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Kivell, Tracy L. and Churchill, Steven E and Kibii, Job M and Schmid, Peter and Berger, Lee R (2018) The hand of Australopithecus sediba. *PaleoAnthropology* . ISSN 1545-0031. (In press)

### DOI

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1   **Title:** THE HAND OF *AUSTRALOPITHECUS SEDIBA*  
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32 **Running title:** The hand of *Australopithecus sediba*  
33

1 **Abstract**

2 Here we describe the functional morphology of the *Australopithecus sediba* hand, including the  
3 almost complete hand of the presumed female Malapa Hominin (MH) 2 skeleton and a single,  
4 juvenile metacarpal from the presumed male MH1 skeleton. Qualitative and quantitative  
5 comparisons with extant hominids and fossil hominins, ranging from *Ardipithecus* to early *Homo*  
6 *sapiens*, reveal that *Au. sediba* presents a unique suite of morphological features that have not  
7 been found in any other known hominin. Analyses of intrinsic hand proportions show that the  
8 MH2 hand has a thumb that is longer relative to its fingers than recent humans and any other  
9 known hominin. Furthermore, the morphology of the hamatometacarpal articulation suggests  
10 that the robust fifth metacarpal was positioned in a slightly more flexed and adducted posture  
11 than is typical of Neandertals and humans. Together, this morphology would have facilitated  
12 opposition of the thumb to the fingers and pad-to-pad precision gripping that is typical of later  
13 *Homo*. However, the remarkably gracile morphology of the first ray and the morphology of the  
14 lateral carpometacarpal region suggest limited force production by the thumb. The distinct  
15 scaphoid-lunate-capitate morphology in MH2 suggests a greater range of abduction at the  
16 radiocarpal joint and perhaps less central-axis loading of the radiocarpal and midcarpal joints  
17 than is interpreted for other fossil hominins, while the morphology of the hamatotriquetrum  
18 articulation suggests enhanced stability of the medial midcarpal joint in extended and/or  
19 adducted wrist postures. The MH2 proximal phalanges show moderate curvature and,  
20 unusually, both the proximal and intermediate phalanges have well-developed flexor sheath  
21 ridges that, in combination with a palmarly-projecting hamate hamulus, suggest powerful flexion  
22 and that some degree of arboreality may have been a functionally important part of the *Au.*  
23 *sediba* locomotor repertoire. Finally, the MH1 and MH2 third metacarpals differ remarkably in  
24 their size and degree of robusticity, but this variation fits comfortably within the sexual  
25 dimorphism documented in recent humans and other fossil hominins, and does not necessarily

1 reflect differences in function or hand use. Overall, the morphology of the current *Au. sediba*  
2 hand bones suggests the capability for use of the hands both for powerful gripping during  
3 locomotion and precision manipulation that is required for tool-related behaviours, but likely with  
4 more limited force production by the thumb than is inferred in humans, Neandertals and  
5 potentially *Homo naledi*.

6

7

## 1 INTRODUCTION

2 Hominin hand morphology has elicited great interest over the last several decades as it has the  
3 potential to reveal information about whether our fossil ancestors and extinct relatives still  
4 engaged in arboreal locomotion, and to provide insights into the evolution of tool-related  
5 behaviours and the extraordinary manipulative abilities of the human hand (e.g. Lemelin and  
6 Schmitt 2016; Marzke 1983, 1997; Napier 1962a,b; Wood Jones 1916). However, until recently,  
7 the early hominin fossil record for hand bones was relatively sparse, composed of primarily  
8 isolated and/or fragmentary hand bones that could not be associated to particular individuals or,  
9 in some cases, particular species (e.g. Bush et al. 1982; Drapeau et al. 2005; Napier 1962a;  
10 Ricklan 1987, 1990; Susman 1988, 1989). Over the last two decades, several discoveries have  
11 fortunately greatly increased our sample of fossil hominin hand bones, including associated  
12 hand skeletons that permit a greater understanding of overall hand function in certain species  
13 (Clarke 1999, 2008, 2013; Kivell et al. 2011, 2015; Lovejoy et al. 2009; Orr et al. 2013; Tocheri  
14 et al. 2007).

15

16 In 2008 two relatively complete and partially articulated skeletons were discovered at the site of  
17 Malapa, South Africa dated to 1.977 million years ago (Ma) (Berger et al. 2010; Dirks et al.  
18 2010; Pickering et al. 2011). Malapa hominin (MH)1 is considered a juvenile male and MH2 is  
19 considered an adult female (Berger et al. 2010). The novel combination of morphologies that  
20 characterised these skeletons established these fossils as a new species, *Australopithecus*  
21 *sediba* (Berger et al. 2010). Included within these fossil remains was a relatively complete right  
22 hand, found in semi-articulation with the remainder of the right upper limb associated with MH2,  
23 as well as a few bones from the left hand of the same individual (Figure 1; Table 1). The MH2  
24 right hand preserves all bones of the hand except the pisiform, trapezium, trapezoid and the  
25 distal phalanges of the fingers, while a capitate, hamate and three partial proximal phalanges

1 are preserved from the left hand. In addition, a juvenile third metacarpal is associated with the  
2 MH1 skeleton. Although Kivell et al. (2011) provided a basic morphological description and  
3 functional interpretation of most of these hand bones, here we provide a more detailed  
4 description and morphological analysis of each bone in a comparative context with extant  
5 humans and African apes, as well as other australopiths, *Ardipithecus*, and early and later  
6 *Homo* fossils, including *Homo naledi*.

7

8 **[INSERT Figure 1 and Table 1 about here]**

9

## 10 **MATERIALS AND METHODS**

11 The *Au. sediba* MH1 and MH2 hand bones were compared qualitatively and quantitatively to  
12 those of extant African apes, recent humans, and a large sample of fossil hominins. The extant  
13 comparative sample is composed of *Gorilla* spp., including *Gorilla gorilla* and *Gorilla beringei*,  
14 *Pan troglodytes* spp., *Pan paniscus*, and recent *Homo sapiens*, including 19<sup>th</sup>-20<sup>th</sup> century  
15 African, European and Tierra del Fuegian populations, 6<sup>th</sup>-11<sup>th</sup> century Nubian Egyptians  
16 (Strouhal 1992), and small-bodied Khoisan individuals.

17 The comparative fossil sample includes data taken from original fossils of *Ardipithecus*  
18 *ramidus*, *Australopithecus* sp. StW 618, *Australopithecus afarensis*, *Australopithecus africanus*,  
19 *Australopithecus (Paranthropus) robustus* TM 1517, the Swartkrans hominin fossils attributed to  
20 either *Au. robustus* or early *Homo*, *Homo habilis* OH 7, *H. naledi*, *Homo neanderthalensis*  
21 (Kebara 2, Amud 1, Tabun 1) and early *H. sapiens* (Qafzeh 8 and 9, Ohalo II H2, Arene  
22 Candide 2, Barma Grande 2). For *Ar. ramidus* specimens, data were either derived from  
23 published values in Lovejoy et al. (2009) or collected on original specimens by TLK and Gen  
24 Suwa. Additional comparative samples include data derived from casts and 3D surface models,  
25 in comparison with published data, on *Australopithecus anamensis* (Ward et al. 2001), cf.

1 *Australopithecus* KNM-WT 22944 (Ward et al. 1999, 2012), *Homo floresiensis* (Larson et al.  
2 2009; Orr et al. 2013; Tocheri et al. 2007), *H. neanderthalensis*, including Shanidar 3 (Trinkaus  
3 1982, 1983), La Ferrassie 1, Regourdou 1, La Chapelle-aux-Staints, and Neandertal 1, and  
4 early *H. sapiens* Tianyuan 1 (Niewoehner 2006; Niewoehner et al. 1997; Trinkaus 1983).

5         The *Au. sediba* fossils were also compared with published data on *Au. afarensis* A.L.  
6 288-1w (Johanson et al. 1982), possible *Homo erectus* specimens including the KNM-WT  
7 51260 third metacarpal (Ward et al. 2013) and OH 86 fifth proximal phalanx (Domínguez-  
8 Rodrigo et al. 2015), *Homo* sp. ATE9-2 fifth proximal phalanx (Lorenzo et al. 2015), *Homo*  
9 *antecessor* isolated hand bones (Lorenzo et al. 1999), *H. neanderthalensis* Shanidar individuals  
10 (Trinkaus 1982, 1983), La Ferrassie 1 and 2, Regourdou 1, La Chapelle-aux-Saints (Heim 1982;  
11 Niewoehner et al. 1997; Niewoehner 2006), Moula-Guercy (Mersey et al. 2013), Krapina (Heim  
12 1982) and Spy (Crevecoeur 2011), and early *H. sapiens*, including Skhul (Kimura 1976), Dolní  
13 Věstonice (Sladek et al. 2000; Trinkaus et al. 2010) and Pavlov (Trinkaus et al. 2010)  
14 individuals. Finally, the fossils were also compared to published images and/or descriptions of  
15 *Orrorin tugenensis* pollical distal phalanx and proximal phalanx (Almecija et al. 2010; Gommery  
16 and Senut 2006; Senut et al. 2001), *Australopithecus prometheus* articulated hand (Clarke  
17 1999, 2008, 2013), *H. erectus* lunate (Weidenreich 1941), KNM-WT 15000 juvenile pollical  
18 proximal phalanx, an intermediate phalanx, and two possible first metacarpals (Walker and  
19 Leakey 1993) and two distal phalanges from Dmanisi (Lordkipanidze et al. 2007), and *H.*  
20 *antecessor* isolated wrist and hand bones from both juveniles and adults (Lorenzo et al. 1999;  
21 Trinkaus 2016).

22         Measurements for the metacarpals and phalanges follow standard metrics described by  
23 Green and Gordon (2008) and Begun (1993), respectively. Linear measurements of the carpal  
24 bones are described in Kivell and Begun (2009), Begun and Kivell (2011), and Kivell et al.

1 (2013a, b). Additional images of how carpal metrics were measured are depicted in box-and-  
2 whisker plots below.

3 Comparisons of size and shape differences across extant and fossil taxa were assessed  
4 via box-and-whisker plots. Most aspects of morphology were assessed as shape ratios, usually  
5 as a ratio of the total length of the bone. For the triquetrum, capitate and hamate, some metrics  
6 were analysed as a shape ratio against a geometric mean of the maximum proximodistal length,  
7 dorsopalmar height and mediolateral breadth of the carpal bone (Jungers et al. 1995; Mosimann  
8 1970). All analyses were conducted in PAST.3.14 (Hammer et al. 2001).

9 Curvature of the dorsal surface of the non-pollical proximal phalanges was quantified  
10 using high-resolution polynomial curve fitting (HR-PCF), following the methods Deane and  
11 colleagues (Deane et al. 2005; Deane and Begun 2008). The HR-PCF method differs from that  
12 of the more traditional included angle measure (Stern et al. 1995) by modelling the surface  
13 curvature and fitting a polynomial function to the dorsal surface of the phalanx. Using  
14 standardised lateral-view photographs of each phalanx, the dorsal surface was digitised and,  
15 from selected end points and a best-fit second order polynomial function, the first polynomial  
16 coefficient was used to describe the nature and degree of longitudinal curvature (Deane et al.  
17 2005).

18 Specimens and sample sizes for comparative analyses varied for each hand element.  
19 Therefore information on the specific sample is provided in the figure legend of each  
20 comparative analysis. In instances where both the left and right sides are preserved for a  
21 particular element for the same individual, the mean value was used.

22

### 23 **ANATOMICAL DESCRIPTION OF *AU. SEDIBA* HAND FOSSILS**

24 All specimens described below are associated with the adult MH2 skeleton, apart from U.W. 88-  
25 112, a juvenile left third metacarpal that is associated with MH1. All of the MH2 hand bones



1 appear externally as adult due to full fusion of epiphyses, complete ossification of carpals (Kivell  
2 2007) and well-defined articular facets. In addition to the MH2 right hand bones being found in  
3 semi-articulation *in situ* (Figure 1), they articulate well together and with the distal radius and  
4 ulna based on the preserved morphology (Figure 2). Metric data for all MH1 and MH2 hand  
5 bones are provided in Tables 2-5. A taphonomic analysis of the MH1 and MH2 skeletons has  
6 revealed numerous perimortem fractures, including several throughout the MH2 upper limb, that  
7 are consistent with falling from a height and bracing with the arm against impact (L'Abbé et al.  
8 2015). Among these perimortem palaeopathologies are two fractures within the MH2 hand; one  
9 on the scaphoid and one on the triquetrum (L'Abbé et al. 2015), which are noted below.

10 A 3D model of the articulated MH2 hand as well as separate 3D data for some of MH2  
11 hand specimens are available on MorphoSource (<https://www.morphosource.org/>). The  
12 following abbreviations are used throughout the morphological descriptions below: proximodistal  
13 (PD), dorsopalmar (DP) and mediolateral (ML).

14

#### 15 **U.W. 88-158 RIGHT SCAPHOID (MH2)**

16 **Preservation** This bone is complete apart from fragments missing from the tip of the tubercle  
17 and the dorsomedial edge of the capitate facet (Figure 3). There are fine cracks running along  
18 the approximate PD midline of the trapezium-trapezoid facet and the DP midline of the capitate  
19 facet, but neither crack distorts the morphology. These cracks have been previously interpreted  
20 as Class II fractures, consistent with a perimortem injury to the wrist (L'Abbé et al. 2015).

21 **Morphology** The U.W. 88-158 scaphoid has a fused os centrale (Figure 3). The tubercle is  
22 robust, conical-shaped, and proximally-oriented. The radial facet is not continuously convex but  
23 instead the point of strongest curvature is proximally-positioned, such that the facet is divided  
24 into a larger distal portion and smaller proximal portion, both of which are mildly convex. A  
25 dorsal ridge at the distal edge of the radial facet is not present. The lunate facet is generally flat,

1 half-moon-shaped, and is confined to the proximodorsal edge of the scaphoid. The capitate  
2 facet is oval-shaped and relatively shallow in its concavity (Table 2). Although a fragment is  
3 missing from the distomedial edge, the capitate facet appears to be “closed” (i.e., there is no  
4 excavation of the distomedial edge of the facet) (Tocheri 2007). The trapezoid and trapezium  
5 facets form a single, continuous facet that is strongly convex both the DP and ML dimensions.  
6 The trapezoid-trapezium facet appears “raised”, divided on the lateral side from the remainder  
7 of the bone by a deep sulcus that extends onto the tubercle. The trapezium facet extends onto  
8 the tubercle, reaching to roughly 3mm from the estimated tip of the scaphoid’s tubercle (as this  
9 region is not well-preserved) (Figure 3).

10

11 **[INSERT Figures 2 & 3 and Table 2 about here]**

12

13 **U.W. 88-159 RIGHT LUNATE (MH2)**

14 **Preservation** This bone is complete apart from a large fragment missing from the palmar-  
15 medial edge of lunate body, and a small fragment from the distodorsal edge of the triquetrum  
16 facet (Figure 4). All articular facets are well-defined.

17 **Morphology** The U.W. 88-159 lunate is small and narrow, although the fragment missing from  
18 the palmar-medial corner over-accentuates its narrowness (Figures 2 and 4; Table 2). The  
19 capitate and radial facets sit roughly parallel to each other. The capitate facet is remarkably ML  
20 narrow relative to its DP height. The palmar portion of the capitate facet (and lunate body) is  
21 more distally extended than the dorsal portion. A separate articulation for the hamate is not  
22 present. The radial facet occupies most of the proximal surface and extends onto the palmar  
23 surface to approximately 5.5mm from the most distal edge of lunate body. The radial facet is ML  
24 broad relative to the breadth of the lunate body and its convexity shows a similar division as  
25 seen in the scaphoid’s radial facet, such that point of peak curvature is proximally-positioned.

1 The scaphoid facet is flat and confined mostly to the dorsal half of the lunate's lateral side. The  
2 scaphoid facet is distolaterally oriented, such that it is positioned more acutely (i.e. less than 90  
3 degrees) to the capitate facet, and can be clearly seen in distal view (Figures 2 and 4). The  
4 triquetrum facet is dorsally-position and generally flat. The dorsal non-articular surface is deeply  
5 excavated for attachment of the dorsal intercarpal and radiotriquetrum liagments (Taleisnik  
6 1976). No foramina or ligamentous attachment sites can be seen on the non-articular palmar  
7 portion of the lunate body.

8

### 9 **U.W. 88-157 RIGHT TRIQUETRUM (MH2)**

10 **Preservation** This bone is complete and undistorted. There are two thin cracks on the medial  
11 surface running dorsopalmarly around the triquetrum body (Figure 5). These cracks have been  
12 previously interpreted as Class II fractures, consistent with a perimortem injury to the wrist  
13 (L'Abbé et al. 2015).

14 **Morphology** The overall shape of the MH2 triquetrum is ML broad and PD narrow, with a  
15 palmar-medially-extended tip (Figure 5; Table 2). The lunate facet is flat, roughly square-  
16 shaped, and is oriented at an approximate right angle to the hamate facet. The hamate facet  
17 has a complex concavoconvex surface; the middle of the facet has the deepest concavity that  
18 extends to a convex surface at the dorsolateral, palmar-lateral and medial borders. The hamate  
19 articulation extends to the dorsal edge of the triquetrum body and to roughly 4.7mm from the  
20 body's most medial extent. The pisiform facet is small (*contra* Kivell et al. 2011) and oval-  
21 shaped. It is positioned on the palmar-medially-projecting extension of the triquetrum body and,  
22 as such, is oriented proximopalmarly. The non-articular palmar portion of the triquetrum body is  
23 deeply excavated by a sulcus running roughly ML across the lateral half of the body (Figure 5).

