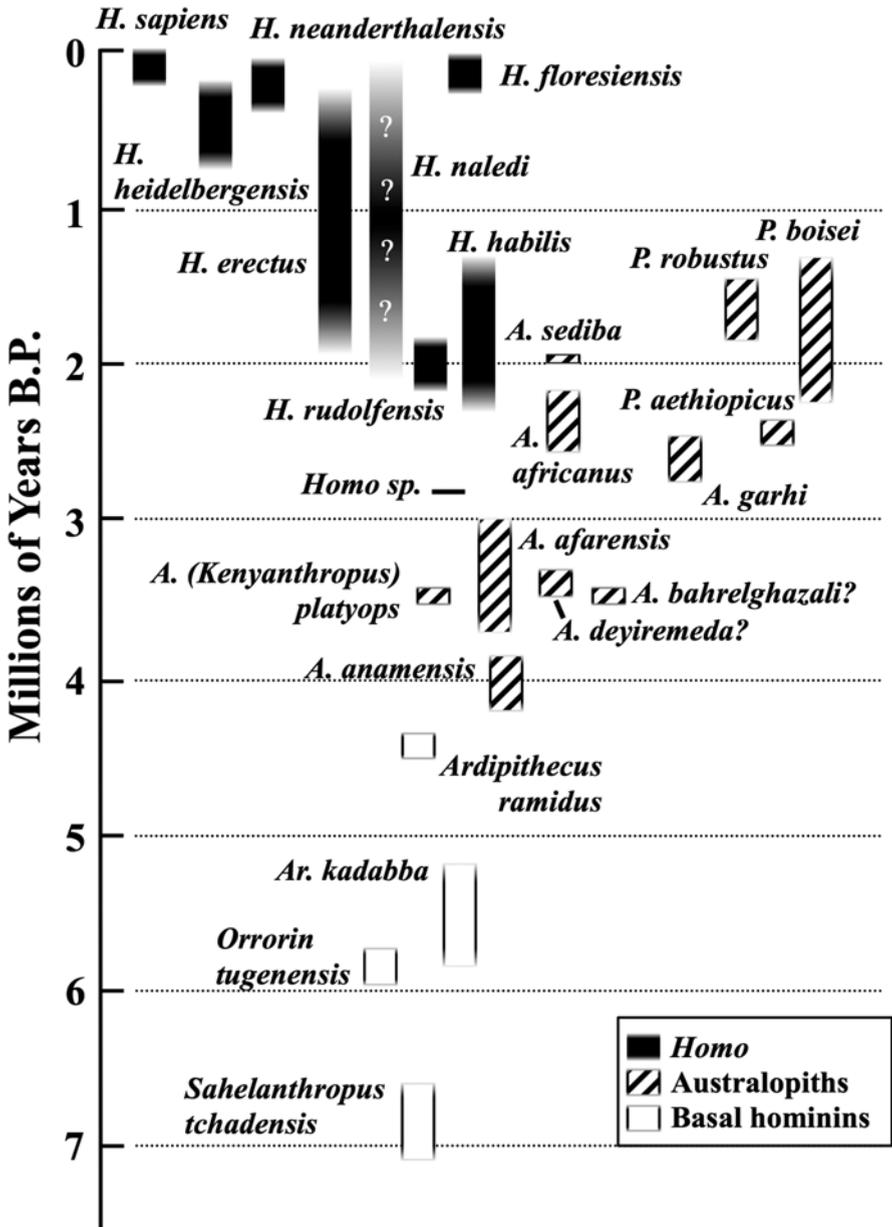
Here we explore the functional significance and evolutionary history of seven anatomical features in the early hominin hand. These are thumb/finger proportions, thumb robusticity, thumb musculature, distal tuberosities (apical tufts), carpal architecture, wrist mobility, and finger curvature. Three of these are features of the thumb that appear at different times and contexts, highlighting the perceived importance of thumb function in human evolution (Napier 1956, 1962; Marzke 1997; Susman 1998). We attempt to bring together this evidence to summarize the current picture of how hand function and anatomy changed over the course of early human evolution, concluding with a discussion of fruitful areas of future research.

2 Anatomy: Function and Evidence from the Fossil Record

2.1 Thumb/Finger Proportions

Hand proportions arguably influence manipulative skills more than any other anatomical characteristic. In particular, a relatively long thumb that more closely approximates finger length allows the thumb to more effectively oppose the fingers. Too much difference between thumb and finger lengths limit pad-to-pad contact in

Fig. 18.1 (continued) share numerous derived characteristics related to bipedalism, as well as hand morphology that includes short fingers relative to some basal hominins. (3) *Homo* is a clade and grade of hominins that share derived human characteristics such as enlarged brain size and aspects of mandible shape. As a clade, *Homo* shows no evidence to date of sharing derived hand anatomy relative to earlier hominins because the hands of earliest *Homo* resemble those of australopiths. Derived hand anatomy only appears later in the *Homo* clade



Common ancestor of hominins and *Pan*

Fig. 18.1 Hominin phylogram. Hominins are organized into three groups or “grades.” (1) “Basal hominins” refer to the most primitive known hominins such as *Ardipithecus ramidus* and probable hominins that are poorly known to date; basal hominins share anatomy related to orthograde posture and derived dental morphology, but it is unclear what aspects of hand anatomy are derived. (2) “Australopithecus” refer to gracile (*Australopithecus*) and robust (*Paranthropus*) australopithecus that

thumb opposition (Marzke and Wullstein 1996; Chap. 12). These proportions are so critical that Napier and Napier (1967) define an “opposability index” as the ratio between thumb and index finger lengths. Definitions of opposability vary widely, but typically refer to Napier’s (1956) description of the ability to rotate the thumb into pad-to-pad contact with other digits or Napier’s (1961) description of the position of the thumb via movements of abduction, flexion, and medial rotation of the first metacarpal (Mc1) at the first carpometacarpal (CM1) joint (see Chap. 2).

Gelada baboons have notable manual dexterity including the ability to use pad-to-pad precision grips during foraging in the wild (Jolly 1970; Rose 1977). It is thought that their high thumb/finger length proportions, while so useful for precision grips, are largely made possible by the evolution of short fingers for terrestrial locomotion. However, some anatomical features, such as short index fingers and hyper-extendable distal interphalangeal joints that facilitate pad-to-pad grip (Etter 1973; Marzke 1997), may enhance their precision grip capabilities.