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25 **[INSERT Figures 4 & 5 about here]**

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**U.W. 88-105 LEFT CAPITATE (MH2)**

**Preservation** This bone is complete and perfectly preserved (Figure 6).

**Morphology** The overall shape of the capitate appears DP tall relative to its PD length (Figure 6; Table 2). The proximal facet is relatively equal in its DP height and ML breadth (Table 2). There is no clear demarcation between the lunate and scaphoid articular areas on the proximal surface and both end distally in a small dorsal ridge. On the lateral surface, the dorsal portion of the scaphoid facet extends further distally than its palmar portion, touching the tip of the dorsal trapezoid facet. The capitate body is deeply excavated between the distal portion of the scaphoid facet and the dorsal trapezoid facet. The capitate body appears moderately “waisted” in palmar view (Figure 6).

There are two trapezoid facets on the lateral side of the capitate; a smaller triangular-shaped facet positioned dorsally and a larger, well-defined, oval-shaped facet placed palmarly (each measuring 4.1 and 3.5mm in PD length and 4.2 and 6mm in DP height, respectively). The capitate’s second metacarpal (Mc2) facet is continuous running most of the DP height of the capitate body. It is slightly concave, especially at its palmar end. The Mc2 articulation is oriented primarily laterally, with only a slight distal orientation. The Mc3 facet occupies the distal surface of the capitate body and is generally flat, with a slight concavity at dorsomedial border. The distodorsolateral border is not excavated to accommodate a Mc3 styloid process (Figure 6). The hamate facet is continuous along the complete dorsal border of the capitate’s medial surface. Most of the hamate articulation is flat apart from the distal 1/3 that curves proximally and palmarly. There is no separate articulation on the capitate for the Mc4.

**U.W. 88-156 RIGHT CAPITATE (MH2)**

1 **Preservation** This bone is complete and well-preserved, apart from small surface fragments  
2 missing from the distopalmar surface of the capitate body, just palmar to the border of the Mc3  
3 facet and the distopalmar surface of the Mc2 facet (Figure 6). There is some abrasion on the  
4 palmar half of the lateral side that obscures the presence of a trapezoid facet and the full dorsal  
5 extent of the Mc2 facet. Although a portion of the distodorsolateral corner of the capitate body  
6 appears to be missing when compared with the left MH2 capitate, the dorsal non-articular  
7 surface appears continuous and undamaged. The capitometacarpal articular surfaces articulate  
8 well with the Mc2 and Mc3, suggesting that the right capitate is generally complete (Figure 7).  
9 Thus, this variation may simply reflect asymmetry between the right and left capitates in MH2.

10 **Morphology** This bone is similar in morphology to that described in the U.W. 88-105 left  
11 capitate, apart from the dorsolateral portion of the capitate body described above (Figure 6;  
12 Table 2). The overall size of the bone and facets are slightly smaller than that of the left  
13 capitate, consistent with bilateral asymmetry within one individual. Due to the preservation of the  
14 lateral side of the capitate, it is unclear if this specimen had both palmar and dorsal trapezoid  
15 facets as in U.W. 88-105. If the absence of distodorsolateral corner of capitate body is not  
16 taphonomical, than is likely that a dorsal trapezoid facet was not present.

17

18 **[INSERT Figures 6 and 7 about here]**

19

#### 20 **U.W. 88-106 LEFT HAMATE (MH2)**

21 **Preservation** This bone is complete and perfectly preserved, except for a small pit at the distal  
22 edge of the dorsal surface (Figure 8).

23 **Morphology** The body of the hamate (excluding the hamulus) appears DP tall relative to PD  
24 length (Figure 8, Table 2). The hamulus projects palmarly much further than it does distally,  
25 such that the hamulus alone measures 7.6mm in DP height but projects distally only 0.2mm

1 from the hamate body. The hamulus is widest in the PD plane and is mediolaterally narrow  
2 (Figures 7 and 8). The triquetrum facet is proximomedially-oriented and extends to the distal  
3 end of the hamate body. The proximal half is convex in both the PD and DP dimensions, while  
4 the distal half is concave and more proximally-oriented. In medial view, the proximal half of the  
5 facet is inclined dorsally, such that the triquetrum would rotate dorsally during extension and/or  
6 adduction of the midcarpal joint.

7         The capitate facet is generally flat, but slightly curved in dorsal view to match the  
8 opposing concavity on the capitate's hamate facet (Figures 6 and 7). The Mc4 facet is  
9 absolutely larger than the Mc5 facet in both the DP and ML dimensions (Table 2). The Mc5  
10 facet is oriented distomedially relative to the Mc4 facet and extends to the dorsal border of the  
11 hamulus (Figure 7). The Mc4 facet is generally flat while the Mc5 facet is strongly concave  
12 dorsopalmarly and slightly concave mediolaterally. There is a space between the palmar border  
13 of the Mc5 facet and the strongest curvature of the hamulus that could potentially accommodate  
14 extension of the pisometacarpal ligament to the Mc3, although no clear groove is present (Lewis  
15 1977).

16

#### 17 **U.W. 88-95 RIGHT HAMATE (MH2)**

18 **Preservation** This bone is complete except for a small fragment missing from the distopalmar  
19 tip of the hamulus (Figure 8).

20 **Morphology** The morphology of the right hamate is identical to that of left side, U.W. 88-106  
21 (Figure 8; Table 2). The overall size of the hamate and its facets are generally slightly smaller  
22 than that of U.W. 88-106, consistent with pattern seen in the MH2 capitates and bilateral  
23 asymmetry within an individual.

24

25 **[INSERT Figure 8 about here]**

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**U.W. 88-119 RIGHT FIRST METACARPAL (MH2)**

**Preservation** This bone is complete and well-preserved (Figure 9). There is a fracture around the approximate midshaft and a smaller crack in the distal half of the shaft, both of which run the circumference of the bone.

**Morphology** The first metacarpal (Mc1) of MH2 appears long and remarkably gracile (Figure 9; Table 3). The dorsal surface of the shaft is mildly convex and the proximal and distal epiphyses project slightly dorsally beyond the shaft. Muscle attachments along the shaft are poorly defined. There is a roughened surface along the lateral shaft for the attachment of the *M. opponens pollicis* tendon, extending from the beginning of the proximal shaft 15.5mm distally, although the distal end of the enthesis is slightly obscured by the midshaft fracture line. The attachment is proximally-positioned and there is no indication of tendon insertion along the distal shaft. The *M. first dorsal interosseous* attachment is equally poorly developed in U.W. 88-119, appearing as a faint ridge along proximal half of the shaft's medial border, measuring 11.8mm in PD length (Kivell et al. 2011).

Relative to interarticular length, the proximal base of U.W. 88-119 is ML narrow relative to its height (Figure 9; Table 3). The tendon attachments at the base appear robust because of the gracility of the shaft; the distolateral border of the base flares laterally with an attachment for the *M. abductor pollicis longus*. The palmar-medial portion of the base is also robust, which is the region of insertion for the *M. palmar interosseous*. A triangular-shaped fossa is found on the palmar-lateral surface between these two tendon attachment sites. The trapezium facet is saddle-shaped; the DP concavity appears slightly more pronounced than its ML convexity. There is no beak-like palmar extension of the proximal epiphysis.

The distal head of U.W. 88-119 is DP tall and ML narrow (Figure 9; Table 3). The head has a prominent beak along the midline of the palmar surface. This beak is flanked by

1 depressions for medial and lateral sesamoid bones, with the medial depression being more  
2 excavated than the lateral, which serve as insertion sites for *Mm. adductor pollicis oblique* and  
3 *flexor pollicis brevis*, respectively (Marzke et al. 1999). The articular surface for the first proximal  
4 phalanx is asymmetric; in palmar view, the dorsal articular surface slopes laterally and the  
5 articular surface extends further proximally on the medial side. In distal view, the dorsal half of  
6 the articular surface is ML narrower than the palmar half. The epicondyles are not prominent.

7

8 **[INSERT Figure 9 and Table 3 about here]**

9

#### 10 **U.W. 88-115 RIGHT SECOND METACARPAL (MH2)**

11 **Preservation** This bone is complete and well-preserved. There is slight erosion on the dorsal  
12 surface of the proximal articular facet and hairline fractures running mediolaterally across the  
13 dorsal half of the proximal facet and proximodistally along the medial side of the shaft from the  
14 proximal end to roughly midshaft (Figure 10).

15 **Morphology** Like the MH2 Mc1, the shaft of U.W. 88-115 appears gracile (Figure 10; Table 3).  
16 In dorsal view, the distal shaft and head are oriented more laterally relative to the remainder of  
17 the Mc2. The dorsal shaft has a prominent crest along the sagittal midline for attachment of the  
18 first and second *Mm. dorsal interossei* that starts at the base-shaft junction and extends 15mm  
19 distally, flattening out just proximal to the midshaft. These crests are prominent on all of the  
20 MH2 medial metacarpal shafts (see below), but the crest is most well-developed on the Mc2.

21 The base of the Mc2 is robust relative to the gracile shaft. The dorsal surface of the  
22 proximal epiphysis has two well-developed tubercles, one dorsolateral for the attachment of the  
23 *M. extensor carpi radialis longus* tendon and one dorsomedial for the attachment of the *M.*  
24 *extensor carpi radialis brevis* tendon. Similarly, the palmar surface of the proximal epiphysis  
25 presents robust and distinct tubercles for the attachment of the *M. flexor carpi radialis* and



1 oblique tendons of the *M. adductor pollicis*. The proximal articular surface for the trapezoid is  
2 roughly triangular in outline in proximal view, although the palmar articular region is relatively  
3 ML broad (measuring 7.3mm) compared with the dorsal portion (measuring 10.2mm), giving it a  
4 somewhat “squared” appearance (Table 3). The trapezoid facet dominates the proximal surface,  
5 although the trapezium and capitate facets can also be seen in proximal view. The trapezoid  
6 facet is V-shaped, with a larger medial portion than lateral portion, that are oriented at roughly  
7 110 degrees to each other in dorsal view.

8         The trapezium facet is flat and oval-shaped (measuring 4.6mm PD and 6mm DP), and  
9 oriented palmar-laterally. Relative to the long axis of the shaft, the trapezium facet is oriented  
10 approximately 35° in proximal view (Drapeau et al. 2005), and approximately 28° in dorsal view  
11 (Kivell et al. 2011). The capitate facet is rectangular in shape, measuring 5mm proximodistally  
12 and 9.6mm dorsopalmarly. It is generally flat in DP dimension but slightly convex in its PD  
13 dimension and runs most of the DP height of the medial side of the proximal epiphysis. The  
14 capitate facet is distinguished from the Mc3 facet by its more proximal orientation. The Mc3  
15 articulation is a continuous, bilobate facet with more distinct palmar and dorsal articular areas  
16 that are connected proximally. The complete Mc3 facet measures 9.9mm dorsopalmarly but is  
17 PD longer at the dorsal end (7mm) than the palmar end (4.3mm).

18         The distal epiphysis of U.W. 88-115 appears ML broad and particularly DP tall (Table 3).  
19 The Mc2 head is strongly asymmetrical; the palmar articular surface is more ML expanded than  
20 the dorsal portion and the palmar articular surface extends further proximally on the lateral side.  
21 There is no ridge along the dorsal articular margin. The medial epicondyle is well-developed and  
22 more proximally positioned compared with the lateral epicondyle.

23

24 **[INSERT Figure 10 about here]**

25

1 **U.W. 88-112 LEFT THIRD METACARPAL (MH1)**

2 **Preservation** This bone is incomplete, missing its epiphyseal head, which was unfused to the  
3 distal shaft (Figure 11). The base is missing a large fragment from the dorsolateral corner and a  
4 smaller fragment from the palmar portion of the proximal articular surface. There is triangular-  
5 shaped hole running through the shaft at roughly midshaft that exposes a cross-section of the  
6 cortex. Additional small surface fragments are missing from the shaft cortex.

7 **Morphology** U.W. 88-112 is a juvenile Mc3 and is thought to be from the left side, *contra*  
8 Berger et al. (2010) and Kivell et al. (2011), which identified it as a right. Because the head and  
9 diagnostic articular surfaces of the base are not preserved, side identification is based on  
10 comparisons with the MH2 U.W. 88-116 right Mc3 and the preservation of a slight lateral torsion  
11 of the distal shaft, protuberance of the dorsolateral tubercle of the base, slight “lipping” of the  
12 mediopalmar edge of the capitate facet, and the orientation of the dorsal Mc4 facet (Figure 11)  
13 all of which suggest U.W. 88-112 is a left Mc3.

14 The distal surface of the metacarpal is irregular and pitted, typical of an unfused  
15 epiphyseal surface (Figure 11). In palmar view, the proximal portion of the shaft is straight but at  
16 midshaft it flares mediolaterally with slight torsion to the lateral side. In dorsal view, the distal  
17 shaft is ML broad and flat both its PD and ML dimensions (Table 3). The flaring of the distal  
18 shaft creates a ridge along the dorsomedial border that extends from the epiphyseal line  
19 proximally 15.1mm. Just palmar to this ridge is a smooth, shallowly concave fossa along the  
20 medial shaft. In lateral view, the dorsal shaft is mildly convex. Although the complete length of  
21 this bone is not preserved, the shaft appears substantially more robust, both in its ML and DP  
22 dimensions, than the Mc3 of the MH2 hand (U.W. 88-116, see below) (Figure 11; Table 3).

23 The preserved morphology of the U.W. 88-112 base is similar in absolute DP height  
24 (13.9mm preserved) to that of MH2 U.W. 88-116 Mc3 but is missing large fragments from its  
25 dorsolateral corner and the palmar border. With these portions preserved, the U.W. 88-112

1 base would be larger both dorsopalmarly and mediolaterally than U.W. 88-116. Much of the  
2 lateral surface of the base is missing and the Mc2 facet(s) is not preserved. The capitate facet,  
3 which is preserved in only the dorsomedial portion of the proximal Mc3 surface, is flat and  
4 slightly dorsally-oriented. In medial view, the slightly palmarly-oriented palmar-medial border of  
5 the capitate facet creates a small lip that is similar to the morphology found in U.W. 88-116  
6 (Figure 11). A dorsal, oval-shaped Mc4 facet is clearly preserved, measuring 6.6mm  
7 proximodistally and 5mm dorsopalmarly, and, although the proximopalmar border of the medial  
8 side is slightly eroded, there does not appear to be a palmar Mc4 facet (unlike U.W. 88-116).

9         The unfused epiphyseal head of this Mc3 is consistent with the stage of juvenile  
10 development found throughout the remainder of the MH1 skeleton (Berger et al. 2010). Fusion  
11 of the Mc3 head occurs at roughly age 9-10 years in chimpanzee (Kerley 1966) and age 14-17  
12 years in humans (Scheuer and Black 2000).

13

#### 14 **U.W. 88-116 RIGHT THIRD METACARPAL (MH2)**

15 **Preservation** This bone is generally well-preserved, apart from a missing fragment at the  
16 dorsomedial edge of the proximal end, a small pit on the palmar surface of the shaft just distal to  
17 the midshaft, a large surface fracture along the palmar surface of the distal articular facet, and a  
18 thin fracture along the lateral side of the distal end, just palmar to the medial epicondyle. The  
19 fracture lines and pit do not distort the original morphology (Figure 11).

20 **Morphology** U.W. 88-116 is a gracile Mc3 that does not have a styloid process (Figure 11). In  
21 palmar view, the shaft is straight and ML narrow (Table 3). Along the proximal half of the dorsal  
22 surface of the shaft there is a small crest running PD 11.1mm along sagittal midline for the  
23 attachment of the second and third *Mm. dorsal interossei*. This crest is not as prominent as that  
24 of the MH2 Mc2 nor does it extend all the way to the base-shaft junction.

1           Relative to the gracile shaft, the Mc3 base appears moderately ML broad and DP tall.  
2   The palmar surface of the base is robust for the attachment for the oblique head of the *M.*  
3   *adductor pollicis* tendon. The proximal articular surface for the capitate is generally smooth and  
4   mildly DP convex, particularly the palmar portion such that part of the capitate facet can be  
5   seen in palmar view of the Mc3. The capitate articulation is generally rectangular in shape; it is  
6   only slightly ML broader dorsally (estimated at 9.3mm) than palmarly (8.1mm), and is  
7   approximately 12.2mm in DP height. The Mc2 articulation is a single, continuous facet  
8   measuring 10.3mm in DP height and 5.4mm in its maximum PD length. It is generally DP  
9   concave to oppose the corresponding articular convexity on the Mc2. The palmar  $\frac{3}{4}$  of the Mc2  
10   facet is oriented mostly laterally and slightly proximopalmarly, while the remaining dorsal portion  
11   is oriented more dorsally and proximally. Just distal to the dorsal portion of the Mc2 facet is a  
12   large tubercle for the attachment of *M. extensor carpi radialis brevis*. Palmar to this tubercle is a  
13   deeply excavated fossa that accentuates the prominence of the tubercle. The medial side of the  
14   base has separate dorsal and palmar articular facets for the Mc4 measuring 5.1mm and 4mm in  
15   PD length and 3.9mm and 5.1mm in DP height, respectively. The palmar facet is mildly concave  
16   and oriented primarily medially but also slightly distodorsally. The dorsal facet is flat and more  
17   distally positioned, and is oriented primarily medially and slightly proximopalmarly.