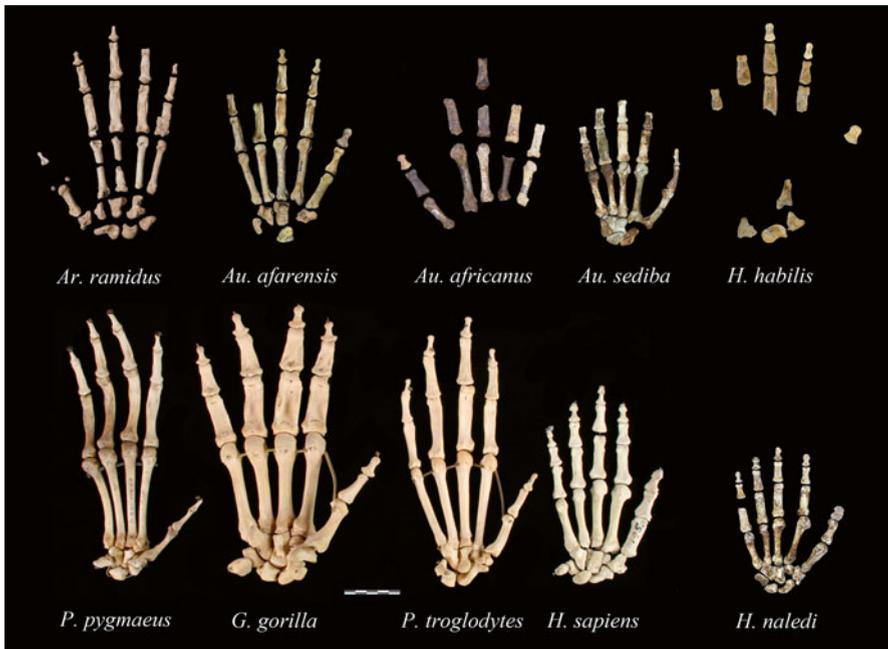


Fig. 18.2 Hand skeletons of extant hominoids and early hominins, illustrating variation in hand proportions. Extant hominoid hands (*bottom left*), all adult, include female *Pongo pygmaeus*, male *Gorilla gorilla gorilla*, female *Pan troglodytes*, and female *Homo sapiens*. Fossil hominin hands, clockwise from *top left*, attributed to *Ardipithecus ramidus* [ARA-VP-6/500 composite of right and left elements, unreversed; photo © and courtesy of T. White (2009)], *Australopithecus afarensis* (A.L. 333 site composite of left and right elements, unreversed; adapted from photos courtesy of T. Kivell), *Australopithecus africanus* (Sterkfontein composite of left and right elements, unreversed), *Australopithecus sediba* (photo © and courtesy of T. Kivell), *Homo habilis* (OH 7, adapted from photos courtesy of T. Kivell), and *Homo naledi* (photo © and courtesy of P. Schmid). All images approximately to scale

The fingers of some apes, such as chimpanzees and orangutans (Fig. 18.2), are so long that when flexed they tend to contact the tip of the thumb rather than its pad. When handling small objects, chimpanzees tend to hold objects in the manner humans typically grip a key, namely, a “two-jaw pad-to-side” grip with the thumb flexed against the side of the index finger (Christel 1993; Marzke and Wullstein 1996; Marzke 1997; see Chap. 12).

In contrast to apes, humans excel in their ability to use pad-to-pad precision grips (e.g., Napier 1956). Marzke (1997) argues that what makes human dexterity unique is the ability to firmly pinch objects, and precisely handle objects, with one hand. Humans have long thumbs relative to their fingers, proportions that are critical to these capabilities (Napier and Napier 1967; see Figs. 18.2 and 18.3).

Evidence of the evolution of hominin thumb/finger proportions is incomplete because associated hand skeletons are rare in the fossil record. *Ardipithecus ramidus* is the earliest hominin taxon with good evidence of hand proportions and the sole data point for such proportions in the basal hominins (Fig. 18.1). The partial

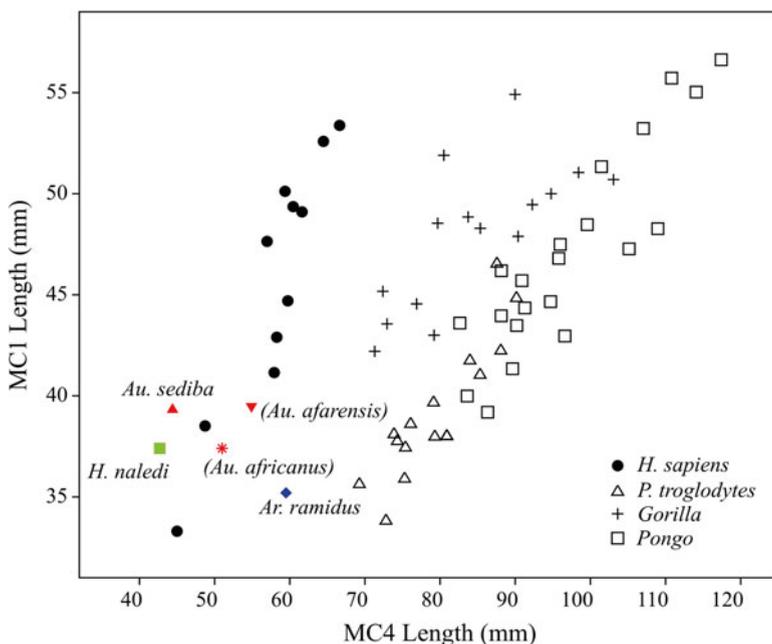


Fig. 18.3 Thumb/finger length proportions in hominoids and fossil hominins. Relative to the fourth metacarpal (Mc4) length, the first metacarpal (Mc1) length is intermediate in gorillas and much longer in modern humans. The australopiths approximate modern humans in relative Mc1 length, whereas *Ardipithecus ramidus* has thumb proportions more similar to gorillas. The long ulnar metacarpals in *Pan* and *Pongo* contribute to their very low relative Mc1 lengths. ARA-VP-6/500 represents *Ar. ramidus* (Lovejoy et al. 2009a), MH2 represents *Australopithecus sediba* (Kivell et al. 2011), and *Australopithecus afarensis* and *Au. africanus* are represented by composites (indicated by parentheses) of isolated hand elements from A.L. 333 and Sterkfontein, respectively

skeleton ARA-VP-6/500 has a short thumb. Relative to fifth metacarpal (Mc5) length, the Mc1 length in ARA-VP-6/500 is much shorter than in humans and appears to be slightly longer than those of great apes (Lovejoy et al. 2009a). Similarly, relative to its fourth metacarpal (Mc4) length, ARA-VP-6/500 has a short Mc1 compared with those of modern humans and several hominin species (Almécija et al. 2015; Fig. 18.3). The intermediate position of ARA-VP-6/500 between apes and later hominins appears to reflect both a short Mc1 and the lack of elongated ulnar (2–5) metacarpals seen in chimpanzees and orangutans (Drapeau et al. 2005; Almécija et al. 2015). When compared with a composite measure of “hand size,” Mc1 length in *Ar. ramidus* is apelike and shorter than those of australopiths and modern humans (Kivell et al. 2011).

The non-pollical phalanges of ARA-VP-6/500 are longer than those of *Gorilla* and shorter than those of *Pan* relative to estimated body size (Lovejoy et al. 2009a). However, when taking into account confidence intervals on estimated body mass (Lovejoy et al. 2009b; Grabowski et al. 2015), relative finger length in *Ar. ramidus* could be equivalent to *Pan* or *Gorilla*. Thus, *Ar. ramidus* appears to have a thumb that is great ape-like in length and, relative to modern human hands, long non-pollical phalanges. While some of this anatomy has been interpreted as revealing the condition of the *Pan-Homo* LCA (Lovejoy et al. 2009b), *Ar. ramidus* occurs millions of years after the likely LCA divergence. Considering evolutionary changes that occur in other hominins over similar spans of time, such as those between *Australopithecus* and *H. erectus* or *H. erectus* and modern humans, it is premature to interpret *Ar. ramidus* as representing the anatomy of the LCA. It is impossible to know the primitive condition without evidence of the earliest basal hominins and the LCA. The metacarpal proportions and somewhat long phalanges suggest that precision grip capabilities in *Ar. ramidus* would more closely resemble those of modern African apes rather than modern humans.

Relative thumb lengths more similar to those of modern humans are first seen in australopiths (Figs. 18.2 and 18.3), consistent with hypotheses that members of this genus were adapted for greater manual dexterity (e.g., Marzke 1997; Panger et al. 2002; Alba et al. 2003). Although no associated hand skeletons of *Australopithecus afarensis* or *Australopithecus africanus* have yet been reported, the large fossil assemblages from Hadar, Ethiopia, and Sterkfontein cave, South Africa, are informative. Using resampling procedures, it is possible to examine the distribution of hand proportions that could produce the fossil assemblage. The results of these analyses show that *Au. afarensis* had a relatively long thumb compared with *Pan* (Alba et al. 2003; Rolian and Gordon 2013). Thumb length relative to other digits appears to be intermediate between modern humans and gorillas (Rolian and Gordon 2014) or essentially the same as in modern humans (Almécija and Alba 2014), depending on whether many of the A.L. 333 hand bones represent one individual and the ray identity of phalanges can be reliably determined based on morphology. This evidence suggests that *Au. afarensis* would have been capable of pad-to-pad precision grips, although likely with less proficiency and force than those of modern humans due to relatively limited thumb mobility and robusticity (Almécija and Alba 2014; Rolian and Gordon 2014; see below).

Later *Australopithecus* species show evidence of humanlike thumb length proportions. No associated hand is yet known for *Au. africanus*, unless StW 573 (“Little Foot”) represents this taxon (Clarke 1999). However, resampling analyses of isolated bones suggest that the length of the Mc1 relative to that of the third metacarpal (Mc3) in *Au. africanus* was similar to that of modern humans, albeit with a more gracile thumb (Green and Gordon 2008). The unusually well-preserved, associated hand skeleton (MH2) of *Australopithecus sediba* shows that the hand proportions were autapomorphic, with longer thumbs than seen in any other higher primate (Jouffroy et al. 1993; Kivell et al. 2011). The great thumb length is due primarily to an elongated Mc1 in a hand that otherwise had digit length proportions similar to those of modern humans (Kivell et al. 2011).

Currently, insufficient evidence is available to know the thumb/finger length proportions in *Paranthropus*.

Relative thumb length in early *Homo* is poorly understood owing to a sparse fossil record. For example, OH 7 does not preserve enough elements to estimate hand proportions for *Homo habilis* (Napier 1962). The only primitive member of the genus *Homo* that preserves sufficient evidence is *Homo naledi*, recently discovered in South Africa (Kivell et al. 2015). It has a long thumb, at the upper end of the modern human range and longer (relative to third ray length) than any other known extinct hominin except for MH2 (*Au. sediba*).

Taken together, the evidence to date shows that, relative to *Ar. ramidus*, *Australopithecus* is characterized by relatively shorter fingers and longer thumbs. This suggests that as *Australopithecus* shifted to more open habitats and derived bipedal locomotion, the importance of arboreal locomotion decreased and that of manual dexterity increased. Furthermore, variation in relative thumb length among *Australopithecus* species tentatively suggests that there may be differences among them in the biomechanics of manipulation.

2.2 Thumb Robusticity

Greater robusticity is functionally related to bone strength and the capacity to withstand external loads (e.g., Ruff et al. 2006). Modern humans have expanded thumb musculature (see below and Chap. 7) that generates strong applied loading forces. Moreover, muscle recruitment creates joint reaction forces that are several times higher than the external applied force. For example, a pinch grip generates forces at the metacarpophalangeal joint that are about five to six times higher than the external force at the thumb tip, and the transarticular forces on the saddle joint (CM1) are about 12 times higher (Cooney and Chao 1977). Stress at these thumb joints can be reduced by lowering muscle force or increasing joint surface area (as $\text{stress} = \text{force} / \text{area}$). In modern humans, the joints of the thumb are significantly larger than those of apes (Fig. 18.4), particularly when compared with the joint sizes of non-pollical digits. Thus, modern humans have robust thumbs thought to be an adaptation to generating and resisting high forces relative to forces experienced by other regions of the

hand (Susman 1994; Williams et al. 2012). Alternatively, it is possible that greater pollical robusticity may also reflect integration with a hallux that is evolving to withstand greater forces from bipedalism (Rolian et al. 2010); in this scenario, the increased robusticity of the thumb has nonetheless the functional consequence of providing enlarged attachment areas for musculature and enhanced resistance to joint stresses.

Twenty years ago, the picture of how thumb robusticity evolved appeared to be relatively simple: australopiths (represented only by A.L. 333w-39, attributed to *Au. afarensis*) resembled apes in having a small Mc1 head breadth relative to length, whereas fossils attributed to *Paranthropus* and *Homo* (at Swartkrans) appeared more humanlike (Susman 1988a, 1994).

Since then, discoveries of numerous isolated and associated hand fossils now show that the evolution of thumb robusticity and morphology might be more complex. Although Mc1s are gracile in all *Australopithecus* taxa (*Au. afarensis*, *Au. africanus*, and *Au. sediba*) for which this bone is known (Bush et al. 1982; Green

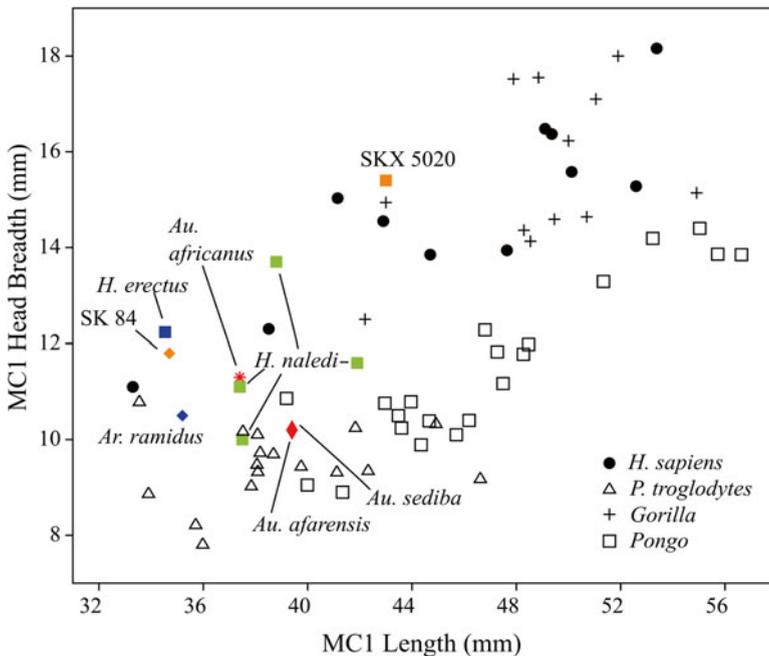


Fig. 18.4 Thumb robusticity in hominoids and fossil hominins. Relative to first metacarpal (Mc1) length, Mc1 head breadth is wider in modern humans and gorillas, although all metacarpals are more robust in the latter. *Australopithecus afarensis* (A.L. 333-39; red inverted triangle) and *Australopithecus sediba* (UW 88-119; red triangle) have gracile Mc1 heads; *Ardipithecus ramidus* (ARA-VP-6/500-015; blue diamond) and *Australopithecus africanus* (StW 418; red asterisk) are somewhat intermediate; and *Homo erectus* (KNM-WT 15000BU; blue square), SKX 5020 (head breadth estimated due to preservation; orange square) and SK 84 (both attributed to either *Paranthropus robustus* or early *Homo*; orange diamond) have wide Mc1 heads similar to modern humans. *H. naledi* (UW 101-007, UW 101-270, UW 101-1282, UW 101-1321) shows variability, overlapping with the distributions of modern humans and chimpanzees

and Gordon 2008; Kivell et al. 2011), *Ar. ramidus* has Mc1 head breadth/length proportions that appear to be slightly greater than in some australopiths (Fig. 18.4). However, *Ar. ramidus* also has a relatively short Mc1, so it would be informative to compare Mc1 head breadth against other variables to assess its relative size. If humanlike Mc1 joints represent the primitive condition for *Australopithecus* (Lovejoy et al. 2009a), then thumb robusticity decreased during the evolution of australopiths, such as *Au. afarensis*. More research is needed to understand this transition and its implications for early hominin hand evolution.