18           The Mc3 head is DP tall and oriented slightly laterally relative to the long axis of the  
19   shaft. The articular surface is asymmetrical with the lateral articulation extending farther  
20   proximally than the medial side. The epicondyles are prominent, with the medial one being  
21   slightly larger. There is no ridge at the dorsal edge of the articular surface (Figure 11).

22

23   **[INSERT Figure 11 about here]**

24

25   **U.W. 88-117 RIGHT FOURTH METACARPAL (MH2)**

1 **Preservation** This bone is complete and perfectly preserved, except for a small fragment  
2 missing from the lateral epicondyle and a thin fracture running the circumference of the shaft  
3 just proximal to midshaft (Figure 12). The proximal end is slightly abraded such that the lateral  
4 and dorsal borders of the hamate facet blend with the non-articular area and do not have a  
5 definitive outline.

6 **Morphology** Like the other MH2 metacarpals, the U.W. 88-117 shaft appears gracile (Figure  
7 12; Table 3). The proximal half of the dorsal shaft presents a prominent *Mm. dorsal interossei*  
8 crest (measuring 13.5mm in PD length) that is more pronounced than that of the MH2 Mc3 but  
9 less so than the Mc2. In palmar view, there is a strong degree of medial torsion in the distal 1/3  
10 of the shaft such that the palmar surface of the head is oriented slightly medially relative to the  
11 base. In lateral view, the dorsal shaft is slightly convex with a peak “bend” in the shaft at roughly  
12 midshaft.

13         The Mc4 base appears DP tall and ML broad relative to the gracile shaft (Figure 12).  
14 The proximal end is dominated by the articulation for the hamate. There is no articulation for the  
15 capitate. The lateral border of the hamate facet is not well-defined, but re-articulation with the  
16 hamate demonstrates that this facet is roughly rectangular shape, with a rounded palmar  
17 border. The hamate facet is generally flat with a mild convexity and its palmar portion of the  
18 hamate facet is estimated to be slightly ML narrower (5.7mm) than its dorsal portion (7.4mm).  
19 Mc5 facet is a single, continuous facet, measuring 8.5mm in DP height and 4.8mm in PD length.  
20 The palmar half of the facet is flat and the dorsal half is strongly concave, such that it flares  
21 medially and can be seen in palmar view. There is a deep pit at the DP centre of the medial  
22 side, just distal to the Mc5 facet. On the lateral side there are two articular facets for the Mc3  
23 divided by a deep sulcus; the palmar facet is larger (4.4mm in PD length, 3mm in DP height),  
24 oval-shaped, flat and faces mostly laterally but also proximopalmarly, while the dorsal facet is  
25 smaller (2.8mm in PD length, 2.9mm in DP height), circular, flat and is more distally placed. The

1 dorsal facet is oriented primarily laterally and slightly distally. These facets correspond well with  
2 the Mc4 articulation on the Mc3 U.W. 88-116.

3 The Mc4 head is DP tall and ML broad relative to the shaft (Figure 12; Table 3). In  
4 palmar view, the head is relatively symmetrical in its proximal extension of the articular surface.  
5 In dorsal view, the medial epicondyle is more proximally positioned than the lateral epicondyle.

6

### 7 **U.W. 88-118 RIGHT FIFTH METACARPAL (MH2)**

8 **Preservation** This bone is complete except for a fragment (6.9mm in PD length) missing from  
9 the ridge for the *M. opponens digiti minimi* tendon attachment on the medial surface at roughly  
10 midshaft (Figure 13). There is a fracture that runs the circumference of the shaft just proximal to  
11 the head. There is also a small surface fragment missing from the palmar shaft, just proximal to  
12 midshaft.

13 **Morphology** Relative to the other MH2 metacarpals, the shaft of U.W. 88-118 appears more  
14 robust (Figure 13). In palmar view, the shaft is straight and the palmar articular surface of the  
15 head is oriented slightly medially relative to the base. In dorsal view, there is small crest for the  
16 fourth *M. dorsal interosseous* running 7.6mm along the proximal portion of the dorsal shaft,  
17 medial to the sagittal midline. This crest is less prominent than that of the MH2 Mc4 and Mc2.  
18 The medial side of the shaft has a well-developed, rugose attachment for the *M. opponens digiti*  
19 *minimi*, running 14.6mm in PD length. Although a large portion is missing from the center of the  
20 entheses, it flares medially at both its proximal and distal ends suggesting that the entheses was  
21 well-developed.

22 The Mc5 base is DP tall and ML broad relative to the shaft (Figure 13; Table 3). The  
23 medial side of the base flares strongly with a robust protuberance for the *M. extensor carpi*  
24 *ulnaris* attachment dorsally and the pisohamate ligament palmarly. The dorsal surface of the  
25 base has a prominent tubercle on the lateral side for the attachment of the dorsal metacarpal

1 ligament. The hamate facet dominates the proximal end of the Mc5 and is strongly DP convex  
2 and generally flat ML, corresponding to the DP concavity of the corresponding articulation on  
3 the hamate. However, the facet is also palmarly-positioned, such that it does not occupy any of  
4 the dorsal portion of Mc5 proximal surface, but instead extends onto the palmar surface of the  
5 base and can be seen clearly in palmar view (Figure 13). The hamate facet is asymmetrical  
6 such that in proximal view, the dorsal portion of the articular surface is slightly ML broader  
7 (8.5mm) than the palmar portion (8.2mm) and the articulation extends farther palmarly on the  
8 medial side than the lateral side. The Mc4 facet is a single, continuous and generally flat facet,  
9 measuring 8.1mm in DP height and 4.2mm in PD length and oriented primarily laterally. The  
10 dorsal portion of the Mc4 facet extends farther distally than the palmar portion, matching the  
11 corresponding articular morphology on the Mc4.

12         The Mc5 head is DP tall and ML broad relative to its shaft (Figure 13). In palmar view,  
13 the head is asymmetric, with the distal outline of the articular surface slanted proximomedially.  
14 The proximal extension of the palmar articular surface is approximately equal on the medial and  
15 lateral sides. The facet tapers strongly towards the sagittal midline as it curves dorsally, such  
16 that the dorsal articular area appears slightly “pinched” between the epicondyles. The lateral  
17 epicondyle is prominent while the medial epicondyle is comparatively small.

18

19 **[INSERT Figures 12 & 13 about here]**

20

## 21 **U.W. 88-91 LEFT POLLICAL PROXIMAL PHALANX (MH2)**

22 **Preservation** This bone is complete and perfectly preserved apart from a fragment missing  
23 from the palmar-medial surface of the trochlea and a small surface fragment missing from the  
24 medial side of the proximal shaft at the junction between the base and shaft (Figure 14).

1 **Morphology** The U.W. 88-91 pollical proximal phalanx (PP1) has a gracile shaft (Figure 14;  
2 Table 4). The dorsal surface of the shaft is PD convex, with greatest curvature along the distal  
3 1/3 of the shaft. The dorsal surface of the shaft is ML broad and flat at its distal end but tapers  
4 proximally, such that the proximal half of the shaft slopes steeply on the medial and lateral sides  
5 from the flat dorsal midline. In sagittal view, the proximal 2/3 of the shaft is DP tall but narrows  
6 strongly just proximal to the trochlea (Figure 14). Most of the palmar shaft surface is generally  
7 ML flat, with a concave fossa just proximal to the trochlea, which gives U.W. 88-91 a “hollowed”  
8 appearance.

9         The PP1 base is strongly asymmetric, with a more proximally-extended lateral portion of  
10 the proximal articular surface and a larger, prominent lateral tubercle for the attachment of the  
11 *Mm. flexor pollicis brevis* and *abductor pollicis brevis* tendons (Figure 14). The medial side of  
12 the base also has a well-developed tubercle for the attachment of the *M. adductor pollicis*  
13 tendon. This tubercle extends distally into a well-defined ridge that is 5.4mm long PD. The  
14 proximal facet is oval-shaped, being ML broader than it is DP tall, and strongly concave,  
15 especially along its lateral border (Table 4). The distal trochlea of U.W. 88-91 is also  
16 asymmetrical; in palmar view, the medial portion of the trochlea extends further distally than the  
17 lateral portion. The articular facet extends proximally onto the dorsal surface 2.3mm.

18

## 19 **U.W. 88-160 RIGHT POLLICAL PROXIMAL PHALANX (MH2)**

20 **Preservation** This bone is less well-preserved than its left counterpart. A large fragment from  
21 the palmar and medial portion of the base and a smaller fragment of the palmar-medial trochlea  
22 are missing, and the remainder of the palmar surface of the trochlea is abraded (Figure 14).

23 **Morphology** The preserved morphology is almost identical to that described for U.W. 88-91,  
24 although most dimensions are slightly smaller, consistent with the bilateral asymmetry found in  
25 the carpal bones (Table 4).



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**[INSERT Figure 14 and Table 4 about here]**

**U.W. 88-164 RIGHT SECOND PROXIMAL PHALANX (MH2)**

**Preservation** This bone is complete and perfectly preserved apart from a crack running ML across the distodorsal surface of the trochlea and slight erosion along the palmar-lateral edge of the lateral trochlea (Figure 15).

**Morphology** U.W. 88-164 is considered to be a PP2 based on its overall length and slightly greater robusticity and asymmetry at the base compared with the other proximal phalanges of the right hand (Figure 15; Table 4). The dorsal surface of this bone is moderately curved, especially at the distal end. The shaft is DP taller at the proximal end and tapers distally and, in palmar view, the medial and lateral sides of the shaft are straight. The palmar surface is PD and ML concave. There is a prominent flexor sheath ridge measuring 8.2mm in PD length, with its centre just distal to midshaft, on the medial edge that extends roughly 1.3mm above the palmar surface of the remaining shaft. The flexor sheath ridge on the lateral side is not distinct.

At the proximal end of U.W. 88-164 both basal tubercles are pronounced, but the lateral basal tubercle is more prominent. In palmar view, the proximolateral border extends farther proximally than that of the medial side. The proximal articular facet is concave, oriented proximally and is oval-shaped, being ML broader than it is tall (Table 4). The head of U.W. 88-164 is generally symmetrical in palmar view, with the medial and lateral trochlear head extending proximally to an equal extent. However, the medial trochlear surface is slightly more ML expanded than that of the lateral side. The dorsal articular surface of the trochlea is ML narrow and expands palmarly.

**[INSERT Figure 15 about here]**

1

2 **U.W. 88-109 LEFT SECOND PROXIMAL PHALANX (MH2)**

3 **Preservation** This bone preserves the full PD length of the medial half of the phalanx, broken  
4 roughly at the sagittal midline (Figure 15). There are two thin fractures; one just distal to the  
5 base-shaft junction and the other distal to the midshaft. The palmar-medial border of the  
6 proximal shaft and flexor sheath ridge is also missing.

7 **Morphology** The preserved morphology is identical to the medial side of PP2 of the right hand.  
8 The flexor sheath ridge measures roughly 7mm PD and appears equally developed and  
9 similarly positioned to that of the medial flexor sheath ridge of U.W. 88-164. The medial trochlea  
10 is better preserved than that of U.W. 88-164 and demonstrates that the distodorsal portion of  
11 the articular surface is more rounded in sagittal view than what is preserved on the right PP2.  
12 The sagittal break along the midline reveals cortical bone in the proximal shaft that is  
13 approximately 2.3mm thick on dorsal and palmar sides and the trabecular structure, although  
14 filled with matrix, appears to extend distally into the shaft roughly 7.2mm.

15

16 **U.W. 88-120 RIGHT THIRD PROXIMAL PHALANX (MH2)**

17 **Preservation** This bone is complete and perfectly preserved except for small fragments missing  
18 from the palmar side of the medial trochlea and the dorsolateral edge of the proximal facet, and  
19 erosion of the palmar-lateral edge of the shaft and flexor sheath ridge (Figure 15).

20 **Morphology** The overall morphology of this bone is similar to that described for U.W. 88-164  
21 right PP2. U.W. 88-120 is considered a PP3 based on its long length and reduced asymmetry  
22 relative to the remaining proximal phalanges of the MH2 right hand (Figure 15; Table 4). In  
23 palmar view, the shaft is PD concave, ML concave at midshaft, but ML flat at the proximal and  
24 distal ends. Both the medial and lateral flexor sheath ridges appear to be well-defined, although  
25 the proximal half of the lateral ridge is eroded. Both ridges extend roughly 1.4mm beyond the

1 palmar surface of the remaining shaft. The PD length of the medial ridge is 14.4mm and the  
2 lateral ridge is roughly 11.4mm. At the PP3 base the lateral basal tubercle is much more  
3 prominent than the medial tubercle. The proximal articular surface is more circular than that of  
4 the PP2, but is still ML broader than it is DP tall. The trochlea is generally symmetrical.

5

#### 6 **U.W. 88-182 LEFT THIRD PROXIMAL PHALANX (MH2)**

7 **Preservation** This specimen is the proximal half of a proximal phalanx. The proximal end is  
8 perfectly preserved and it broken at an angle just distal to the midshaft (Figure 15).

9 **Morphology** This bone is identified as a left PP3 based on its similar size and morphology to the  
10 right PP3, U.W. 88-120 (Figure 15; Table 4). In palmar view, the flexor sheath ridges are well-  
11 developed on both sides. The medial ridge is completely preserved and measures 11.5mm PD  
12 length. The portion of the lateral ridge that is preserved (7.6mm in PD length) is similar in its  
13 development to that of the medial ridge. The basal tubercles are less asymmetrical than those  
14 of the right PP3.

15

#### 16 **U.W. 88-108 RIGHT FOURTH PROXIMAL PHALANX (MH2)**

17 **Preservation** This bone is complete and well-preserved apart from erosion to the palmar  
18 portion of the basal tubercles and fragments missing from the palmar-lateral and palmar-medial  
19 surfaces of the trochlea (Figure 15).

20 **Morphology** This bone is identified as the PP4 based on its relative length, slightly less robust  
21 base and slight asymmetry of the trochlea compared with the other proximal phalanges (Figure  
22 15; Table 4). Its overall morphology is generally similar to that described for the PP2 and PP3.  
23 The palmar surface of the shaft is PD concave and is ML concave at the proximal end and,  
24 especially, at midshaft, while the distal portion is ML flat. The flexor sheath ridges are very well-  
25 developed on both sides, more so than in any other ray. The lateral flexor ridge is more palmarly

1 and PD extended than the medial ridge, measuring 14.9mm in PD length and extending roughly  
2 2.2mm above the remainder of the palmar surface of the shaft. The medial flexor ridge is 8.9mm  
3 in PD length and 1.9mm extended above the palmar surface of the shaft. The base is slightly  
4 asymmetric; the medial side of the proximal facet and base extend more proximally than the  
5 lateral side and the preserved morphology suggests that the medial tubercle was slightly more  
6 prominent. The preserved morphology of the trochlea displays slight asymmetry with the lateral  
7 articular surface extending more distally than the medial side.

8

#### 9 **U.W. 88-110 LEFT FOURTH PROXIMAL PHALANX (MH2)**

10 **Preservation** This bone preserves only the dorsolateral portion of the proximal end of a  
11 proximal phalanx, including the dorsal half of the proximal facet and the dorsolateral side of the  
12 base (Figure 15).

13 **Morphology** The bone is identified as a likely left PP4 based on its similarity in size and  
14 morphology with the complete right PP4 U.W. 88-108 (Figure 15; Table 4). The DP height of the  
15 preserved portion of the proximal shaft as well as the curvature, size and proximal orientation of  
16 the articular surface are all comparable to that of U.W. 88-108.

17

#### 18 **U.W. 88-121 RIGHT FIFTH PROXIMAL PHALANX (MH2)**

19 **Preservation** This bone is complete apart from strong erosion of the trochlea, a small surface  
20 fragment missing from the palmar-medial edge of the proximal border of the base, and  
21 fragments missing from both flexor sheath ridges. There is small, square piece of sediment still  
22 attached to the dorsal surface of the shaft, just proximal to the trochlea (Figure 15).

23 **Morphology** This bone is identified as a PP5 based on its small size and morphology relative to  
24 the other proximal phalanges (Figure 15; Table 4). The overall morphology is generally similar  
25 to the other MH2 proximal phalanges with a few distinct differences; the palmar surface is

1 largely convex ML with a well-developed “bar” that extends from the medial basal tubercle  
2 proximally to roughly 3mm from the sagittal midline of the distal articular surface. Along the  
3 palmar surface of the medial tubercle, the convex bar turns into a prominent ridge. There is an  
4 outline of white exposed cortex where the flexor sheath ridges have eroded on both the medial  
5 and lateral sides. The lateral flexor ridge extends an estimated 12.3mm distally from the lateral  
6 tubercle. At the tubercle the ridge appears to curve proximally and medially around the palmar  
7 surface of the shaft to form a teardrop-shaped concavity lateral to the convex “bar” described  
8 above (Figure 15). Compared with the lateral ridge, the medial flexor ridge appears not to  
9 extend as far distally (estimated at 7.7mm in PD length), although erosion of the surface makes  
10 this difficult to determine with certainty. The PP5 base is asymmetric with the medial tubercle  
11 being more prominent and medial portion of the articular surface being more proximally  
12 extended than on the lateral side. Much of the distal trochlea is eroded and thus the degree of  
13 asymmetry cannot be assessed.