All known fossils potentially attributable to *Homo* have robust thumbs, with relatively broad Mc1 heads and broad shafts, typically with well-developed opponens pollicis insertions (note that no Mc1 of *H. habilis* is known). The oldest of these are two Swartkrans fossils, SK 84 and SKX 5020 (Fig. 18.4), at roughly 2 Ma. There is some debate about the taxonomic attribution of these fossils (Susman 1988a; Trinkaus and Long 1990). Comparative evidence (e.g., from Mc1s of the early *H. erectus* KNM-WT15000 skeleton and MH2; Richmond et al. 2009; Kivell et al. 2011) now suggests that SKX 5020 likely represents *Homo* and SK 84 might represent *Paranthropus robustus*, rather than the reverse (Susman 1988a, 1994). However, this does not diminish Susman's (1994: 1570) conclusion that *P. robustus* had hand anatomy capable of "advanced precision grasping" for making and using tools. It is notable that humanlike thumb robusticity evolved well after the first appearance of making and using stone tools (McPherron et al. 2010; Harmand et al. 2015).

The well-preserved *H. naledi* fossils have unique Mc1 morphology, represented by six individuals, with unusually small proximal bases and saddle joints for the trapezium, combined with humanlike broad Mc1 heads and shafts with pronounced attachments for the opponens pollicis and dorsal interossei (Kivell et al. 2015). Thus, *H. naledi* appears to have most of the derived anatomy for forceful precision pinch grips, but would not have been capable of withstanding as much force compared with the thumbs of later *Homo*.

2.3 Thumb Musculature

Modern humans have elaborate thumb musculature. Humans do not have unique muscles, as every major muscle attached to the human thumb can be found in other primate taxa. However, more muscles attach to the thumb in humans than in almost all other primates (Diogo et al. 2012; see also Chap. 7), and thumb muscles constitute a much larger proportion of total hand muscle mass in humans compared with other hominoids (Tuttle 1969).

Humans have two major extrinsic thumb muscles that are normally absent in the great apes: the flexor pollicis longus and extensor pollicis brevis (e.g., Diogo et al. 2012 and references therein). These two muscles are present in hylobatids, raising questions about whether these muscles were independently lost in three great ape lineages, were lost at the Hominidae node (great ape and human clade) and re-evolved in hominins, or were independently gained in hylobatids and hominins, perhaps associated with their relatively long thumbs (Chap. 7). Humans and African apes also share a third, intrinsic

thumb muscle almost never observed in other primates, a structure sometimes called the first volar interosseous muscle of Henle (Susman 1994; Susman et al. 1999), more accurately named the accessory adductor pollicis muscle (Diogo et al. 2012).

The most important muscle for force production during thumb flexion is the flexor pollicis longus (FPL). In most nonhuman primates, this muscle (when present) is not fully separated from the flexor digitorum profundus (FDP) muscles attaching to the other digits, meaning that the thumb would flex during forceful flexion of the fingers. In humans [and hylobatids (Diogo et al. 2012)], it is more fully separated from other muscles, so that the thumb can be forcefully flexed independently from the other digits and vice-versa. This capability confers obvious advantages during manipulation. However, to date, there is no way to detect the relative independence of the FPL from skeletal evidence alone. Because of this, a visible insertion site on the thumb's distal phalanx merely provides evidence of the attachment of the long tendon of an extrinsic flexor muscle, but cannot distinguish whether it is independent (FPL) or not (i.e., belly connected to the rest of FDP). It is interesting to note that even in humans, about 31% of individuals lack a completely independent FPL (Lindburg and Comstock 1979).

Because great apes generally lack an extrinsic thumb flexor muscle, parsimony suggests that the LCA lacked it as well (Tocheri et al. 2008). However, the insertion site is present in most, if not all, fossil hominins to date (Fig. 18.5), including the distal phalanges (DP1s) attributed to *Orrorin* (Gommery and Senut 2006; Almécija et al. 2010), *Ar. ramidus* (Lovejoy et al. 2009a), *Au. afarensis* (Ward et al. 2012), *Au. africanus* (Ricklan 1987), *Au. sediba* (Kivell et al. 2011), *P. robustus* or early *Homo* at Swartkrans (Susman 1988b), *H. naledi* (Kivell et al. 2015), and *H. habilis* (Napier 1962). Thus, an extrinsic thumb flexor muscle is present very early in the hominin lineage, if not in the LCA, but there is no evidence regarding when the FPL became independent from the FDP muscle to the other digits.

The morphology of the FPL attachment in humans (Fig. 18.5) is distinctive in ways that may influence its function. For example, the FPL tendon inserts in a gable-shaped pattern with a consistently longer radial side. Shrewsbury et al. (2003) argue that this contributes to opposition against the fingers, together with an asymmetric interphalangeal joint that slightly pronates the distal phalanx during flexion. The distal phalanx BAR 1901'01 displays these characteristics and appears remarkably humanlike (Almécija et al. 2010). If it is correctly attributed to *Orrorin*, this suggests that a humanlike FPL attachment was present at or near the base of the hominin lineage. Australopiths (post *Au. afarensis*) and early *Homo* DP1s tend to have much larger palmar fossae and more distal FPL attachments (e.g., Kivell et al. 2011), although the specific morphology of the FPL attachment and overall morphology of the DP1 (see below) are quite variable across australopiths and early *Homo*.

Fossil Mc1s attributed to *Homo* often bear a prominent opponens pollicis muscle attachment site, developing into an opponens "flange" in later archaic *Homo* (Chap. 19). While it may seem logical to interpret the prominent attachment as indicating a large and/or intensively used opponens pollicis muscle, efforts to examine the relationships between muscle size, activity, and insertion sites have found no association (Zumwalt 2006; Rabey et al. 2015), including those specifically examining hand muscle size and



Fig. 18.5 Images of pollical (DP1) (left) and non-pollical (right) distal phalanges of humans, apes, and fossil hominins. Fossil phalanges attributed to *Orrorin tugenensis* (DP1 only, BAR 1901'01; adapted from Gommery and Senut 2006), *Ardipithecus ramidus* (ARA-VP-6/500-049, ARA-VP-6/500-050; adapted from Lovejoy et al. 2009a; photo © and courtesy of T. White [2009]), *Australopithecus afarensis* (A.L. 333-159, A.L. 333w-50), *Australopithecus africanus* (DP1 only, StW 294), *Australopithecus sediba* (DP1 only, UW 88-124, adapted from Kivell et al. 2011), *Homo habilis* (OH 7: FLK NN-A, FLK NN-B), and *Homo naledi* (DH1: UW 101-1351, UW 101-1329)

insertion morphology (Marzke et al. 2007; Williams-Hatala et al. 2016). A radial extension of the opponens crest does, however, have the biomechanical consequence of increasing the rotational moment arm of the muscle (Maki and Trinkaus 2011), and the more distally extended dorsal interosseous attachment in humans provides a longer moment arm for adduction (Tocheri et al. 2008).

2.4 Broad Distal Tuberosities

Fingertips are responsible for precision grips and handling, so it is no surprise that humans have derived distal phalanges. Humans have broad fingertips, nails, and underlying distal tuberosities (also called “apical tufts”) compared with other hominoids (Mittra et al. 2007; Chaps. 4 and 8 and references therein). Shrewsbury and colleagues (Shrewsbury and Johnson 1983; Shrewsbury et al. 2003) describe a “functional compartmentalization” of the thumb tip, with a larger, thick, mobile proximal portion and a smaller, more stable distal portion. The border between these “compartments” lies at the proximal end of the tuberosity. The distal portion has more fibers and less fat content and is anchored to the tuberosity and supported by the nail, whereas the proximal portion has greater fat content and is supported by the lateral intraosseous ligaments that attach to the unguis spines on either side of the tuberosity. The proximal portion also contains neurovascular bundles and corpuscles that provide sensory information during manipulation (Shrewsbury and Johnson 1983; see Chaps. 6 and 8).

Broader fingertips increase the surface area for precision grips between the thumb and other digits. The breadth of the soft tissue of the fingertip is correlated with the breadth of the underlying DP distal tuberosity (Mittra et al. 2007), reflecting the functional role played by the distal tuberosities in supporting the stability of the nail dorsally and fleshy fingertip palmarly.

In his analysis of the OH 7 hand, part of the *H. habilis* holotype, Napier (1962) highlighted the broad terminal phalanges as a key requirement for precision grip capabilities, but noted that the “set” of the trapezium left open doubt about whether thumb opposition was exactly like that of modern humans. Finding a hand with functional signatures of precision grips, together with some of the oldest stone tools at the time, was cited as evidence for the hypothesis that OH 7 belonged in the genus *Homo* (Leakey et al. 1964). Since then, discoveries have shown that stone tools occur substantially earlier, at 3.3–3.4 Ma (McPherron et al. 2010; Harmand et al. 2015), and broad distal tuberosities may occur even earlier.

The c. 5.8 Ma DP1 attributed to *Orrorin tugenensis*, BAR 1901'01, has remarkably humanlike anatomy, much more so than the morphology of fossils securely attributed to *Ardipithecus* and some *Australopithecus* taxa. Like human DP1s, BAR 1901'01 has a broad, distinct tuberosity with ungual spines and well-developed basal tubercles that form the attachments of the lateral intraosseous ligaments (Almécija et al. 2010) and are functionally related to the mobile proximal pulp compartment (Shrewsbury et al. 2003). The DP1 of *Ar. ramidus* (ARA-VP-6/500-049), on the other hand, appears much more like those of great apes, with a narrow distal tuberosity without ungual spines (Lovejoy et al. 2009a). Given the modern humanlike morphology of BAR 1901'01, it is surprising that the morphology in *Ar. ramidus* appears so much more primitive and potentially raises concern over the reliability of the attribution of BAR 1901'01 to *Orrorin*. More fossil evidence is needed to clarify the evolution of this anatomy near the base of the hominin clade.

Aside from the DP of *Au. afarensis*, the DPs of all gracile and robust australopithecids and most members of the genus *Homo* have substantially broader distal tuberosities than the DPs of modern humans (Fig. 18.5). These taxa include *Au. africanus*, *Au. sediba*, *H. habilis*, and *H. naledi*, as well as *Homo heidelbergensis* and *Homo neanderthalensis* (Fig. 18.5; Chap. 19). This raises questions about the functional significance of the broader apical tufts in earlier hominins and why modern humans have evolved narrower apical tufts. Are modern humans less dextrous in this respect?

2.5 Carpal Architecture

One of the few osteological synapomorphies of humans and African apes occurs in the wrist, namely, the fusion of the os centrale to the scaphoid (Weinert 1932; Corruccini 1978; Richmond et al. 2001; Kivell and Begun 2007). Among anthropoids, this feature is occasionally observed in *Pongo*, but only in African apes and

humans does it occur in virtually all individuals and develop very early in ontogeny (Kivell and Begun 2007). Wood Jones (1916) proposed that os centrale fusion was functionally related to stability at the base of the index finger in African apes and in humans, two groups considered to be distantly related at the time. Lovejoy et al. (2009a) proposed a nonfunctional hypothesis, positing that fusion of the os centrale may have been a pleiotropic effect of an elongation of the scaphoid tubercle and deepened carpal tunnel.

Currently, the predominant functional hypothesis for its evolution posits that the fused os centrale/scaphoid decreases mobility and improves the ability to transmit forces between the manual rays and radius during knuckle-walking (Marzke 1971; Tuttle 1975; Sarmiento 1988; Gebo 1996; Richmond et al. 2001). This is particularly important in African apes, which lack a weight-bearing articulation between the carpals and ulna and use a hand posture in which ground reaction forces travel along a “column” of metacarpals, carpals, and the radius. Some support for this hypothesis can be found in the convergent evolution of carpal fusion in knuckle-walking giant anteaters (Orr 2005), as well as chalicotheres (Richmond et al. 2001; Begun 2004). Of course, it is well known that some lemurs, including suspensory subfossil lemurs such as *Palaeopropithecus*, also show convergence in os centrale fusion (Jouffroy 1975; Hamrick et al. 2000; Chap. 15). This observation, along with other factors, leads some to question a knuckle-walking hypothesis for os centrale fusion in the African ape-human clade (e.g., Kivell and Schmitt 2009), while others argue that the wrist structure and function in lemurs is distinct enough to have evolved for different reasons (e.g., Begun 2004). This area deserves more research.

The presence of a fused os centrale/scaphoid in all known hominin fossils to date, including the *Ar. ramidus* partial skeleton ARA-VP-6/500 (Lovejoy et al. 2009a), suggests that it did not evolve independently in hominins and African apes. In contrast, Miocene apes such as *Rudapithecus* (Kivell and Begun 2009) and *Pierolapithecus* (Moyà-Solà et al. 2004) have an independent os centrale. The growing fossil record suggests that os centrale fusion most likely evolved once at, or near, the base of the African ape and human clade, begging an alternative explanation if the knuckle-walking hypothesis is incorrect.

In addition to os centrale fusion, modern humans have a carpal architecture that is quite distinct from other primates. In most anthropoids, the trapezoid is wedge shaped, with the narrow end of the wedge projecting palmarly. In humans, the palmar portion of the trapezoid is substantially expanded (Tocheri et al. 2007). This expansion effectively supinates the trapezium and brings the distal carpal row into greater radioulnar alignment (Tocheri 2007). This realignment influenced the morphology of many of the intercarpal and carpometacarpal joints on the radial side and has been hypothesized to improve the biomechanics of resisting radioulnarly oriented forces acting across the radial side of the wrist during forceful contraction of the enlarged thenar musculature (Tocheri 2007; Tocheri et al. 2008).

All non-*Homo* hominin taxa and the most primitive members of the genus *Homo*, including *H. habilis* and *Homo floresiensis*, show evidence of the primitive anthropoid wrist configuration (Tocheri et al. 2007). In contrast, later members of the genus *Homo*, including *H. neanderthalensis* and early modern humans, show evidence of a shared, derived wrist configuration (Tocheri et al. 2008). Interestingly, the wrist anatomy of

H. naledi shares the same derived anatomy with Neanderthals and modern humans (Kivell et al. 2015). Unfortunately, wrist anatomy is poorly preserved for *H. erectus*, so it remains unclear exactly when and in what context this anatomy evolved.

Humans also have a prominent styloid process on the base of the Mc3, a feature that might be linked with this radial carpal reconfiguration and was present at least 1.4 Ma in KNM-WT 51260 from West Turkana, Kenya (Ward et al. 2014). Marzke and Marzke (1987) proposed that the styloid process evolved to stabilize the carpo-metacarpal joint to prevent subluxation, especially due to palmarly oriented external forces experienced during stone tool use. The functional significance of this feature deserves more attention.

2.6 Wrist Mobility

Humans have more mobile wrists in some directions than do African apes and in this regard more closely resemble the Asian apes (Bradley and Sunderland 1953; Tuttle 1969; Richmond 2006). Schreiber (1936) was the first to report limited wrist mobility in chimpanzees, and Tuttle (1969) demonstrated this based on the passive mobility of upper limb joints in a large sample of extant apes. He noted that African apes, particularly *Pan troglodytes*, have much lower ranges of mobility in wrist extension and proposed that this limited range of motion represented a functional adaptation to knuckle-walking in order to provide a stable, weight-bearing column between the hand and arm.