14

#### 15 **U.W. 88-123 RIGHT SECOND INTERMEDIATE PHALANX (MH2)**

16 **Preservation** The bone is largely complete but the dorsal portion of the proximal half is still  
17 encased in sediment (to preserve the remaining morphology), and the dorsal portion of the  
18 distal half is missing. The trochlea is eroded on the distal and palmar surfaces. The bone is  
19 broken ML just distal to the base such that the distal 2/3 of the bone is shifted slightly proximally  
20 and palmarly, resting just on the edge the remaining proximal 1/3 of the bone. This orientation  
21 makes the bone appear slightly shorter than its true overall length (Figure 16).

22 **Morphology** This bone is considered a second intermediate phalanx (IP2) based on its  
23 relatively short estimated length compared to the remaining intermediate phalanges of the MH2  
24 right hand (Figure 16; Table 5). Given the preservation and degree of preparation of U.W. 88-  
25 123, only the morphology the palmar surface can be described. Like the other intermediate

1 phalanges of the MH2 right hand (see below), the morphology of U.W. 88-123 is best described  
2 as a smaller version of a proximal phalanx. The palmar surface is mildly concave in both the PD  
3 and ML dimensions. There is a thick flexor sheath ridge along the lateral shaft and a thinner,  
4 shorter (though slightly obscured) ridge along the medial shaft. A median bar or lateral fossae  
5 are not present. The proximal palmar surface appears hollowed, with a concave area just distal  
6 to a thick ridge along the proximal border of the phalanx.

7

8 **[INSERT Figure 16 and Table 5 about here]**

9

#### 10 **U.W. 88-161 RIGHT THIRD INTERMEDIATE PHALANX (MH2)**

11 **Preservation** The bone is complete and perfectly preserved, except for small surface fragments  
12 missing from the dorsal surface of the trochlea and the medial border of the proximal facet.  
13 There are thin fractures along the sagittal midline of the medial trochlea and running ML along  
14 the dorsal surface of the proximal shaft (Figure 16).

15 **Morphology** This bone is considered an IP3 based on its long length and large overall size  
16 relative to the other MH2 intermediate phalanges (Figure 16; Table 5). Its morphology is similar  
17 to that described above for U.W. 88-123, although this specimen is much better preserved. The  
18 dorsal surface is mildly convex longitudinally, with stronger convexity at the distal end, and in  
19 dorsal or palmar view, the sides of the shaft are straight. Both flexor sheath ridges are well-  
20 developed; the lateral ridge is larger than that of the medial side, extending 8.8mm distally from  
21 the base and extending approximately 2mm from the palmar surface. The medial flexor ridge is  
22 smaller, extending 4mm from the base and extending approximately 1mm from the palmar  
23 surface of the shaft. A palmar median bar and lateral fossae are not present.

24 The proximal end of the bone appears “scooped”, such that the palmar surface is ML  
25 concave and then slanted palmarly up to a thick proximal border (Figure 16). In sagittal view,

1 the dorsal border of the base flares dorsally in sagittal view. The proximal articular surface  
2 extends onto the palmar and dorsal flaring portions, creating a PD tall but still ML broad facet  
3 (Table 5). The condyles of the proximal facet are roughly equal in size and DP concave. The  
4 trochlea is more ML expanded than the distal shaft. The articular surface extends just to the  
5 distal edge of the dorsal surface. The medial trochlea appears slightly more distally and  
6 palmarly extended than the lateral trochlea, although this asymmetry may be accentuated by  
7 the eroded dorsal surface of the articular facet.

8

#### 9 **U.W. 88-122 RIGHT FOURTH INTERMEDIATE PHALANX (MH2)**

10 **Preservation** This bone is complete and well-preserved except for a fragment missing from  
11 palmar surface of the proximal border of the base and a small surface fragment missing from  
12 the palmar surface of the trochlea (Figure 16).

13 **Morphology** This bone is considered to be from the fourth ray based on its large size and being  
14 only slightly smaller than U.W. 88-161 (Figure 16; Table 5). The preserved morphology of this  
15 bone is virtually identical to that of U.W. 88-161. The lateral flexor sheath ridge is slightly more  
16 pronounced, extending 8.4mm distally from the base and roughly 1.5mm from the palmar  
17 surface of the shaft. The medial flexor ridge extends 8mm distally from the base and is roughly  
18 the same height as the lateral ridge. The dorsal border of the base is dorsally flaring, but less so  
19 than that of U.W. 88-161. The condyles of the distal trochlea are symmetrical and the articular  
20 surface extends onto the dorsum 3.1mm.

21

#### 22 **U.W. 88-162 RIGHT FIFTH INTERMEDIATE PHALANX (MH2)**

23 **Preservation** This bone is complete apart from a fragment missing from the palmar surface of  
24 the base, and small fragments from the dorsomedial surface and palmar-medial border of the  
25 trochlea (Figure 16).

1 **Morphology** This bone is identified as an IP5 because of its small size and morphology  
2 compared with the other MH2 intermediate phalanges (Figure 16; Table 5). Its morphology is  
3 similar to that described for the other intermediate phalanges. The flexor sheath ridges are not  
4 as pronounced; both are 4.4mm in PD length and extend only slightly above the palmar surface  
5 in sagittal view. In palmar view, the short ridges slope medially toward the midline, such that the  
6 palmar surface of the midshaft is only mildly concave. The dorsal surface of the proximal end  
7 flares less than that of U.W. 88-122 and U.W. 88-161.

8

9 **U.W. 88-124 RIGHT POLLICAL DISTAL PHALANX**

10 **Preservation** This bone is approximately half complete, preserving most of the PD length of the  
11 bone and its lateral side. Much of the medial half is missing as well as lateral corner of the  
12 proximal end (Figure 17).

13 **Morphology** This bone is identified as a distal pollical phalanx (DP1) based on the presence of  
14 well-developed proximal and distal fossae, a *M. flexor pollicis longus* (FPL) tendon attachment,  
15 and its ML broad apical tuft (Figure 17). The dorsal shaft is longitudinally straight with slight  
16 dorsal flaring at the proximal end. In palmar view, the proximal portion of the palmar surface is  
17 dominated by a deeply concave proximal fossa, measuring approximately 4.6mm in PD length.  
18 The distal border of this fossa is palmarly extended well above the remainder of the shaft,  
19 creating a ridge roughly 1.8mm PD for the attachment of the FPL tendon. The distal half of the  
20 bone is dominated by what appears to be a ML broad apical tuft that is DP thick (Table 5). Just  
21 proximal to the apical tuft is a concave distal fossa, measuring 3mm in PD length and roughly  
22 3.4mm in ML breadth, for the palmar ungual pulp.

23

24 **[INSERT Figure 17 about here]**

25



## 1    **COMPARATIVE MORPHOLOGY**

2

### 3    **SCAPHOID**

4    The U.W. 88-158 scaphoid is smaller in absolute size than the *Australopithecus* sp. StW 618  
5    and *H. habilis* OH 7 scaphoids, but slightly DP taller than that of *H. naledi*. The tubercle is much  
6    shorter and less robust than that of *Ar. ramidus* but longer and more robust than that of *H.*  
7    *naledi*. The U.W. 88-158 tubercle is most similar in morphology to that of StW 618, apart from  
8    the tubercle being more proximally-oriented and the base being slightly less robust (Figure 3).  
9    The relative size and shape of the radial facet is generally most similar to *Homo*; it is DP tall  
10    relative to the DP height of the scaphoid body and relative to the PD length of the facet (Figure  
11    18). In contrast, *Ar. ramidus*, StW 618 and African apes tend to have relatively short radial  
12    facets, making them more round, rather than oval, in their overall shape. The lunate facet of  
13    U.W. 88-158 is confined to the proximodorsal corner of the scaphoid body, which is most similar  
14    to *H. naledi* and typical of humans and some Neandertals. This morphology is unlike the more  
15    distally-extended lunate facet of OH 7 and StW 618 (Figure 3).

16           The shape of the *Au. sediba* capitate facet falls out as intermediate among the  
17    comparative sample, being most similar to the median values of *P. troglodytes*, early *Homo* and  
18    recent humans, although there is substantial overlap across all taxa (Figure 18). StW 618 and  
19    *H. naledi* have a relatively long PD length of the capitate facet, whereas OH 7 is relatively short.  
20    The shallow concavity of the capitate facet in U.W. 88-158 is unlike the deeply concave, circular  
21    capitate facet of *Ar. ramidus* and StW 618, or the more rectangular-shaped facet of OH 7  
22    (Figure 3). The distomedial edge of the capitate facet appears more “closed”, which is most  
23    similar to StW 618, OH 7 and *H. naledi*, rather than the “open” border of humans and  
24    Neandertals (Tocheri 2007).

1           Finally, the trapezium-trapezoid facet of U.W. 88-158 is highly convex in both the DP  
2 and ML dimensions, and appears “raised” off of the bone due to deep sulcus running parallel to  
3 its proximodorsal border (Figure 3). This morphology is similar to what is preserved in OH 7, and  
4 unlike the flatter facet of *Ar. ramidus* and StW 618. The trapezium facet also extends much  
5 further onto the tubercle than that of *Ar. ramidus* and StW 618, but is less extended than that of  
6 *H. naledi*, Neandertals and *H. sapiens*. The trapezoid facet is more extensive distomedially,  
7 reflecting the more “closed” border of the capitate facet, than that typically found in humans and  
8 Neandertals, and in this way appears most similar to OH 7 and *H. naledi*.

9

## 10 **LUNATE**

11 The MH2 lunate is remarkably ML narrow both in the overall size of the lunate body and its  
12 capitate facet (Figures 4 and 19). In this way, U.W. 88-159 is distinctly different from the  
13 spherical lunates of cf. *Australopithecus* KNM WT 22944-J (Ward et al. 1999) and *Au. afarensis*  
14 (Ward et al. 2012), and the generally broader lunates of African apes, humans and most other  
15 fossil hominins (Figure 19). The narrowness of the U.W. 88-159, although accentuated by the  
16 missing fragment from the palmar-medial portion of the lunate (Figure 4), is more reminiscent of  
17 Miocene apes like *Proconsul* (Schön and Ziemer 1973) and *Afropithecus* (Leakey et al. 1988).  
18 The lack of a separate articulation for the hamate in MH2 is shared with KNM WT 22944-J and  
19 *H. naledi*, and is common in African apes (Marzke et al. 1994), while a lunatohamate articulation  
20 is present in *Ar. ramidus*, *Au. afarensis* and most Neandertals and recent humans (Marzke et al.  
21 1994).

22           The U.W. 88-159 radial facet is ML broad relative to its DP height and to the breadth of  
23 the lunate body (Figure 19). This morphology is similar to other extant and fossil hominins, and  
24 different from the relatively narrow radial facet of African apes. The scaphoid facet of U.W. 88-  
25 159 lunate is notably more distally-oriented than the typically laterally-facing scaphoid facets

1 (i.e. oriented at approximately 90° angle to the capitate facet) of African apes, *Ar. ramidus*, *Au.*  
2 *afarensis*, most Neandertals, and humans.

3

4 **[INSERT Figures 18 & 19 about here]**

5

## 6 **TRIQUETRUM**

7 The MH2 triquetrum presents a distinct morphology that is not seen in other known hominin  
8 triquetra. The U.W. 88-157 triquetrum body is relatively (i.e. divided by a geometric mean) PD  
9 narrow and ML broad compared with the more blocky triquetra typical of extant humans and  
10 African apes (Figure 20). In this way, the overall shape of U.W. 88-157 is similar to other fossil  
11 hominins, particularly *Ar. ramidus*, SKX 3498 and Neandertals. Its hamate facet is also DP tall  
12 relative to its ML breadth and in this way is more similar to Neandertals and *H. sapiens*, rather  
13 than the ML broader hamate facets of SKX 3498 and *H. naledi* (Figure 20). The concavoconvex  
14 complexity of the hamate facet is more accentuated than that of SKX 3498 (Kivell 2011), *H.*  
15 *naledi* and Neandertals, and is consistent with the opposing morphology of the triquetrum facet  
16 on the MH2 hamate (Figure 8).

17 U.W. 88-157 is distinct in having an almost tubercle-like palmar-medial extension to the  
18 triquetrum body that is not known in any other hominin (Figure 5). This extension orients the  
19 small pisiform facet in a proximopalmar direction. As such, this morphology suggests, especially  
20 when the ulna is in anatomical position (Figure 2), that the pisiform was small, unlike the rod-  
21 shaped pisiform of African apes and *Au. afarensis* (Bush et al. 1982). However, any correlation  
22 that might exist between the size of the pisiform and the size and shape of the pisiform's  
23 articular facet on the triquetrum is unknown.

24

## 25 **CAPITATE**

1 The MH2 capitates are larger in absolute size than *Au. afarensis* A.L. 288-1w but smaller than  
2 cf. *Australopithecus* KNM-WT 22944-H and *Au. afarensis* A.L. 333-40. The absolute length is  
3 similar to *Au. africanus* TM 1526 but the MH2 capitates are ML broader at both the proximal and  
4 distal ends. The MH2 capitate body is DP tall relative to its PD length and overall size (i.e. a  
5 geometric mean), compared with other australopiths and the particularly short capitates of *H.*  
6 *floresiensis* and *H. naledi* (Figure 21). Like other australopiths, *H. naledi* and *H. floresiensis*, the  
7 distodorsolateral border is not excavated to accommodate a Mc3 styloid process, which is found  
8 in the KNM-WT 51260 Mc3 possibly attributed to *H. erectus* (Ward et al. 2013) and later *Homo*  
9 (Lorenzo et al. 1999; Trinkaus 1983). The capitate body is “waisted” in palmar view to a similar  
10 degree as that found in *Ar. ramidus*, other australopiths and *H. naledi*, being less waisted than  
11 that of KNM-WT 22944-H and African apes but more so than is typical for recent humans  
12 (Figures 6 and 21). The proximal facet is ML expanded to the same degree as most other  
13 hominins and extant humans (Figure 21), but does not have the bulbous appearance of KNM-  
14 WT 22944-H, which is accentuated by its strong degree of waisting. The capitate body is deeply  
15 excavated between the distal portion of the scaphoid facet and the dorsal trapezoid facet, and  
16 unlike the continuous articulation found in humans (Figure 6). However, the scaphoid facet does  
17 not have a well-developed, concave J-hook morphology at its distal border, as is found in *Pan*,  
18 *Au. afarensis* and *H. floresiensis* (Orr et al. 2013).

19 The presence of both a dorsal and palmar trapezoid facet on the lateral side of the  
20 capitate (at least in the better preserved left capitate, U.W. 88-105) is similar to the condition  
21 described in *H. antecessor* (Lorenzo et al. 1999) and that is found in some Neandertals (e.g.  
22 Tabun 1) and rarely in humans (Lewis 1989; Tocheri 2007). KNM-WT 22944-H, *Au. afarensis*  
23 A.L. 333-40 and possibly *Ar. ramidus* demonstrate similar morphology, suggesting that a dual  
24 trapezoid articulation may be primitive for the hominin clade (although *Au. africanus* TM 1526  
25 does not have a palmar capitate-trapezoid articulation).

1           The primarily lateral orientation of the Mc2 facet on the MH2 capitates is similar to  
2 African apes, *Ar. ramidus* (Lovejoy et al. 2009), *Au. anamensis* KNM-KP 31724 (Ward et al.  
3 2001), *H. floresiensis* (Orr et al. 2013; Tocheri et al. 2007), and what has been inferred for OH 7  
4 (Tocheri et al. 2003). It is less distally-orientated than A.L. 333-40, TM 1526 and *H. naledi*  
5 (Kivell et al. 2011, 2015). The generally flat morphology of the capitate's Mc3 articulation is  
6 similar to that of humans and Neandertals, and is less concavoconvex than African apes, *Ar.*  
7 *ramidus*, *Au. afarensis*, TM 1526, or what is preserved in KNM-WT 22944-H.

8           The U.W 88-95 right capitate differs from the left in missing a portion of the capitate body  
9 at the distodorsolateral border (Figure 6). Although taphonomic damage for this missing portion  
10 cannot be ruled out, the morphology of this region appears to be complete. This is the same  
11 region that is truncated in humans and Neandertals to accommodate the Mc3 styloid process,  
12 however the preserved morphology in U.W. 88-95 capitate is not similar. Instead, the dorsal  
13 surface of U.W. 88-95 appears non-articular rather than the dorsally-extended articular surface  
14 of the Mc3 facet that is typical of humans and Neandertals. Furthermore, the MH2 Mc3 U.W. 88-  
15 116 does not have a styloid process (Figure 11). If this morphology is not due to taphonomic  
16 damage, it is possible that a separate ossification centre between the capitate and Mc3  
17 (O'Rahilly 1953) was present on the right side only. Either way, there was likely little difference  
18 in overall function of this carpometacarpal joint between the left and right hands.

19

20 **[INSERT Figures 20 & 21 about here]**

21

## 22 **HAMATE**

23 The hamate body of MH2 is DP taller relative to its PD length than that of *Au. afarensis* and  
24 Neandertals, falling within upper range of variation of *H. sapiens* and *Pan*. In this way, MH2 is  
25 most similar to cf. *Australopithecus* KNM-WT 22944-I and *Gorilla* (Figure 22). The hamulus

1 projects primarily palmarly and to a similar degree found in *H. naledi*, *H. sapiens* and *Gorilla*.  
2 Relative to hamate size (i.e. a geometric mean), it is more palmarly-projecting than that of *Au.*  
3 *afarensis* and KNM-WT 22944-1, but less so than Neandertals. However, distal projection of the  
4 MH2 hamulus is minimal like that of *H. sapiens*, while all other fossil hominins are more distally  
5 extended (Figure 22). Similarly, the PD long but ML narrow shape of the hamulus, creating an  
6 oval-shaped cross-section, is most similar to the human condition and unlike the ML broader  
7 hamuli of African apes, *Au. afarensis*, KNM-WT 22944-I, *H. naledi* and *H. floresiensis* (Orr et al.  
8 2013; Figure 8).

9         Although the Mc4 facet is absolutely larger than the Mc5 facet in the MH2 hamates, a  
10 ratio of Mc5/Mc4 facet ML breadth reveals that MH2 has a relatively broader Mc5 facet than  
11 *Pan*, KNM-WT 22944-I and *Au. afarensis* (Figure 22). In this way, MH2 is most similar to  
12 condition found in *H. naledi* and Neandertals, but also overlaps with that of *Gorilla*. The MH2  
13 hamatometacarpal articulation differs from *Ar. ramidus*, KNM-WT 22944-I and *Au. afarensis* in  
14 having a generally flat, rather than concave, Mc4 facet and an Mc5 facet that does not extend  
15 onto the hamulus. In this way, MH2 is more similar to *H. naledi* and later *Homo*. MH2 does not  
16 show a saddle-shaped Mc5 facet as in *H. naledi* or typically found in recent humans (Kivell et al.  
17 2015; Marzke and Marzke 2000). There is a space between the palmar border of the Mc5 facet  
18 and the most dorsal edge of the hamulus (which is particularly marked on the left hamate with a  
19 more well-preserved hamulus) that could accommodate the extension of the pisometacarpal  
20 ligament to the Mc3, as is found in humans (Lewis 1977) and has been described in *Au.*  
21 *afarensis* (Marzke and Marzke 1987; Figure 7). In medial view, the proximal half of the  
22 triquetrum facet is inclined dorsally, such that proximal border of the hamate appears somewhat  
23 pointed (Figure 8). This differs from the rounded profile of the more proximally-oriented  
24 triquetrum facets of *Ar. ramidus*, KNM-WT 22944-I, *Au. afarensis*, *H. naledi* and that is typical of  
25 *H. sapiens*.

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**[INSERT Figure 22 about here]**

**FIRST METACARPAL**

The MH2 first metacarpal is remarkably long in its PD length. Relative to the length of the Mc3, U.W. 88-119 falls outside the range of variation and well-above the regression lines for recent humans (including smaller-bodied individuals), with a much longer Mc1 for its size (Kivell et al. 2011) (Figure 23). The same pattern holds true for thumb length (i.e. including the PP1) relative to PD length of the third ray (Figure 23). The Mc1 and thumb of MH2 are longer relative to the Mc3 and third ray, respectively, than the estimated proportions of the *Au. afarensis* composite hand, Neandertals and early *H. sapiens*. The only fossil hominin (for which associated hand bones are known) to come close to the same relative Mc1 or thumb length as MH2 is *H. naledi*.

The Mc1 shaft is also remarkably gracile; relative to interarticular length, the midshaft ML breadth and DP height are smaller than all other fossil hominins and falling only within the lower range of variation in *Pan* (Figure 24). The poorly-developed muscle attachments along the shaft are similar to that of *Ar. ramidus* ARA-VP-6/500-15 and *Au. afarensis* A.L. 333-39w. The U.W. 88-119 entheses morphology contrasts the more robust or flaring flanges for the *M. opponens pollicis* insertion found in *Ar. ramidus* ARA-VP 6/1638, *Au. africanus* StW 418, the *Au. robustus*/early *Homo* SKX 5020 and SK 84 specimens from Swartkans, *H. naledi* and Neandertals. Furthermore, the *M. opponens pollicis* insertion is proximally-positioned in U.W. 88-119, with no indication of attachment along the distal shaft. This is distinctly different from the distally-placed attachment in *Ar. ramidus*, *Au. afarensis*, *Au. africanus*, SK 84, SKX 5020 and *H. naledi*, which is similar to the positioning found in *Pan* (although the entheses is not nearly as rugose in *Pan*), or the larger insertion of humans, which extends the entire PD length of the Mc1's lateral shaft (Jacofsky 2009). The first *M. dorsal interosseous* attachment is equally

1 poorly developed in U.W. 88-119, however this enthesis is also not well-defined in humans and  
2 most early fossil hominins (e.g. A.L. 333-39w, StW 418 or SKX 5020). Swartkrans specimen SK  
3 84, with a rugose *M. first dorsal interosseous* insertion, is a notable exception. The positioning  
4 of the *M. first dorsal interosseous* enthesis in MH2 is similar to that of other hominins (e.g. StW  
5 418, SK 84, SKX 5020) and humans, being distally extended and distinct from the localized  
6 proximo-medial insertion of *Pan* (Jacofsky 2009).

7         Relative to interarticular length, the base of U.W. 88-119 is more ML narrow than all  
8 other fossil hominins except *H. naledi* (Kivell et al. 2015) (Figure 24). However, the relative DP  
9 height of the base is taller than *Au. africanus* and most similar to SKX 5020, extant humans and  
10 *Pan*. The DP curvature of the trapezium facet appears similar to that of *Ar. ramidus*, *Au.*  
11 *africanus*, and SK 84, and is more curved than SKX 5020 or humans. The U.W. 88-119  
12 proximal articulation also appears to be distinct from the strongly DP concave and “V-shaped”  
13 articulation described for *Au. prometheus* (Clarke 1999), although a formal description of the  
14 StW 573 Mc1 morphology has not been published. U.W. 88-119 does not have a beak-like  
15 extension of the palmar base as is found in *Au. afarensis* A.L. 333-58 (Bush et al. 1982).

16         U.W. 88-119 has a relatively ML narrower breadth of the Mc1 head than all other fossil  
17 hominins except *Au. afarensis*, falling closest to the mean values of African apes, although still  
18 within the lower range of variation found in recent humans (Figure 24). The DP height of the  
19 head is comparatively taller, being most similar to *Au. afarensis*, Neandertals and *H. sapiens*,  
20 although also falling within the upper range of variation in African apes (Figure 24). The  
21 prominent palmar beak that characterises the U.W. 88-119 Mc1 head is also present in SK 84  
22 (Susman 1988b, 1989, 1994; Trinkaus and Long 1990). It has been suggested that the KNM-  
23 WT 15000 *H. erectus* juvenile Mc1s and SKX 5020 also have this beak (Walker and Leakey  
24 1993; Susman 1988b, 1989), however all of these specimens are missing the majority of the



1 proximal epiphysis. A beak is not present in *Ar. ramidus*, *Au. afarensis* (A.L. 333w-39), *Au.*  
2 *africanus* (StW 418 and StW 583), *H. naledi* or Neandertals.

3

4 **[INSERT Figures 23 & 24 about here]**

5

## 6 **SECOND METACARPAL**

7 The MH2 Mc2 shaft is gracile compared with other fossil hominins and modern humans.

8 Relative to interarticular length, the ML breadth at midshaft in U.W. 88-115 is much narrower  
9 than that of *Au. afarensis*, *Au. africanus*, and especially *H. naledi*, although it falls within the  
10 lower range of variation in Neandertals and *H. sapiens* (Figure 25). The proximal portion of the  
11 shaft is also absolutely more gracile than what is preserved in the OH 7 Mc2. The Mc2 has a  
12 particularly prominent *M. dorsal interossei* crest compared to the other MH2 metacarpals, in  
13 which two *Mm. dorsal interossei* attachments joint to form a single crest. This morphology is  
14 similar to *Pan* and is occasionally found in muscularly robust humans (Drapeau et al. 2005), but  
15 is not seen in other known australopiths (*Au. afarensis* or *Au. africanus*) or *H. naledi*.

16 Despite the gracility of the shaft, the base of U.W. 88-115 is robust relative to its  
17 interarticular length. It is ML broader than *Au. afarensis* and *Au. africanus*, and DP taller than  
18 *Au. afarensis*, being most similar to Neandertals and *H. sapiens* (Figure 25). The dorsal muscle  
19 attachments on the proximal epiphysis appear more well-developed than in *Au. afarensis*, *Au.*  
20 *africanus* and *H. naledi*. The trapezoid facet is more “squared” (i.e. ML broad) at its palmar  
21 portion than that of *Au. afarensis*. The orientation of the U.W. 88-115 trapezium facet (relative to  
22 the long axis of the shaft) in proximal view (35 degrees) is more palmarly oriented than that of  
23 *Au. africanus* StW 382, but more laterally oriented than that of *H. naledi*, and is most similar to  
24 *Au. afarensis*, recent humans and *Gorilla* (Drapeau et al. 2005). When viewed dorsally, the  
25 U.W. 88-115 trapezium facet is more proximally-oriented (28 degrees) than *Au. afarensis* but

1 less so than *H. naledi*, and falls out as intermediate between the more laterally-facing facet of  
2 African apes and more proximally-oriented facet of humans (Drapeau et al. 2005). The capitate  
3 and Mc3 articulation is similar to that of *Au. afarensis*, being intermediate between the African  
4 ape condition and the typically continuous and dorsopalmarly-convex capitate-Mc3 articulation  
5 of humans and *H. naledi*.

6 Relative to its interarticular length, the U.W. 88-115 head is as ML broad as that of all  
7 other fossil hominins and recent humans, but is DP taller than all other hominins, falling only  
8 within the upper range of variation of Neandertals (Figure 25). The Mc2 head is strongly  
9 asymmetrical, slightly more so than the *Au. afarensis* Mc2s from A.L. 333 but similar to the A.L.  
10 438-1 specimens, *Au. africanus* and *H. naledi*.

11

### 12 **THIRD METACARPAL**

13 The Mc3 is the only bone that is preserved for both MH1 and MH2 (Figure 11). The Mc3 of  
14 MH1, U.W. 88-112, is juvenile, with an unfused epiphyseal head that is consistent with the stage  
15 of juvenile development (estimated to be 12-13 years old by human standards) found  
16 throughout the remainder of the MH1 skeleton (Berger et al. 2010). Fusion of the Mc3 head  
17 occurs at roughly 9-10 years of age in chimpanzee (Kerley 1966) and 14-17 years of age in  
18 humans (Scheuer and Black 2000). Although U.W. 88-112 is missing its proximal epiphysis, the  
19 total preserved length is similar to the complete adult Mc3, U.W. 88-116, of MH2 (Figure 11;  
20 Table 3). For comparative analyses, the complete length of the U.W. 88-112 (i.e., including a  
21 proximal epiphysis) was estimated to be 53mm (preserved length is 44.7mm). This estimate is  
22 based on the fact that the metacarpal proximal epiphysis is in the process of fusing with the  
23 diaphysis in 12-13 year-old human males and thus the overall length of the metacarpal shaft is  
24 generally adult-like (Greulich et al. 1971; Gilsanz and Ratib 2005). Although this is just an  
25 estimation, comparative analyses reveal sexual dimorphism between MH1 and MH2.

1           Qualitative comparisons between MH1 U.W. 88-112 and MH2 U.W. 88-116 Mc3s clearly  
2 show a substantial difference in shaft robusticity. Indeed, relative to (estimated) interarticular  
3 length, ML breadth at midshaft in MH2 is narrower than all other hominins, including *Au.*  
4 *afarensis*, *Au. africanus*, *H. naledi* and most Neandertals and is slightly narrower than *H.*  
5 *erectus* KNM-WT 51260. In contrast, MH1 is ML broader than *Au. afarensis*, KNM-WT 51260,  
6 and the average breadth of Neandertals and *H. sapiens*. However, both Mc3 specimens fall  
7 within the lower (MH2) and upper (MH1) ranges of variation of Neandertals and *H. sapiens*  
8 (Figure 26).

9           A styloid process is not present at the proximal end of either Mc3 specimen, which is  
10 similar to morphology found in other australopiths (Bush et al. 1982; Tocheri et al. 2008; Ward  
11 et al. 2012; *contra* Susman 1988b; Ricklan 1987), and unlike the possibly *H. erectus* specimen  
12 KNM-WT 51260 (Ward et al. 2013) and later *Homo* (Lorenzo et al. 1999; Trinkaus 2016).  
13 Comparison of the relative size of the Mc3 base shows that the MH1 and MH2 Mc3s share a  
14 similar ML breadth, which is intermediate between *Au. afarensis* and all other fossil hominins  
15 and most similar to the median values of *H. sapiens* (Figure 26). The DP height of the base is  
16 relatively larger in MH1 compared with MH2, but both specimens are taller than *Au. afarensis*,  
17 *H. naledi* and *H. erectus*. The smooth and mildly convex capitulate articular surface in both  
18 specimens is unlike the more concavoconvex topography of the *Au. afarensis* A.L. 333  
19 specimens or SKX 3646 from Swartkrans. The MH1 and MH2 Mc3s differ in their Mc4 articular  
20 morphology, such that MH1 is missing a palmar Mc4 facet that is present in MH2. This articular  
21 variation is common within the hominin fossil record; *Au. afarensis* A.L. 438-1d and A.L. 333-  
22 122, Swartkrans SKX 3646 and *H. naledi* U.W. 101-1319 have a dorsal Mc4 facet only, while  
23 both dorsal and palmar facets are found in *Ar. ramidus* ARA-VP-6/500-6, *Au. afarensis* A.L.  
24 333-16 and A.L. 333w-6, and *Au. africanus* StW 64 and StW 68.

1 MH2 also demonstrates a remarkably tall DP height of the Mc3 head, being taller than all  
2 other fossil hominins and falling only within the upper range of variation in *H. sapiens* and  
3 *Gorilla* (Figure 26).

4  
5 **[INSERT Figures 25 & 26 about here]**

#### 6 7 **FOURTH METACARPAL**

8 Like the other MH2 metacarpals, the U.W. 88-117 Mc4 shaft is gracile (Figure 12). However,  
9 relative to its interarticular length, the Mc4 is comparatively more robust in most dimensions  
10 than the MH2 Mc2 and Mc3 (Figure 27). Relative ML breadth at midshaft is similar to (rather  
11 than narrower than, as in the Mc2 and Mc3) all other fossil hominins and modern humans, apart  
12 from *H. naledi* and, especially, SKX 2954 from Swartkrans. The prominent *Mm. dorsal interossei*  
13 crest on the dorsal shaft of U.W. 88-117 is more developed than that of *Au. afarensis*, SKX  
14 2954 and later hominins. The dorsal “bend” in the Mc4 shaft is similar to that seen in StW 330  
15 and not as accentuated as that of SKX 2954.

16 Relative to interarticular length, the U.W. 88-117 base is as ML broad as Neandertals  
17 and *H. sapiens* and broader than all other fossil hominins (Figure 27). The base is relatively  
18 taller than all other fossil hominins in DP height, falling only within the extreme upper range of  
19 variation in recent humans. The mildly convex morphology of the hamate articulation is similar  
20 to SKX 2954, *H. naledi* and *H. sapiens* and unlike the more concavoconvex morphology of *Au.*  
21 *afarensis*, *Au. africanus* StW 65, and *Pan*. The U.W. 88-117 head is remarkably ML broad and  
22 DP tall, particularly in contrast to its relatively narrow shaft (Figure 12). For example, in absolute  
23 dimensions, U.W. 88-117 is almost identical in head size (10mm in ML breadth, 10.9mm in DP  
24 height) to that of SK 85 (10.2mm and 10.8mm, respectively) and SKX 2954 (10.1mm and  
25 10.5mm, respectively) despite having a much more gracile shaft (5.2mm in ML breadth, 6.6mm

1 in DP height, compared with 7.3mm and 7.8mm, respectively, in SK 85 and 6mm and 8.1mm,  
2 respectively, in SKX 2954). Relative to interarticular length, the MH2 Mc4 head is broader (and  
3 DP taller) than all other fossil hominins apart from *H. naledi* and falling only within the extreme  
4 upper range of variation of recent humans (Figure 27).

5

## 6 **FIFTH METACARPAL**

7 The U.W. 88-118 Mc5 is the most robust metacarpal for its length compared with the other MH2  
8 metacarpals. Compared with other hominins, the U.W. 88-118 ML midshaft breadth is similar to  
9 that of Neandertals and *H. sapiens*, broader than *Au. afarensis* and *Ar. ramidus*, but narrower  
10 than *Au. africanus* StW 63 and SK(W)14147 from Swartkrans (Figure 28). The *M. opponens*  
11 *digiti minimi* entheses along the medial side of U.W. 88-118 is more well-developed and  
12 proximally-extended than that of *Au. africanus* StW 63, but it is less developed than that of *Au.*  
13 *afarensis*, SK(W) 14147, and *H. naledi* (Figure 13).

14 The MH2 Mc5 base is ML broader than that of all other hominins, including Neandertals  
15 and early *H. sapiens*, and is most similar to *Au. africanus* and SK(W) 14147 (Figure 28). The DP  
16 height of the U.W. 88-118 base is also taller than all other hominins except SK(W) 14147 and  
17 falls only within the upper range of variation in recent humans. This robusticity is largely due to  
18 an extremely well-developed medial protuberance for the *M. extensor carpi ulnaris* dorsally and  
19 the pisohamate ligament palmarly, which is most similar to *Au. africanus* StW 63, and more  
20 protruding than that of *Ar. ramidus*, *Au. afarensis*, SK(W) 14147 and *H. naledi*. The strongly  
21 convex, palmarly-extended and asymmetrical hamate facet is most similar to articular  
22 morphology found in SK(W) 14147. In *Ar. ramidus* and *Au. afarensis* the hamate articular  
23 surface also extends onto the palmar Mc5 surface, but the palmar border of the facet is more  
24 symmetrical. The hamate facet of U.W. 88-118 is unlike the saddle-shaped articulation found in  
25 *H. naledi*, Neandertals and *H. sapiens*.