Range of motion is difficult to predict from skeletal anatomy alone because of the critical roles played by ligaments and other soft tissues. However, the anatomy of joints also plays a crucial role in joint mobility and stability (Hamrick 1996). Systematic assessment of the movements of individual carpals when cadaveric wrists are flexed and extended shows that the morphology of the distal radius and midcarpal joint (e.g., lunate-capitate arc curvature) correlates significantly with range of motion in wrist extension (Orr et al. 2010; see Chap. 9).

Morphology of the radiocarpal and midcarpal joints suggests that early hominins had less wrist mobility in extension compared with modern humans. *Ar. ramidus*, *Australopithecus anamensis*, and *Au. afarensis* have distal radii with palmar inclinations formed in part by distally projecting dorsal ridges, or margins, similar to the morphology in modern African apes (Richmond and Strait 2000; Richmond et al. 2001; Orr 2013). The midcarpal joint morphology, such as the curvature of the lunate-capitate joint, shows that *Ar. ramidus* had restricted wrist extension (Orr 2013; *contra* Lovejoy et al. 2009a). This restricted wrist extension supports the hypothesis that the LCA practiced knuckle-walking as well as climbing (Washburn 1967; Richmond et al. 2001; Williams 2010). Nevertheless, the locomotor behavior of the LCA is still a matter of debate (e.g., Schmitt 2003; Begun et al. 2007; Thorpe et al. 2007; Kivell and Schmitt 2009; Lovejoy et al. 2009b; Williams, 2010) and will remain so until forelimb fossils of the *Pan-Homo* LCA are found.

By the late Pliocene, hominin taxa such as *Au. africanus* and *P. robustus* had radii with distally oriented ends without projecting dorsal margins (Richmond et al. 2001). Further analyses of early hominin wrist joint anatomy will help to clarify the timing and pattern of changes in wrist joint mobility during human evolution (Chap. 9). It is not clear what led to the changes in wrist mobility, but two hypotheses propose that the changes are influenced by relaxed selection for the use of the upper limb in locomotion and/or selection for manual manipulation or throwing (Marzke 1971; Ambrose 2001; Richmond et al. 2001; Roach et al. 2013). In humans today, many manipulative activities involve a high degree of wrist mobility. Mobility in wrist extension has been shown to play an important role in stone toolmaking (Williams et al. 2010, 2014; see Chap. 11) and throwing (Wolfe et al. 2006; Roach and Lieberman, 2014).

2.7 *Phalangeal Curvature*

There is a well-documented association between longitudinal curvature of proximal and middle phalanges and arboreal and, especially, suspensory behavior among primate taxa (Stern and Susman 1983; Jungers et al. 1997; Matarazzo 2008; Rein 2011). Biomechanical modeling based on in vivo data show that phalangeal curvature substantially reduces bending stresses during highly flexed finger postures, such as those involved in grasping branches during suspensory locomotion (Preuschoft 1970; Richmond 2007; Nguyen et al. 2014). This seems to be attributable to the counteracting influences of the palmarly oriented force of the extrinsic flexor tendons that tend to bend “open” (in the direction of straightening) the proximal phalanx and the proximo-distal component of the joint reaction forces that tend to bend the phalanx “closed” (in the direction of increasing the curvature). In contrast, straighter phalanges reduce bending when fingers use more extended postures, such as those used by primates when traveling on the ground (Richmond 1998). Longitudinal curvature is sensitive to changes in behavior during growth and, therefore, serves as a good indicator for degree of arboreal behavior during primate development (Richmond 1998; Jungers et al. 2001; Congdon 2012).

The functional morphology of phalangeal curvature is still not completely understood. Some taxa (e.g., gibbons) that are highly suspensory have lower levels of curvature than others (e.g., orangutans; Fig. 18.6). Size and scaling may play a role, especially regarding how hand size and arboreal support size influence finger postures during locomotion; for example, small primates may not use very flexed finger postures during arboreal locomotion because the supports are large relative to their hands. Very little is currently known about hand and finger postures during locomotion and during ontogeny (but see Sarringhaus 2013). At present, evidence shows that curved phalanges occur in primate taxa that climb and suspend from arboreal supports and that curvature is somewhat sensitive to changes in locomotor behavior during growth.

Among modern hominoids, curvature in proximal phalanges varies from extremely curved in orangutans to lower levels, in decreasing order, in siamangs, gibbons, bonobos, chimpanzees, and gorillas, with the straightest phalanges in

modern humans (Fig. 18.6). Finger curvature is moderately high, more or less like that of chimpanzees, in basal hominins such as *Orrorin* (Richmond and Jungers 2008) and early australopiths such as *Au. afarensis* (Stern and Susman 1983). Enough fossils are now known to see that phalangeal curvature varied among early hominin taxa (Fig. 18.6). For example, it appears that phalangeal curvature is greater in *Au. afarensis* than in *Au. africanus* and *Au. sediba* (Kivell et al. 2015). The latter taxa have moderate phalangeal curvature, and more fossils will be needed to assess how some of these taxa differed from one another and how the degree of phalangeal curvature fits with the remaining morphology of the hand.



Fig. 18.6 Extant anthropoid (*left*) and early fossil hominin (*right*) manual proximal phalanges (PPs), illustrating variation in phalangeal curvature. PPs are arranged roughly from straighter at the top to those with greater curvature toward the bottom, scaled to equivalent lengths. PPs of extant taxa include (a) modern human, (b) baboon, (c) gorilla, (d) chimpanzee, (e) gibbon, and (f) orangutan. Fossil PPs include (g) Hominini gen. et sp. indet. (OH 86; adapted from Domínguez-Rodrigo et al. 2015), (h) *Australopithecus africanus* (StW 293; adapted from Kivell et al. 2011), (i) *Australopithecus sediba* (UW 88-120 of MH2; adapted from Kivell et al. 2011), (j) *Homo habilis* (OH 7, cast), (k) *Homo naledi* (UW 101-1327; adapted from Kivell et al. 2015), (l) *Australopithecus afarensis* (A.L. 333-57), and (m) *Ardipithecus ramidus* (ARA-VP-6/500-022; adapted from Lovejoy et al. 2009a; photo © and courtesy of T. White [2009])

Differences between species in phalangeal curvature and other characteristics may reflect slight but significant differences in positional behavior (Green et al. 2007), not unlike the differences in anatomy and behavior observed between species of *Pan* (Doran 1993).

The oldest evidence of humanlike low phalangeal curvature is seen in a manual proximal phalanx (OH 86) from Olduvai found in deposits over 1.84 Ma (Domínguez-Rodrigo et al. 2015). This phalanx differs substantially from the OH 7 phalanges, attributed to *H. habilis*, pointing to diversity in hand function at that time. Low phalangeal curvature is seen in later *Homo* fossils, such as ATE9-2 from c. 1.2 to 1.3 Ma deposits at Sima del Elefante (Lorenzo et al. 2015). Very few hand bones are securely attributed to *H. erectus*. However, based on the loss of other ape-like, “arboreal” traits and the presence of a humanlike Mc3 styloid process (Ward et al. 2014), it would not be surprising if future discoveries show that *H. erectus* had straight proximal and middle phalanges, but this anatomy will remain unknown until fossil evidence is recovered.

How to interpret the behavioral and adaptive implications of phalangeal curvature has been a matter of considerable debate, despite having a better understanding of its functional significance than that of many anatomical characteristics. Primitive anatomy can be retained without the continuation of primitive behaviors (e.g., a highly mobile, ape-like shoulder in modern humans), complicating the interpretation of primitive anatomy (Latimer, 1990; Stern 2000; Ward 2002). However, comparative and developmental evidence suggest that the *Pan*-like levels of manual (and pedal) phalangeal curvature in *Orrorin*, *Ardipithecus*, *Australopithecus*, and early *Homo* are evidence that climbing trees, probably to obtain food and avoid predation, was a significant component of the behavioral repertoire of these taxa (e.g., Stern and Susman 1983; Richmond 1998; Kivell et al. 2015).

3 Changes in Hominin Hand Functions: A Process, Not an Event

This review of changes in hominin hand anatomy drives home the point that the two major functional changes—the loss of hand use for locomotion and the intensification of hand use in manipulation—are better characterized as “processes” than “events.” What do we mean by “process”? We use the term process in the same sense that Mike Rose (1991) used it to argue that the origin of bipedalism was a process rather than an event. In that example, it is extremely unlikely that the earliest hominins switched, across a single species transition, from a locomotor repertoire involving a small proportion of bipedalism (comparable to that seen in modern great apes) to one that was exclusively bipedal like that seen in modern humans. Instead, it is far more likely that bipedalism became a more important component in the locomotor repertoires of some hominin descendants of the *Pan-Homo* LCA. However, the increase in the importance of bipedalism was not necessarily linear, nor was the decrease in arboreality and increase in manual manipulation capabilities. Different species, even different

populations, may have varied in the importance of bipedalism and arboreality as components of their locomotor repertoires, just as African ape species, subspecies, and populations differ in the relative proportions of suspension, climbing, knuckle-walking, and bipedalism in their repertoires (e.g., Doran 1993, 1996) and in related functional anatomy. An example can be seen in the variation in medial cuneiform morphology and locomotor behavior among gorilla species and subspecies (Tocheri et al. 2011). The many factors that influence modern primate locomotion would also have influenced the repertoires of the earliest hominin taxa. Therefore, we argue that the “null hypothesis” for the pattern of early hominin locomotor evolution should be one in which different species (or smaller divisions if we could accurately reconstruct them) differ in important, and perhaps subtle, ways from one another depending on their ecological settings, diets, body sizes, and other factors.

The mosaic pattern observed in the changes in functional complexes of the hand, including the seven reviewed above, supports the hypothesis that the evolution of locomotor and manipulative hand function was complex.

3.1 Changes in Locomotion

As locomotor mode changed over the course of human evolution, so too must have the selective forces acting on the hand. The locomotor behavior of the LCA is a matter of considerable debate (e.g., Richmond and Strait 2000; Begun et al. 2007; Thorpe et al. 2007; Kivell and Schmitt 2009; Lovejoy et al. 2009b; Williams 2010). However, there is broad consensus that arboreal climbing and suspension were very important components of the LCA’s behavior and that bipedalism was likely no more important than that seen in the repertoires of modern great apes. There is some evidence that bipedality was a relatively greater component of the repertoires of the earliest basal hominins, including *Sahelanthropus*, *Orrorin*, and *Ardipithecus kadabba*, but the evidence is frustratingly fragmentary (reviewed in Richmond and Hatala 2013). By 4.4 Ma, there is much more abundant evidence of the anatomy of *Ar. ramidus* (White et al. 2009). Arboreal locomotion was likely a very important part of the repertoire in *Ar. ramidus*, which had curved manual and pedal phalanges and a divergent, grasping hallux (Lovejoy et al. 2009a, c). However, evidence of a stiff foot and short pelvis suggests that bipedalism was also an important component of the locomotor adaptation of *Ar. ramidus*, likely more so than in any extant great ape (Lovejoy et al. 2009c, d).

Derived anatomy in *Australopithecus* shows that bipedalism played a greater role in the repertoires of australopiths than those of basal hominins. However, the role of arboreality continues to be a matter of enduring debate based mainly on differences in interpretation of the functional significance of primitive traits (e.g., Ward 2002). Regardless, some species of *Australopithecus* differ in these apelike traits, showing that they underwent evolutionary changes. Although one could invoke genetic drift to explain interspecific differences, some characteristics (phalangeal curvature, limb joint size proportions) differ among closely related anthropoid taxa in ways

that reflect significant differences in locomotor repertoires (Fleagle 1977; Doran 1993). Therefore, some of the differences between *Australopithecus* species may reflect differences in the relative degrees of arboreal behavior in the repertoire (Green et al. 2007). Similarly, there is compelling evidence of different locomotor repertoires between neighboring hominins living at c. 3.5 Ma, with greater emphasis on bipedalism in *Au. afarensis* at Hadar and greater emphasis on arboreal locomotion in another hominin taxon (*Ardipithecus* sp. or *Australopithecus deyiremeda*?) at nearby Burtele (Haile-Selassie et al. 2012, 2015).

The oldest evidence from hand fossils that hominins abandoned arboreal behavior comes from the over 1.84 Ma straight proximal phalanx at Olduvai (Domínguez-Rodrigo et al. 2015). However, based on the loss of morphology and cross-sectional geometry related to arboreality from other anatomical regions, there is broad consensus that by the early Pleistocene the locomotor repertoire of *H. erectus* comprised only bipedalism with no significant arboreal component (e.g., Jungers 1988; Ruff and Walker 1993; Bramble and Lieberman 2004; Ruff 2009). Current evidence suggests that the role of arboreality decreased from *Ar. ramidus* to *Australopithecus* to *H. erectus*. However, the pattern is certainly more complex, including broadly contemporaneous lineages that differ in their repertoires (e.g., hominins at Hadar and Burtele) and likely diversity among australopiths and early *Homo* in the degree of arboreality.

While the details of the evolutionary history must await more fossil discoveries, it is clear that hominins essentially stopped using their hands for locomotion “for good” by the time of *H. erectus* or possibly earlier.¹ This represents one of two fundamental changes in the functional and biological roles (sensu Bock and von Wahlert 1965) of the hominin hand.

3.2 Changes in Hand Manipulation

The review of changes in hominin hand anatomy also highlights the mosaic pattern in which the human hand has been shaped by evolution for greater manual dexterity, particularly in the anatomy and function of the thumb. However, investigating *how* the hand might be adapted for dexterity is challenging. In addition to a sparse fossil record, the uniqueness of human hand function limits the ability to use the comparative approach, arguably the most potent tool for investigating adaptation in extinct species. For example, long, curved fingers are good examples of adaptations to arboreal locomotion because this morphology evolved independently in South American atelines and Asian apes (Erickson 1963; Jungers et al. 1997), taxa that share the functional similarity of engaging in relatively high frequencies of suspensory behavior in their locomotor repertoires. In contrast, since humans are the only

¹We note, of course, that hands are used for crawling in humans during a brief period of development, and some people occasionally use their hands to climb trees in natural settings (Kraft et al. 2014). However, these instances of hand-based locomotion are rare.

natural stone toolmakers, no other taxa are available to examine structure-function relationships specific to this behavior (Susman 1998). Furthermore, the unique morphology in the hands of early hominins complicates attempts to infer their hand function based on experiments replicating primitive tools, because the human subjects in these experiments obviously have modern, not early hominin, hand morphology and cognitive abilities.

Despite these challenges, there are several lines of evidence regarding the evolution of manual dexterity and tool use. First, the fossil record demonstrates where and when hand morphologies existed, including characteristics that have functional consequences. Second, in some cases the fossil record preserves evidence of hand function, such as the pattern of trabecular bone density in metacarpal heads from Sterkfontein attributed to *Au. africanus* (Skinner et al. 2015). Third, the archeological record of tool use, such as cut marks and percussion marks on bones, and tools themselves demonstrates the products of hominin hand function. Fourth, experimental evidence of the manipulative skills needed to make and use tools, and the mechanical demands involved, provide an important context for understanding the functional morphology of making and using tools (see Chap. 11). Finally, studies of living human and nonhuman primate tool use, toolmaking, and carrying in natural settings provide important perspectives on the behavioral and ecological contexts of hand manipulation (e.g., Carvalho et al. 2013; Koops et al. 2014; Chap. 12).