1 Relative to interarticular length, U.W. 88-118 head is DP taller than all other hominins,  
2 falling outside even the upper range of variation in recent humans (Figure 28). The ML head  
3 breadth is also relatively broad, being similar to that of Neandertals and *H. sapiens* and broader  
4 than all other hominins except SK(W) 14147. The distal articular outline of U.W. 88-118 head in  
5 palmar view is most similar to SK(W) 14147, being more asymmetrical than *Au. afarensis*, but  
6 less so than that of *Au. africanus* StW 63, *H. naledi* and other later *Homo*.

7  
8 **[INSERT Figures 27 & 28 about here]**  
9

#### 10 **POLLICAL PROXIMAL PHALANX**

11 The MH2 proximal pollical phalanx (PP1) appears more gracile, curved and asymmetrical  
12 compared with many other fossil hominins (Figure 14). Relative to total PP1 length, the ML  
13 breadth at midshaft in both MH2 PP1s is narrower than that of all other fossil hominins, apart  
14 from *Ar. ramidus*, and is almost identical to that of *Au. afarensis* A.L. 333-69 (although it differs  
15 substantially from the more robust, but incomplete, A.L. 438-4) (Figure 29). The dorsal surface  
16 of the MH2 PP1s is mildly PD convex, especially at the distal end, like that of *Ar. ramidus*, *Au.*  
17 *afarensis*, *Au. africanus* StW 575, and is more curved than that of *H. naledi* and other *Homo*  
18 specimens. In sagittal view, the palmar surface is strongly PD concave due to a dramatic  
19 narrowing in the DP height of the shaft just proximal to the trochlea; this narrowing and  
20 curvature is more accentuated than that of all other known fossil hominin PP1s. The “hollowed”  
21 appearance of the palmar shaft surface differs from slightly convex surface in *Au. afarensis* and  
22 *H. naledi* and strongly convex surface of *Au. africanus*.

23 Despite a gracile shaft, the relative ML breadth of the MH2 PP1 base is similar to all  
24 other hominins, apart from *Ar. ramidus*, which is narrower, and Neandertals, which are much  
25 broader (**Figure 29**). In relative DP basal height, U.W. 88-91 is also taller than all other fossil

1 hominins, apart from Neandertals, although all early hominins fall within range of recent human  
2 and *Pan* variation. The basal asymmetry of the MH2 PP1s is much more pronounced than that  
3 of *Ar. ramidus*, *Au. afarensis* and *Au. africanus*, both in the development of the tubercles and,  
4 especially, the proximal extension of the metacarpal facet (Figure 14). Relative to total PP1  
5 length, ML breadth and DP height of the MH2 PP1 trochlea are smaller than all other fossil  
6 hominins, being most similar to *Au. afarensis* (Figure 29).

7         Comparison of the intrinsic proportions within the thumb shows that, relative to the  
8 length of the Mc1, MH2 has a short PP1 that is most similar to Neandertals, particularly the  
9 Shanidar 4 specimen (Table 6). The MH2 PP1 is shorter than the estimate for *Au. afarensis*  
10 (A.L. 333-69 and A.L. 333w-39; Marzke 1983), *H. naledi*, and *H. sapiens*.

11  
12 **[INSERT Figure 29 & Table 6 about here]**

#### 14 **NON-POLLICAL PROXIMAL PHALANGES**

15 Overall, the MH2 non-pollical proximal phalanges show moderate PD curvature of the dorsal  
16 surface, and are relatively gracile and short in absolute length compared with most other  
17 hominins (**Figure 30**). Although there is substantial overlap in the degree of curvature across  
18 the comparative sample, *Au. sediba* curvature is less than the median value of *Ar. ramidus*, *Au.*  
19 *afarensis*, *H. naledi* and OH 7, but greater than that of *Au. africanus* and hominins from  
20 Swartkrans (Figure 30). Phalangeal curvature in *Au. prometheus* is also reportedly “strong”  
21 (Clarke 2013:116) and similar to *Au. afarensis* (Clarke 1999:479), but measurements of the  
22 curvature have not yet been published. Relative to metacarpal length, the MH2 proximal  
23 phalanges are of similar length to those of modern humans: the PP3 is 71.7% of the Mc3  
24 interarticular length and the PP4 is 75.5% the Mc4 total length, compared with mean values of  
25 71.5% and 74.7% in recent humans, respectively (Table 6). In comparison, *Ar. ramidus* (ray 4

1 only), *H. naledi* and *H. sapiens* specimen Qafzeh 9 have relatively longer proximal phalanges  
2 than MH2, while African apes and the *Au. afarensis* composite hand have relatively shorter  
3 proximal phalanges.

4         Relative to PP total length, the MH2 bases fall out as intermediate in ML breadth (and  
5 DP height), being most similar to *Au. africanus*, the PPs from Swartkrans, *H. naledi*, *H.*  
6 *floresiensis*, *H. sapiens* and *Gorilla*. In contrast, *Ar. ramidus* and *Au. afarensis* have ML narrow  
7 PP bases for their length, while OH 86 (Domínguez-Rodrigo et al. 2015), ATE9-2 (Lorenzo et al.  
8 2015) and Neandertals are relatively broader (Figure 31). In relative ML breadth at midshaft,  
9 the MH2 proximal phalanges, again, fall out as intermediate, being most similar to *H. naledi*, the  
10 Swartkrans specimens, and ATE9-2, and relatively broader than *Ar. ramidus*, *Au. afarensis* and  
11 recent *H. sapiens*, but narrower than *Au. africanus*, OH 86 and Neandertals (Figure 31).  
12 However, the palmar surfaces of the MH2 PP2-PP4 shafts are concave both ML and PD,  
13 making them appear gracile compared to the ML flat or mildly convex palmar surfaces of the *Ar.*  
14 *ramidus* (e.g. ARA-VP-6/500-30 and -69), *Au. afarensis* (e.g. A.L. 1044-1, A.L. 444-4), *Au.*  
15 *africanus* (e.g. StW 28 and - 293), the Swartkrans specimens (e.g. SKX 5018 and -15468), *H.*  
16 *habilis* (OH 7) and *H. naledi*, and the strongly convex palmar surface of the *H. floresiensis*  
17 proximal phalanges (Larson et al. 2009). The concave palmar surface morphology of the MH2  
18 proximal phalanges makes the flexor sheath ridges particularly prominent (especially on the  
19 PP4) relative to most *Au. afarensis*, *Au. africanus*, Swartkrans, *H. naledi* and *H. floresiensis*  
20 specimens. The MH2 PP5 (U.W. 88-121) morphology differs from that of the other proximal  
21 phalanges, in having a ML flatter palmar surface that is more similar to other fossil hominins,  
22 and a well-developed convex “bar” extending from the medial basal tubercle (Figure 15). This  
23 morphology is not seen in other potential PP5s from *Au. afarensis* (A.L. 333-62) and OH 86  
24 (Domínguez-Rodrigo et al. 2015), or *H. naledi*.



1           The relative ML breadth and DP height of the MH2 PP trochlea are generally similar to  
2 all other fossil hominins and recent humans, apart from *Ar. ramidus* and *Au. afarensis*, which  
3 are relatively smaller in both dimensions, and Neandertals, which are relatively bigger (Figure  
4 31).

5

6 **[INSERT Figures 30 & 31 about here]**

7

### 8 **INTERMEDIATE PHALANGES**

9 Overall, the morphology of the MH2 intermediate phalanges is unique among hominins; the  
10 palmar surface is generally concave, both ML and PD, and the flexor sheath ridges are well-  
11 developed, with no indication of median bar and lateral fossae (Figure 16). In this way, MH2  
12 looks superficially most similar to the Miocene hominoid *Sivapithecus* (Madar et al. 2002) rather  
13 than other hominins. Although Marzke et al. (2007) demonstrated a high degree of variability in  
14 primate intermediate phalanx morphology and *M. flexor digitorum superficialis* tendon  
15 attachment, all of the fossil hominin middle phalanges recovered to date demonstrate a palmar  
16 median bar and lateral fossae that is typical of human intermediate phalanges, including *Ar.*  
17 *kadabba*, *Ar. ramidus*, *Au. afarensis*, *Au. africanus*, Swartkrans specimens, *H. habilis*, *H.*  
18 *erectus*, *H. naledi*, *H. floresiensis*, and other later *Homo* (e.g. Bush et al. 1982; Larson et al.  
19 2009; Lorenzo et al. 1999; Susman and Creel 1979; Walker and Leakey 1993). The concave  
20 palmar morphology and tall flexor ridges of the MH2 intermediate phalanges – described by  
21 Marzke et al. (2007) as a “palmar median fossa” – was found in only two humans and one adult  
22 chimpanzee in their hominoid sample. The FDS tendons attach primarily to the lateral margins  
23 of the middle phalanx (i.e., not to the lateral fossa, *contra* Susman and Creel 1979; Susman and  
24 Stern 1979). Furthermore, in palmar or dorsal view, the sides of the MH2 intermediate phalanx  
25 shafts are relatively straight, which is more similar to typical proximal phalanx morphology.

1 Instead, in all other known hominin specimens the shaft sides taper distally, such that the distal  
2 shaft is ML narrower than the proximal shaft in *Ar. ramidus*, *Au. afarensis*, *Au. africanus*,  
3 Swartkrans specimens, *H. naledi* and *H. floresiensis* (Larson et al. 2009). The MH2 intermediate  
4 phalanges are distinctly different from the bottle-shaped shaft (Susman and Creel 1979: 391) of  
5 the OH 7 *H. habilis* intermediate phalanges.

6 Quantitatively, the relative length of IP3 to Mc3 is similar to that of *H. sapiens*, as well as  
7 *H. naledi*, while the *Au. afarensis* composite hand and Neandertals have a relatively shorter IP3  
8 (Table 6). Relative to total length of the IP, the MH2 IP bases fall out as intermediate in their ML  
9 breadth, being most similar to *H. naledi*, *H. sapiens* and *Gorilla* (Figure 32). *Ar. ramidus*, *Au.*  
10 *afarensis*, *Au. africanus*, and *H. floresiensis* have relatively ML narrower bases, while most  
11 specimens from Swartkrans and Neandertals are relatively broader. The MH2 IP relative ML  
12 breadth at midshaft is most similar to *Au. afarensis*, *Au. africanus*, and *H. sapiens*, while all  
13 other hominins, apart from *Ar. ramidus*, are broader. Comparative analysis of the distal trochlea  
14 reveals limited variation in trochlea DP height across all hominins (only *Ar. ramidus* and *H.*  
15 *floresiensis* are relatively short), while the MH2 IPs have relatively ML broad trochlea compared  
16 with earlier hominins, being most similar to the Swartkrans specimens, *H. naledi* and *H. sapiens*  
17 (Figure 32).

18

## 19 **DISTAL POLLICAL PHALANX**

20 Although the MH2 distal pollical phalanx is not complete, enough of the lateral proportion and its  
21 total length are preserved to confidently estimate its overall size and to identify key  
22 morphological features that can be compared with other hominins (Figure 17). Relative to the  
23 total estimated DP1 length, U.W. 88-124 has a ML expanded apical tuft that is most similar to  
24 *Au. africanus* StW 294 and Swartkrans specimen SKX 5016 (Figure 33). The MH2 DP1 apical  
25 tuft is more ML expanded than that of *Ar. ramidus*, *Au. afarensis*, Neandertals and *H. sapiens*,

1 but less expanded than *Au. robustus* TM 1517k, *H. habilis* OH 7 and *H. naledi*. This is generally  
2 consistent with the qualitative comparisons in which the relative ML narrow but DP tall shaft of  
3 U.W. 88-124 is more similar to morphology to StW 294 than the ML broader and DP flatter DP1  
4 morphology typical of OH 7, TM 1517k and *H. naledi* (although SKX 5016 would fall into the  
5 latter category as well). MH2, however, differs from StW 294, as well as TM 1517k, OH 7 and  
6 SKX 5016, in having both a well-developed proximal and distal (ungual) fossae and a more well-  
7 developed gable for the FPL tendon attachment on its palmar surface. MH2 shares a similar  
8 palmar morphology with that described in *Orrorin tugenensis*, although the apical tuft is less ML  
9 expanded in the latter (Almecija et al. 2010).

10

11 **[INSERT Figures 32 & 33 about here]**

12

## 13 **DISCUSSION AND CONCLUSION**

14

15 The rare occurrence of semi-articulated hand skeleton in association with a relatively complete  
16 skeleton affords a unique opportunity to investigate potential hand function within an  
17 australopith individual. The MH2 hand presents morphological features that are similar to both  
18 earlier and later hominins, as well as some features that are distinct to *Au. sediba* (Table 7).  
19 Together, the combination of features found in the MH2 hand skeleton is not found in any other  
20 known hominin. Below, we describe some of the potential functional implications of the MH2  
21 hand, divided by anatomical region.

22

### 23 **The thumb and lateral carpometacarpal articulations**

24 Although the trapezium and trapezoid are not yet known for *Au. sediba*, some functional  
25 inferences can be drawn from the lateral carpometacarpal articulations and thumb morphology.

1 The mosaic morphology of the MH2 scaphoid, capitate and Mc1-Mc3 suggest a unique pattern  
2 of load transmission through the thumb, lateral wrist and palm compared with that of other fossil  
3 hominins and humans. Features that are shared typically with *Pan*, *Ar. ramidus*, and the  
4 preserved elements of early australopiths (*Australopithecus* sp., *Au. anamensis*, *Au. afarensis*  
5 and/or *Au. africanus*), as well as *H. floresiensis*, include a relatively large trapezoid facet on the  
6 scaphoid (associated with a “closed” distal border of the scaphoid’s capitate facet), a small  
7 trapezium-Mc1 articulation, a gracile Mc1 shaft, absence of a large, palmarly-positioned  
8 trapezoid-capitate articulation, a Mc2-capitate articulation that is more laterally facing, and the  
9 absence of a Mc3 styloid process (Bush et al. 1982; Kibii et al. 2011; Lovejoy et al. 2009;  
10 Marzke 1983; Marzke et al. 1992; McHenry 1983; Tocheri 2007; Tocheri et al. 2007, 2008;  
11 Ward et al. 1999, 2001, 2012). The *Au. sediba* MH2 hand shares all of these morphological  
12 features with other early fossil hominins (and *H. floresiensis*) that together suggest relatively  
13 small force production by the thumb and limited ability to pronate the Mc2, both of which are  
14 considered important for forceful precision gripping in humans (Marzke 1983, 1997; Marzke et  
15 al. 1992, 1998; Marzke and Marzke 2000; Tocheri 2007; Tocheri et al. 2008). In fact, the MH2  
16 Mc1 shaft is the most gracile shaft for its length of all known fossil hominins (Figure 24), strongly  
17 supporting an interpretation of limited force production by the thumb.

18 The MH2 hand, however, also shows morphological features that indicate a mosaic  
19 evolution of the lateral carpometacarpal region and suggest that function of this region was  
20 somewhat different from that of other australopiths. Although MH2 has a dorsal capitate-  
21 trapezoid articulation as in African apes, it also has a small palmar trapezoid facet like that of  
22 some other early and later hominins, including cf. *Australopithecus* sp. KNM-WT 22944-H, *Au.*  
23 *afarensis* A.L. 333-40, *H. antecessor* (Lorenzo et al. 1999) and possibly *Ar. ramidus*. This  
24 morphology is intermediate between the single dorsally-positioned facet of *Pan* and some  
25 australopiths (*Au. africanus* TM 1526, *Au. afarensis* A.L. 288-1w) and the single, expanded

1 palmar capitate-trapezoid articulation typical of recent humans and Neandertals (Lewis 1989;  
2 Tocheri 2007). Furthermore, MH2 lacks a J-hook scaphoid facet on the capitate that is found in  
3 *Pan*, *Au. afarensis*, and *H. floresiensis* (Orr et al. 2013) and the trapezium facet extends further  
4 onto the scaphoid tubercle than in *Australopithecus* sp. StW 618, OH 7 and *H. floresiensis* (Kibii  
5 et al. 2011; Tocheri et al. 2007). The MH2 Mc1 shaft is uniquely gracile (Figure 24) and the  
6 entheses are poorly developed (but see below). MH2 is similar to most other hominins in the  
7 weak expression of the *M. first dorsal interosseous* enthesis (SK 84, *H. naledi*, and Neandertals  
8 being notable exceptions) that is distally-extended, which provides a longer moment arm for  
9 adduction of the thumb than that of African apes (Jacofsky 2009; Tocheri et al. 2008). However,  
10 the MH2 *M. opponens pollicis* (OP) insertion is distinct in being proximally-positioned and poorly  
11 developed. The MH2 insertion differs from the distally-positioned OP enthesis of *Pan*, *Ar.*  
12 *ramdius*, other australopiths and *H. naledi*, and from the more extended enthesis of humans that  
13 runs the entire length of the Mc1 lateral shaft (Jacofsky 2009). Jacofsky (2009:128) noted that  
14 the proximal portion of the human OP insertion had a larger abduction moment arm when the  
15 thumb was extended, while the distal OP insertion had a larger abduction moment arm when  
16 the thumb was flexed. This may suggest subtle differences in OP muscle efficiency and thumb  
17 function in MH2 relative to other fossil hominins. It is important to note, however, that no  
18 consistent relationship has been found between OP enthesis morphology and several aspects  
19 of the muscle size and architecture in human cadaveric specimens (Williams-Hatala et al.  
20 2016), and that several recent studies have highlighted the complexity of inferring muscle size,  
21 function and even presence/absence from enthesis morphology (Eliot and Jungers 2000;  
22 Marzke et al. 2007; Rabey et al. 2015; Zumwalt 2006; but see Karakostis et al. 2017).

23         The MH2 Mc1 also has a prominent intersesamoid beak on the palmar surface of the  
24 head that is not preserved in any other known hominin Mc1 specimens (*contra* Susman 1988a,  
25 b), apart from SK 84 from Swartkrans (Napier 1959; Trinkaus and Long 1990). If the

1 prominence of the beak is correlated with an increased size of the medial and lateral  
2 sesamoids, then the morphology of the MH2 (and SK 84) Mc1 may suggest well-developed  
3 pulleys for the *Mm. adductor pollicis oblique* and *flexor pollicis brevis* and thus enhanced  
4 adduction and flexion of the thumb (Marzke et al. 1999).

5         Finally, and perhaps most notably, the MH2 thumb, and particularly the Mc1, is  
6 exceptionally long relative to the length of the fingers, being relatively longer than that of recent  
7 humans (i.e. outside the range of variation in our sample) and all known fossil hominins (Figure  
8 23; Kivell et al. 2011). Intrinsic hand proportions are strongly linked with precision grip capability  
9 (Feix et al. 2015; Lui et al. 2016) and, indeed, the relatively long thumb in humans has long  
10 been considered key to pad-to-pad precision abilities (e.g Marzke 1997; Napier 1960, 1962b;  
11 Susman 1998). Thus, despite the gracility of the MH2 PP1 and, particularly, the Mc1, such a  
12 relatively long thumb would have facilitated precision opposition of the thumb to the fingers.  
13 Indeed, kinematic modelling as shown that if range of motion at the MH2 trapezium-Mc1 joint is  
14 assumed to be more limited, like chimpanzees, or more mobile, like humans, the manipulative  
15 “workspace” between the thumb and index finger is similar to or greater than that of recent  
16 humans (Feix et al. 2015).

17         Together, the morphology found in MH2 suggests at least some repositioning of the  
18 trapezoid-trapezium within the lateral carpometacarpal complex (which was also likely occurring  
19 in earlier hominins as well; Tocheri et al. 2008), perhaps with some degree of palmar expansion  
20 of the trapezoid (compared with the wedge-shaped trapezoid of African apes and *H.*  
21 *floresiensis*), and an enhanced ability to perform precision grips between the thumb and fingers.  
22 However, the small trapezium-Mc1 joint, extremely gracile Mc1 (and PP1) shafts, and absence  
23 of a Mc3 styloid process, strongly suggest that the manipulative capabilities of MH2 had limited  
24 force production. The full expression of the lateral carpometacarpal features in humans and  
25 Neandertals, and to a large extent in *H. naledi* (Kivell et al. 2015) results in a more proximodistal

1 alignment of the joint surfaces, that is thought to facilitate better transmission of high transverse  
2 loads from the thumb during manipulative activities (Marzke et al. 2010; Tocheri 2007). The  
3 combination of morphological features in MH2 lateral carpometacarpal region suggest that *Au.*  
4 *sediba* was clearly not capable of forceful precision manipulation to the same degree as  
5 humans, Neandertals, and potentially *H. naledi*, but that its precision abilities were enhanced  
6 relative to African apes, *H. floresiensis*, and what is currently known from most other  
7 australopiths.

8

### 9 **Radiocarpal and midcarpal joints**

10 Associated wrist bones are rare in the early fossil hominin record (Clarke 1999; Lovejoy et al.  
11 2009). As such, MH2 provides the first opportunity to investigate wrist function in an  
12 australopith. The MH2 scaphoid incorporates a fused os centrale, as in humans, African apes  
13 (Kivell and Begun 2007) and all other known fossil hominins (e.g. Kibii et al. 2011; Kivell et al.  
14 2015; Lovejoy et al. 2009; Napier 1962a) (Figure 3). Similarly, MH2 has a relatively larger radial  
15 facet on the lunate than that of the scaphoid, which is similar to the pattern found in humans,  
16 Neandertals, *H. naledi* and the unassociated carpal and radial remains of other australopiths  
17 (Heinrich et al. 1993; Johanson et al. 1982; Kibii et al. 2011; Ward et al. 2001, 2012). This  
18 morphology in MH2 is consistent with the radiocarpal articulation of the associated MH2 distal  
19 radius (Churchill et al. 2013; this volume). The opposite relationship is typical of African apes, in  
20 which they have a relatively larger scaphoid-radial articulation (Heinrich et al. 1993; Ward et al.  
21 1999, 2012). The radiocarpal articular pattern in humans and fossil hominins is thought to reflect  
22 loading along a more central axis of the wrist rather than then the more radial loading of African  
23 apes (Ward et al. 2012).

24         However, in MH2 this central-axis loading does not appear to translate through to the  
25 midcarpal joint in same way as other australopiths or *Ar. ramidus* given its ML narrow lunate

1 body, remarkably small (in both ML and DP dimensions) lunate-capitate articulation, and more  
2 distally-oriented scapholunate articulation. The narrow lunate morphology in MH2 differs from  
3 the ML broad lunates of *Ar. ramidus*, KNM-WT 22944-J, *Au. afarensis* and *H. erectus* (Lovejoy  
4 et al. 2009; Ward et al. 1999, 2012; Weidenrich 1941). Although the distinction between the  
5 lunate and scaphoid articular surfaces of the capitate is not well-defined, rearticulation of the  
6 midcarpal joint (**Figure 2**; see also Fig. 5 in Kivell et al. 2011) suggests that the articulation for  
7 the lunate was relatively small compared with that of the scaphoid. This differs from the larger  
8 capitate facets of *Ar. ramidus*, *Au. afarensis*, and *H. naledi* lunates (Figure 19), as well as the  
9 articular morphology of the ML broad capitate heads of other australopiths (KNM-WT 22944-H,  
10 A.L. 333-40, TM 1526) in which the lunate facet is relatively larger than that of the scaphoid,  
11 while the opposite relationship is typical of African apes (Jenkins and Fleagle 1975; Corruccini  
12 1978). Furthermore, the more distally-oriented scaphoid facet positions the scaphoid in a more  
13 distomedially-rotated position relative to the lunate, which is distinct from the more laterally-  
14 facing scapholunate articulation found in *Ar. ramidus* and *Au. afarensis*. This scapholunate  
15 articulation in MH2 is consistent with a more medially-facing radiocarpal articulation of the MH2  
16 distal radius relative to the human condition (Churchill et al. this volume). Altogether, the  
17 scaphoid-lunate-capitate morphology in MH2 might allow for a greater range of abduction at the  
18 radiocarpal joint and suggests less central-axis loading of the radiocarpal and midcarpal joints  
19 than that of other australopiths.

20         Within the medial aspect of the MH2 carpus, MH2 has a DP tall and strongly  
21 concavoconvex articulation between the triquetrum and hamate (Figures 5 and 8), which differs  
22 from the less complex articular morphology seen in SKX 3498, *H. naledi* and Neandertals.  
23 Furthermore, the proximal half of the hamate's triquetrum facet is inclined dorsally, which differs  
24 from the more proximally-oriented triquetrum facets of *Ar. ramidus*, KNM-WT 22944-I, *Au.*  
25 *afarensis*, *H. naledi* and that is typical of *H. sapiens*. As such, the MH2 triquetrum would rotate



1 dorsally onto the hamate during extension and/or adduction of the midcarpal joint, suggesting  
2 enhanced stability in the medial midcarpal joint in extended and/or adducted wrist postures  
3 relative to other hominins.

4

## 5 **Flexor apparatus**

6 The tubercles of the scaphoid and trapezium laterally, and the pisiform and hamate hamulus  
7 medially form the “walls” of the carpal tunnel. In African apes, all of these morphological  
8 features are palmarly extended (e.g. large tubercles, rod-shaped pisiform) to create a deep  
9 carpal tunnel that accommodates well-developed flexor tendons, while the opposite condition is  
10 typical of humans (Corruccini 1978; Kivell 2016; Lewis 1989; Niewoehner 2006; Sarmiento  
11 1988; Tuttle 1969). In the MH2 hand, although the trapezium is not preserved, the size of the  
12 scaphoid tubercle is smaller and less palmarly-oriented than that of *Ar. ramidus*, StW 618 and  
13 some Neandertals, but larger than *H. naledi* and *H. sapiens* (Kivell et al. 2011; Trinkaus 1983)  
14 (Figure 3; Table 2). The MH2 triquetrum is unusual in having a tubercle-like mediopalmar  
15 projection that is not found in any of known fossil hominin triquetra, although there are few  
16 preserved (i.e. *Ar. ramidus*, SKX 3498, *H. naledi* and Neandertals). This projection orients the  
17 small pisiform facet proximopalmarly. When the MH2 carpus is articulated with the associated  
18 ulna, there is minimal space between the ulnar styloid process and the triquetrum, suggesting  
19 the pisiform was smaller than the rod-shaped pisiform of *Au. afarensis* (Bush et al. 1982) and  
20 African apes. Finally, the hamate hamulus projects strongly palmarly, but its distal projection  
21 and oval-shaped cross-section is most similar to the human and Neandertal condition (Figure  
22 22) (although KNM-WT 22994-H also has an oval-shaped cross-section; Orr et al. 2013). Its  
23 greater palmar projection may enhance the capacity of the *M. flexor carpi ulnaris* to act as a  
24 flexor and increase the moment arm of the *Mm. opponens digiti minimi* and *flexor digiti minimi*  
25 (Niewoehner 2006; Ward et al. 1999), although more research is needed to understand the

1 relationship, if any, between hamulus shape and extrinsic and intrinsic flexor muscle  
2 morphology (Orr et al. 2013). Together, the preserved morphology of the MH2 carpus suggests  
3 a moderately developed carpal tunnel, intermediate between the deep carpal tunnels of *Ar.*  
4 *ramidus*, *Au. afarensis*, and Neandertals, the shallow morphology of *H. naledi* and *H. sapiens*.

5         That being said, there appear to be potential trade-offs in the bony morphology of the  
6 carpal tunnel among hominins that, without a complete and associated carpus, make functional  
7 interpretations difficult. For example, *Ar. ramidus* has large, projecting tubercles on the  
8 scaphoid, trapezium and hamate (Lovejoy et al. 2009); unassociated specimens of *Au.*  
9 *afarensis* show a rod-shaped pisiform but a less palmarly-projecting hamulus relative to hamate  
10 size (the A.L. 333-80 trapezium does not preserve its tubercle); the *H. naledi* Hand 1 has a  
11 relatively small scaphoid tubercle and hamate hamulus, but a large, projecting tubercle on the  
12 trapezium; while most Neandertals generally have large, projecting tubercles on scaphoid,  
13 trapezium and hamate, but a pea-shaped pisiform (McCown and Keith 1939; Trinkaus 1982,  
14 1983; but see Kivell et al. 2018). Thus it is unclear how the different combinations of  
15 morphology across the four bones of the carpal tunnel might translate into potential functional  
16 differences, if any, of the flexor apparatus at the hominin wrist joint.

17         The proximal and, unusually, the intermediate phalanges of the MH2 hand have well-  
18 developed flexor sheath ridges, indicating strong flexion of all of the fingers, and particularly the  
19 fourth and fifth digits. The proximal and intermediate phalanges are also moderately curved,  
20 suggesting some degree of arboreality was still a functionally important part of the MH2  
21 locomotor repertoire (Jungers et al. 1995b; Kivell et al. 2015; Nguyen et al. 2014; Richmond  
22 1998). However, although there is a large degree of overlap in the degree of phalangeal  
23 curvature across extant and fossil taxa, the MH2 phalanges are less curved than those *Au.*  
24 *afarensis* and *Ar. kadaba*, suggesting less dependence on arboreality than in earlier hominins.  
25 Furthermore, the proximal phalanges are absolutely short and, relative to the length of the palm,

1 similar in length to modern humans and Neandertals (Kebara 2) (and actually shorter than early  
2 *H. sapiens* Qafzeh 9). Finally, although the distinct flexor sheath ridges of the MH2 intermediate  
3 phalanges suggests enhanced flexion at the interphalangeal joints, it is the DP thickening of the  
4 shaft created by a palmar median bar that likely reflects high dorsopalmarly-directed bending  
5 stress of the phalanges (Begun et al. 1994; Marzke et al. 2007). The absence of the median bar  
6 in MH2 suggests lower loading/bending stress during grasping (either during locomotor or  
7 manipulative behaviours) than in other hominins. The MH2 morphology is particularly distinct  
8 from the robust phalanges –both proximal and, especially, intermediate— of the OH 7 *H. habilis*  
9 hand (Napier 1962a) and the strongly curved phalanges of *H. naledi* (Kivell et al. 2015).  
10 Together, the few associated fossil hominin hand skeletons reveal varied mosaics of  
11 morphologies that suggest potentially different selective pressures on finger morphology, or  
12 different morphological solutions to similar selective pressures, across australopiths and *Homo*.

13

#### 14 **The medial metacarpus**

15 Like the Mc1, the MH2 medial metacarpal shafts appear remarkably gracile (Figures 10-13).  
16 Indeed, relative to their lengths, the medial metacarpal midshaft breadths are ML narrow  
17 compared to other australopiths and *H. naledi* (Figs. 25-28). However, the MH2 relative  
18 midshaft breadths fall close to the median values or within the range of variation found in  
19 Neandertals and *H. sapiens*. Furthermore, the proximal bases and distal heads of the medial  
20 metacarpals are among the largest in our comparative sample; for example, the relative DP  
21 height of the Mc2-Mc5 heads are taller than all other hominins, apart from *H. naledi*, and fall  
22 only within the extreme upper range of variation found in recent humans. The dorsal surface of  
23 the MH2 medial metacarpal shafts also have prominent attachments for the *Mm. dorsal*  
24 *interossei*. These entheses may be accentuated due to the relatively gracile shafts and/or  
25 indicate powerful abduction of the fingers.

1           The MH2 Mc2 and Mc3 are comparatively more gracile than its Mc4 and Mc5 and the  
2 overall morphology of both metacarpals is generally similar to other australopiths (Figures 25-  
3 28). The strongly asymmetrical Mc2 head would facilitate opposition of the index finger to the  
4 thumb as in other australopiths (Drapeau et al. 2005; Marzke 1983). The more laterally-facing  
5 Mc2-capitate articulation than that of humans suggests that MH2 may have had more limited  
6 pronation of the second digit, which is considered particularly important for cupping the palm  
7 during precision grasping in humans (Marzke 1997). The same functional interpretation has  
8 been made for the relatively laterally-facing Mc2 facet typical of Neandertals (Niewoehner 2006;  
9 Niewoehner et al. 1997). The Mc3 lacks a styloid process as in all other australopiths and *H.*  
10 *naledi* (Bush et al. 1982; Drapeau et al. 2005; Kivell et al. 2015; Marzke and Marzke 2000) and  
11 the capitometacarpal articulation is ML broad like that of other South African hominins (*Au.*  
12 *africanus* and SKX 3646 from Swartkrans) and humans (Rein and Harvati 2013). The generally  
13 flat morphology of the Mc3-capitate articulation is similar to that of humans and Neandertals,  
14 and distinct from the more concavoconvex morphology of African apes, *Ar. ramidus*, A.L. 333-  
15 40, TM 1526, and what is preserved in KNM-WT 22944-H, which is interpreted as reducing  
16 sliding and rotation at the capitometacarpal joint (Lovejoy et al. 2009; Marzke and Marzke 1987;  
17 Selby et al. 2016). Altogether, the MH2 morphology suggests greater mobility at the  
18 capitometacarpal articulation than the concavoconvex joints of earlier hominins, but also greater  
19 mobility than what is found in humans and Neandertals (and possibly *H. erectus*; Ward et al.  
20 2013), in which their joints are further stabilized via the styloid process (Marzke and Marzke  
21 1987, 2000).

22           The MH2 Mc5 is particularly robust (Figure 28). The ML broad and DP tall Mc5 base  
23 suggests well-developed extrinsic and intrinsic musculature to the fifth digit, including the *Mm.*  
24 *extensor carpi ulnaris* and *flexor carpi ulnaris*, via the pisohamate ligament, while the rugose  
25 entheses along the medial shaft may suggest a well-developed *M. opponens digiti minimi*. This

1 morphology is consistent with the robust insertion for the *M. flexor carpi ulnaris* on the proximal  
2 ulna (Churchill et al. 2013, this volume). The Mc5-hamate articulation is DP convex and extends  
3 onto the palmar surface of the shaft, while the corresponding facet of the hamate is constrained  
4 to the hamate body (i.e. does not extend onto the hamulus) and is distomedially oriented. This  
5 morphology differs from the proximally-oriented and saddle-shaped Mc5 hamate facet that is  
6 typical of humans and Neandertals (Marzke and Marzke 2000) and *H. naledi* (Kivell et al. 2015).  
7 The articular morphology of MH2 suggests that the Mc5 was positioned in a slightly more flexed  
8 and abducted position on the hamate than is typical of humans and Neandertals. This is  
9 consistent with the limited distal- but strong palmar projection of the hamulus found in the MH2  
10 hamate. Altogether, this morphology in combination with an asymmetric Mc5 head, suggests  
11 substantial mobility at the hamatometacarpal joint with strong flexion of the wrist and strong  
12 flexion and opposition of the fifth digit, but without the Mc5 rotation that is possible with a  
13 saddle-shaped hamatometacarpal articulation.