These various lines of evidence suggest the following hypothesis for the evolution of hominin hand manipulation and tool use. Basal hominins likely used and made tools or at least had the capacity to do so in the right ecological settings; modern great apes in the wild make and use tools, and parsimony suggests that this capability was present in the *Pan-Homo* LCA as well (Panger et al. 2002). Basal hominins in the late Miocene may have had slightly better manipulative abilities than modern great apes, as suggested by distal pollical anatomy (Almécija et al. 2010) and potentially by hand proportions less derived than in great apes (Almécija et al. 2015), but this hypothesis remains very tentative until more fossil evidence is recovered. The oldest direct evidence of manipulation and tool use comes from the archeological record, including cut marks and percussion marks on large mammal bones from 3.4 Ma sediments at Dikika, Ethiopia (McPherron et al. 2010), and c. 3.3 Ma stone tools from Lomekwi, Kenya (Harmand et al. 2015), predating the earliest evidence of the genus *Homo* (Villmoare et al. 2015). This Pliocene archeological record is consistent with evidence that australopiths had greater manipulative capabilities than modern apes, mainly because australopiths had fairly humanlike thumb/finger proportions, broad distal tuberosities on fingertips, and an extrinsic flexor muscle to the thumb. Australopiths are derived relative to *Ar. ramidus* in having more humanlike thumb/finger proportions.

In the early Pleistocene, the hand of *H. habilis* is similar to that of australopiths, despite the name “handy man.” *H. habilis* is found in association with primitive Oldowan stone tools, but so is *Paranthropus*, leaving open the possibility that both engaged in this behavior. Wrist mobility appears to have increased by the early Pleistocene in *Au. africanus* and *P. robustus* (Richmond and Strait 2000; Richmond et al. 2001). Wrist mobility improves the accuracy of throwing

and accuracy and force production during stone toolmaking (Williams et al. 2010, 2014; Roach et al. 2013; Roach and Lieberman 2014), suggesting that these australopiths had greater manual capabilities than their predecessors. Rearrangement of carpal architecture is seen in *H. naledi* but not in *H. habilis* or *H. floresiensis*, pointing to major changes in force transmission patterns through the hand after the origin of *Homo*.

More sophisticated Acheulean stone tools date to c. 1.7 Ma (Lepre et al. 2011) and are first found in association with *H. erectus* (and *Paranthropus*). These tools require greater manipulative and cognitive skills than earlier Oldowan tools, and a hand anatomy suited to make and use them. Hand fossil elements that can be reliably attributed to *H. erectus* are scarce, but Mc1s associated with the Nariokotome skeleton indicate a robust thumb capable of generating higher forces and resisting greater stresses associated with strong thumb flexion (Fig. 18.4). The oldest evidence of a hand with essentially modern human anatomy comes after a substantial chronological gap, later in the early Pleistocene at 0.8 Ma (see Chap. 19). Much would be learned about the timing, context, and potential selective pressures responsible for more humanlike morphology from the recovery of hand fossils securely attributed to *H. erectus* and *Paranthropus*.

It is clear that morphology related to forceful precision grips evolved in a mosaic fashion, with derived features appearing in multiple species of *Australopithecus*, possibly *Paranthropus*, and multiple species of *Homo*. It is notable that several modern human features, such as a robust thumb, greater wrist mobility, reorganized carpal architecture, and straight phalanges, appear well after stone tools first appear. This supports the hypothesis that *intensification* of making and using tools, rather than the origin of these behaviors, drove much of the evolution of derived human hand anatomy.

4 Conclusions and Future Directions

In conclusion, the fossil record preserves evidence of hominin hand anatomy spanning about 6 million years. When examined in a comparative and functional context, it is clear that the anatomy of the hominin hand evolved in a complex, mosaic fashion.

This review highlights several major conclusions:

1. Two major functional changes occurred during human evolution: the loss of a locomotor role and the intensification of manipulation.
2. These two changes in function were not abrupt. The abandonment of arboreal locomotion and rise of manipulative capabilities evolved over considerable spans of time, in varied contexts, and in a nonlinear manner.
3. Differences in hand morphology among early hominin species suggest differences in their locomotor repertoires and manipulative abilities, not unlike differences in behavior seen among closely related species today (e.g., bonobos and chimpanzees).

4. Evidence supports the hypothesis that the *intensification* of manipulation, rather than the origin of stone tool making, drove the evolution of a number of derived aspects of human hand anatomy.

4.1 *Future Directions I: Is the Human Thumb “Hyper-opposable”?*

In the process of reviewing what we currently know about the early evolution of the human hand, it became clear that there is considerable variation in what is meant by an “opposable” thumb, and this topic deserves further attention. There is broad consensus that a thumb capable of opposing the other digits is a key characteristic of primates (e.g., see Chap. 14) and that humans are derived in the ability to oppose the thumb for precision gripping and handling. Definitions of opposability vary widely, but typically defer to Napier’s traditional definitions describing the ability to rotate the thumb into pad-to-pad contact with other digits (Napier 1956) or position the thumb via movements at the CM1 joint (Napier 1961). It would be useful to have a separate term that describes the derived ability in humans to produce an extensive area of contact between the thumb and other digits and forcefully secure and precisely handle objects between the thumb and other digits through pad-to-pad contact (Marzke 1997). We propose the term *hyper-opposable* to describe this derived human condition.

4.2 *Future Directions II: Other Areas of Research*

It goes without saying that more fossils are needed to document the evolution of human hand anatomy, although some fossils would be more valuable than others. Efforts to reconstruct the *Pan-Homo* LCA have preoccupied scholars for well over a century, so fossil evidence of the LCA and its close relatives (including fossil *Pan* and *Gorilla*) would be particularly enlightening, despite the challenges in reaching consensus among scientists regarding the systematics and phylogenetic position of fossils near the LCA once they are found. Other notable gaps in the fossil record include the lack of hand fossils, especially associated elements, that are securely attributed to *Paranthropus*, *H. erectus*, and other early *Homo* species. In addition to finding fossils of taxa for which we currently know virtually nothing about their hand morphology, a more complete fossil and archeological record will improve our knowledge about the timing and context of the changes in hominin hand function.

A second area of research that deserves more attention is primate functional morphology. While primate hand morphology is relatively well characterized, our understanding of hand function, especially in natural settings, is still in its infancy.

Very little is known about how primates use their hands during locomotion and how hand postures and forces vary with support size and orientation, types of locomotion, speed, body size, and other factors (see Chaps. 10 and 13). Categories used to describe locomotion in the wild, such as “arboreal” and “terrestrial,” are limited in their utility for understanding hand biomechanics. For example, for a small primate, the biomechanics of the hand can differ more between locomotion on large versus small arboreal supports than between a large arboreal support and the ground. What we need is a “hands-eye” view of a primate’s world to understand the functional demands that hands face.

Similarly, too little is known about the biomechanics of the human hand when engaged in functions that were likely to be important during human evolution. A number of studies have examined aspects of biomechanics involved in making primitive stone tools, and research in this area is growing in sophistication (see Chap. 11). More research is needed to examine the biomechanics of other activities, such as the use of spears, digging sticks, food processing, and throwing, as well as the use of various forms of stone tools and flakes in different settings. In a similar vein, more research is needed on the ecological and behavioral context of making and using tools, and carrying, in humans as well as nonhuman primates in natural settings.

Finally, a better understanding of the factors that influence skeletal morphology during growth and in adulthood will improve our ability to make robust inferences about behavior from external morphology, cortical geometry, and trabecular structure.

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