14

### 15 **Comparison between MH1 and MH2 third metacarpals**

16 Although the MH1 juvenile individual preserves only an incomplete Mc3, its association with a  
17 relatively complete skeleton that can be identified as presumably male provides a rare  
18 opportunity to investigate variation in hand morphology between sexes in early hominins. The  
19 MH1 Mc3 is missing its distal epiphysis but its absolute length is just slightly shorter than the  
20 fully adult Mc3 of MH2. Given the estimated age of MH1, the adult length of the Mc3 can be  
21 reasonably estimated and is approximately 8% longer than that of the MH2 Mc3. For  
22 comparison, there are only two complete Mc3s each known for the following hominin taxa,  
23 although, unlike *Au. sediba*, none is associated with other skeletal remains from which sex can  
24 be confidently estimated: *Au. afarensis*, in which A.L. 438-1d (64.8mm) is 7.1% longer than A.L.  
25 333-16 (60.2mm), *Au. africanus*, in which the total length of StW 64 (55.8mm) is 2.9% longer

1 than StW 68 (54.2mm), and *H. naledi*, in which U.W. 101-1319 (49mm) is approximately 6%  
2 longer than U.W. 101-1651+1628 (estimated at 46mm). Within our human samples, the total  
3 (and interarticular) length of male Mc3s are, on average, 3.6% longer than females, and within  
4 small-bodied humans, male Mc3s are, on average, 7.5% longer than females. Thus, the sexual  
5 dimorphism in Mc3 length between MH1 and MH2 is consistent with that of small-bodied recent  
6 humans and potentially other fossil hominins.

7         The MH1 Mc3 shaft is notably more robust than that of MH2 (Figures 11 and 26).  
8 Relative to length, the MH1 Mc3 midshaft breadth is among the broadest in our comparative  
9 sample, being similar to *Au. africanus* and *H. naledi*, while the MH2 Mc3 is among the  
10 narrowest, but similar to the absolutely long KNM-WT 51260. However, importantly, both Mc3  
11 specimens fall within the range of variation documented in Neandertals and *H. sapiens*.  
12 Therefore, although the two *Au. sediba* Mc3 specimens appear remarkably different in their  
13 robusticity, their variation comfortably fits within the sexual dimorphism documented in other  
14 fossil hominins and recent humans and does not necessarily reflect differences in function or  
15 hand use. This morphological variability between sexes is important to consider when drawing  
16 functional or taxonomic interpretations from isolated specimens (Trinkaus and Long 1990).

17

## 18 **ACKNOWLEDGEMENTS**

19 For this study, we are grateful to the institutions and curators that have provided access to  
20 specimens in their care, including: F. Mayer and S. Jancke (Berlin Natural History Museum), C.  
21 Boesch (Max Planck Institute for Evolutionary Anthropology), M. Teschler-Nicola and R. Muehl  
22 (Vienna Natural History Museum), E. Gilissen, M. Louette and W. Wendelin (Royal Museum for  
23 Central Africa), J. Moggi Cecchi and S. Bortoluzzi (University of Florence), M. Harman (Powell-  
24 Cotton Museum), L. Gordon and D. Hunt (Smithsonian Institution), Y. Haile-Selassie and L.  
25 Jellema (Cleveland Museum of Natural History), P. Reed (University of Toronto), J. Eger and S.

1 Woodward (Royal Ontario Museum), B. Zipfel (University of the Witwatersrand), S. Potze and L.  
2 Kgasi (Ditsong National Museum of Natural History), A. Kweka and A. Gidna (National Museum  
3 of Tanzania), B. Kimbel, T. White, B. Asfaw, G. Suwa and G. Shimelies (National Museum of  
4 Ethiopia), Y. Rak and I. Hershkovitz (Tel Aviv University). We thank Nick Stephens for sharing  
5 comparative data of Barma Grande 2 and Arene Candide 2 and Matt Tocheri for sharing surface  
6 models for several Neandertal and early *H. sapiens* carpal bones. We are grateful to Andrew  
7 Deane for his comparative analysis of phalangeal curvature. This research was funded by  
8 Natural Science and Engineering Research Council of Canada (TLK), General Motors Women  
9 and Mathematics and Sciences Award (TLK), Max Planck Society (TLK) and the European  
10 Research Council Starting Grant 336301 (TLK). For the Malapa project in general, we thank the  
11 South African Heritage Resources Agency for the permits to work at the Malapa  
12 site; the Nash family for granting access to the Malapa site and continued support of research  
13 on the Malapa and John Nash nature reserves; the South African National Centre of Excellence  
14 in Palaeosciences, the Lyda Hill Foundation, South African Department of Science and  
15 Technology, the South African National Research Foundation, the Evolutionary Studies  
16 Institute, University of the Witwatersrand, the University of the Witwatersrand's Vice  
17 Chancellor's Discretionary Fund, the National Geographic Society, the Palaeontological  
18 Scientific Trust, the Andrew W. Mellon Foundation, the Ford Foundation, the U.S. Diplomatic  
19 Mission to South Africa, the French embassy of South Africa, the Oppenheimer and Ackerman  
20 families, and Sir Richard Branson for funding; the University of the Witwatersrand's Schools of  
21 Geosciences and Anatomical Sciences and the Bernard Price Institute for Palaeontology for  
22 support and facilities; the Gauteng Government, Gauteng Department of Agriculture,  
23 Conservation and Environment and the Cradle of Humankind Management Authority; the  
24 University of Zurich 2010 Field School. Numerous individuals have been involved in the  
25 ongoing preparation and excavation of these fossils, including C. Dube, C. Kemp, M. Kgasi, M.

1 Languza, J. Malaza, G. Mokoma, P. Mukanela, T. Nemvhundi, M. Ngcamphalala, S. Jirah, S.  
2 Tshabalala, and C. Yates. Other individuals who have given significant support  
3 to this project include B. de Klerk, W. Lawrence, C. Steininger, B. Kuhn, L. Pollarolo, J. Kretzen,  
4 D. Conforti, C. Dlamini, H. Visser, B. Nkosi, B. Louw, L. Backwell, F. Thackeray, and M. Peltier.  
5 Finally, we thank Scott Williams and Jeremy DeSilva for co-editing this special issue and  
6 Jeremy DeSilva and two anonymous reviewers for helpful comments that have greatly improved  
7 this manuscript.

8  
9

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- 5

1 **FIGURE**

2

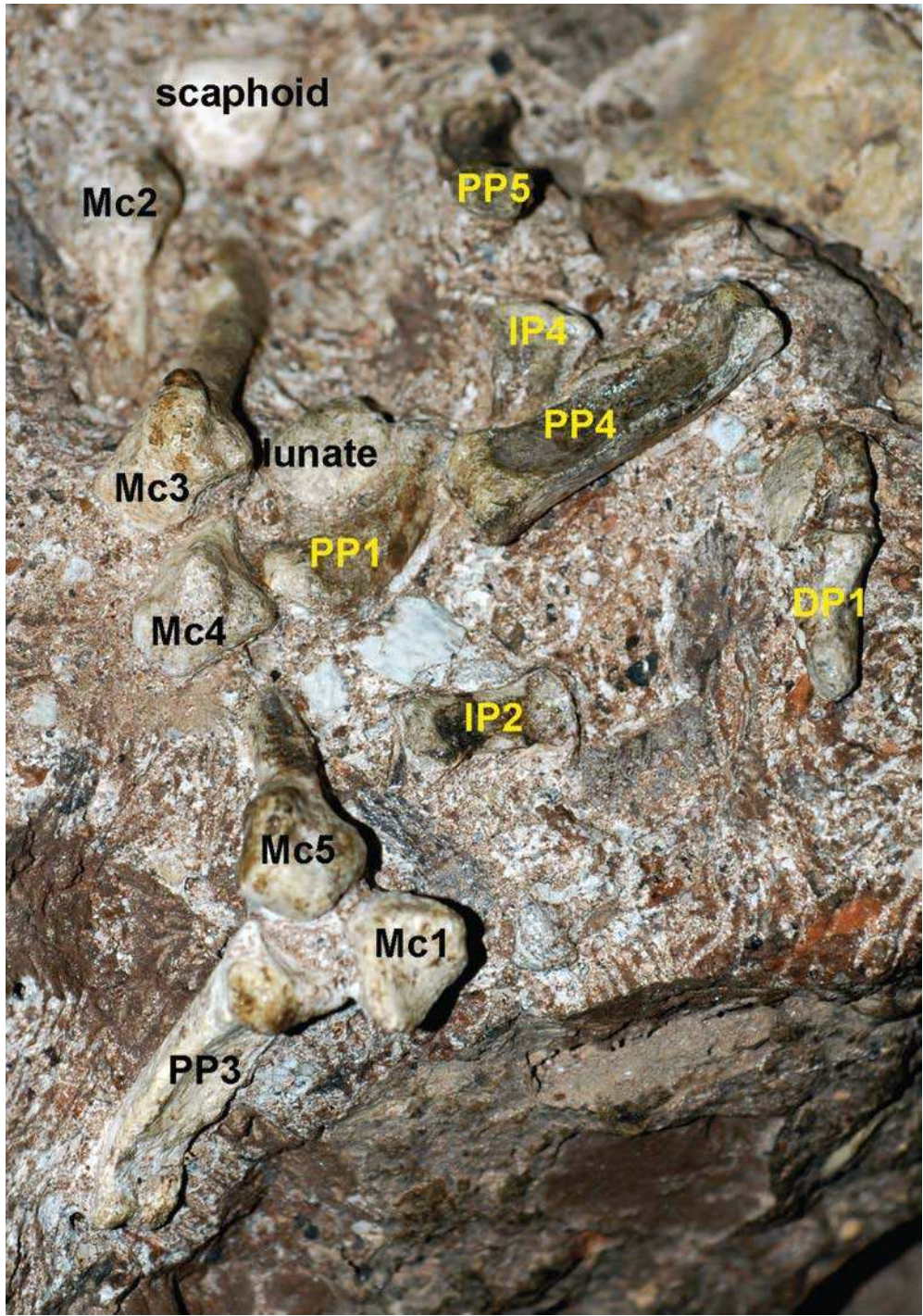
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4 *Figure 1. MH2 right hand bones in situ, showing the scaphoid, lunate, metacarpals (Mc),*

5 *proximal phalanges (PP), intermediate phalanges (IP) and the distal pollical phalanx (DP1).*

6

7



8

1 *Figure 2. Articulated MH2 carpus with the associated radius (U.W. 88-85) and ulna (U.W. 88-62)*  
2 *in palmar (left) and dorsal (right) views. See also Churchill et al. (this volume).*



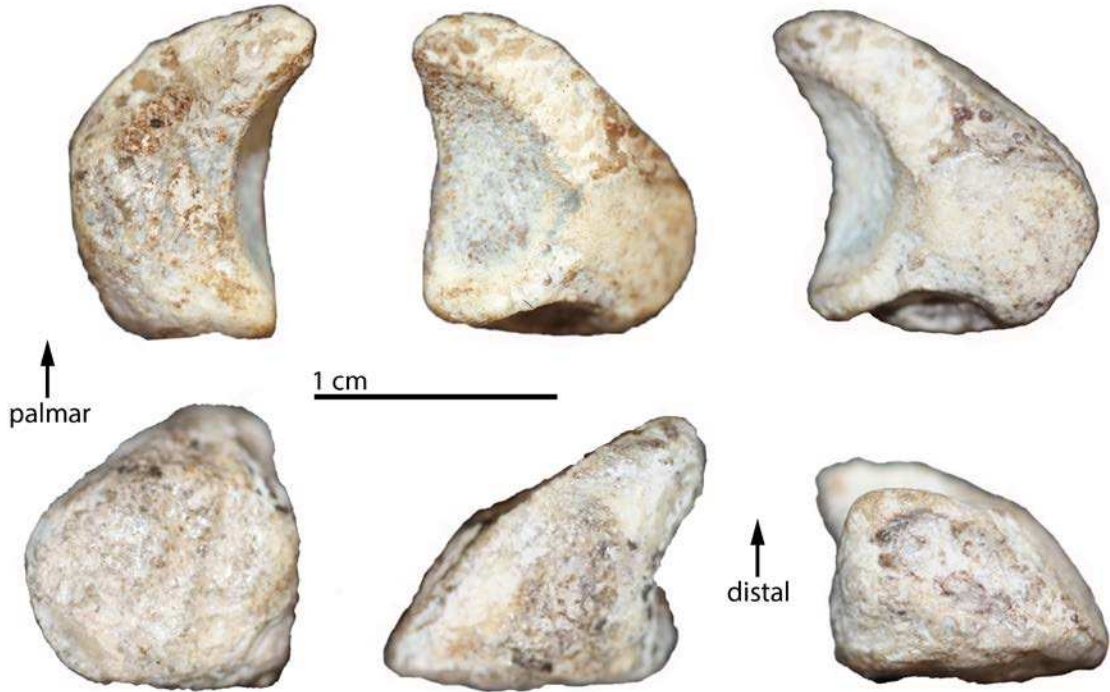
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1 *Figure 3. MH2 right scaphoid U.W. 88-158 in, from left to right, approximate dorsal view,*  
2 *showing most of radial facet, palmar view showing trapezium facet, distal view of trapezium-*  
3 *trapezoid facet, medial view of capitate and lunate facets, proximal view of non-articular surface,*  
4 *and lateral view showing radial and trapezium-trapezoid facets. In the first two images on the*  
5 *left, proximal is towards the top; in the latter four images, palmar is towards the top.*



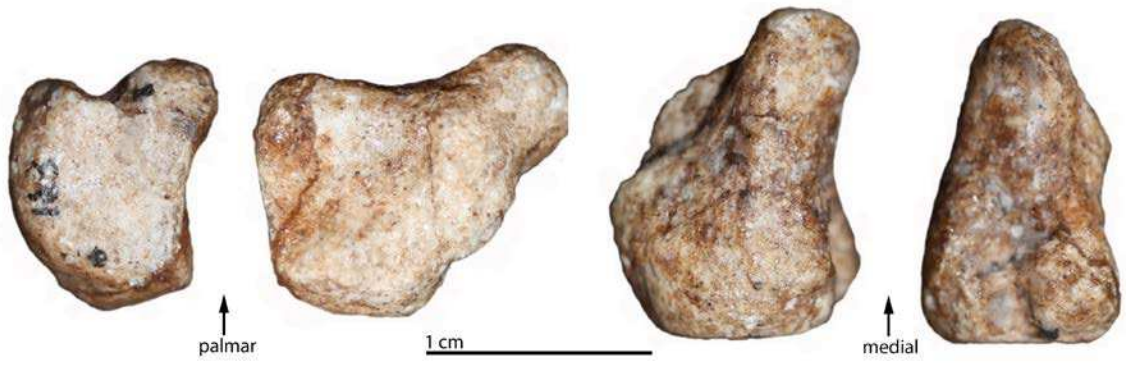
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1 *Figure 4. MH2 right lunate U.W. 88-159 in, from left to right in the top row, lateral view of*  
2 *scaphoid facet, distomedial view of capitate and triquetrum facets, medial view of triquetrum*  
3 *facet, and in the bottom row, proximal view of the radial facet, and palmar and dorsal views of*  
4 *non-articular surface.*



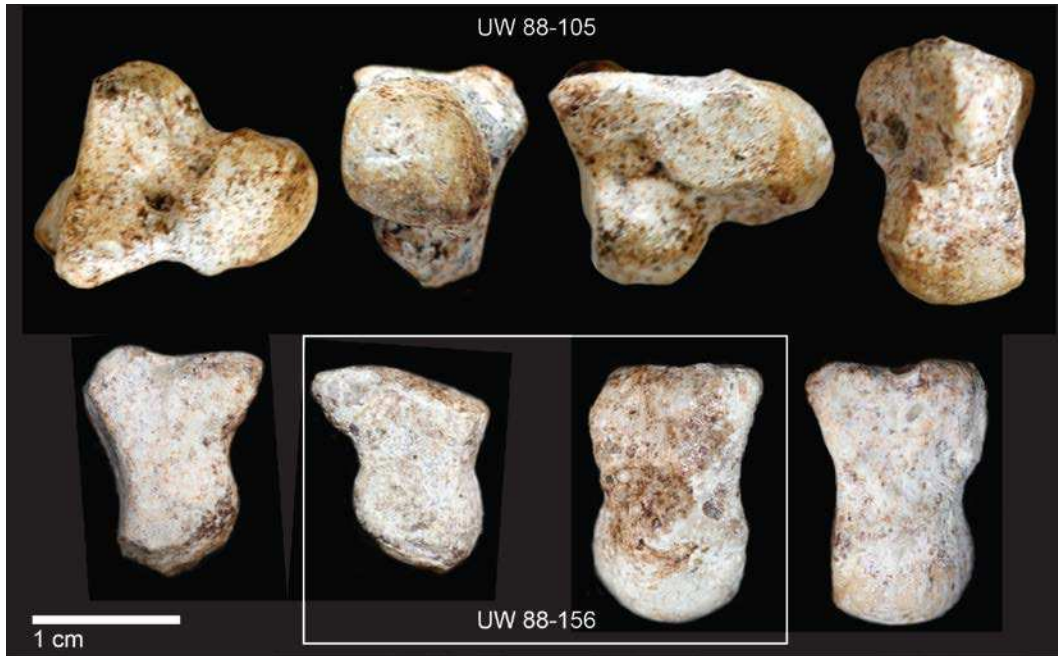
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1 *Figure 5. MH2 right triquetrum U.W. 88-157 in, from left to right, lateral view of lunate facet,*  
2 *distal view of hamate facet, medial view of non-articular surface, and palmar view of the pisiform*  
3 *facet.*



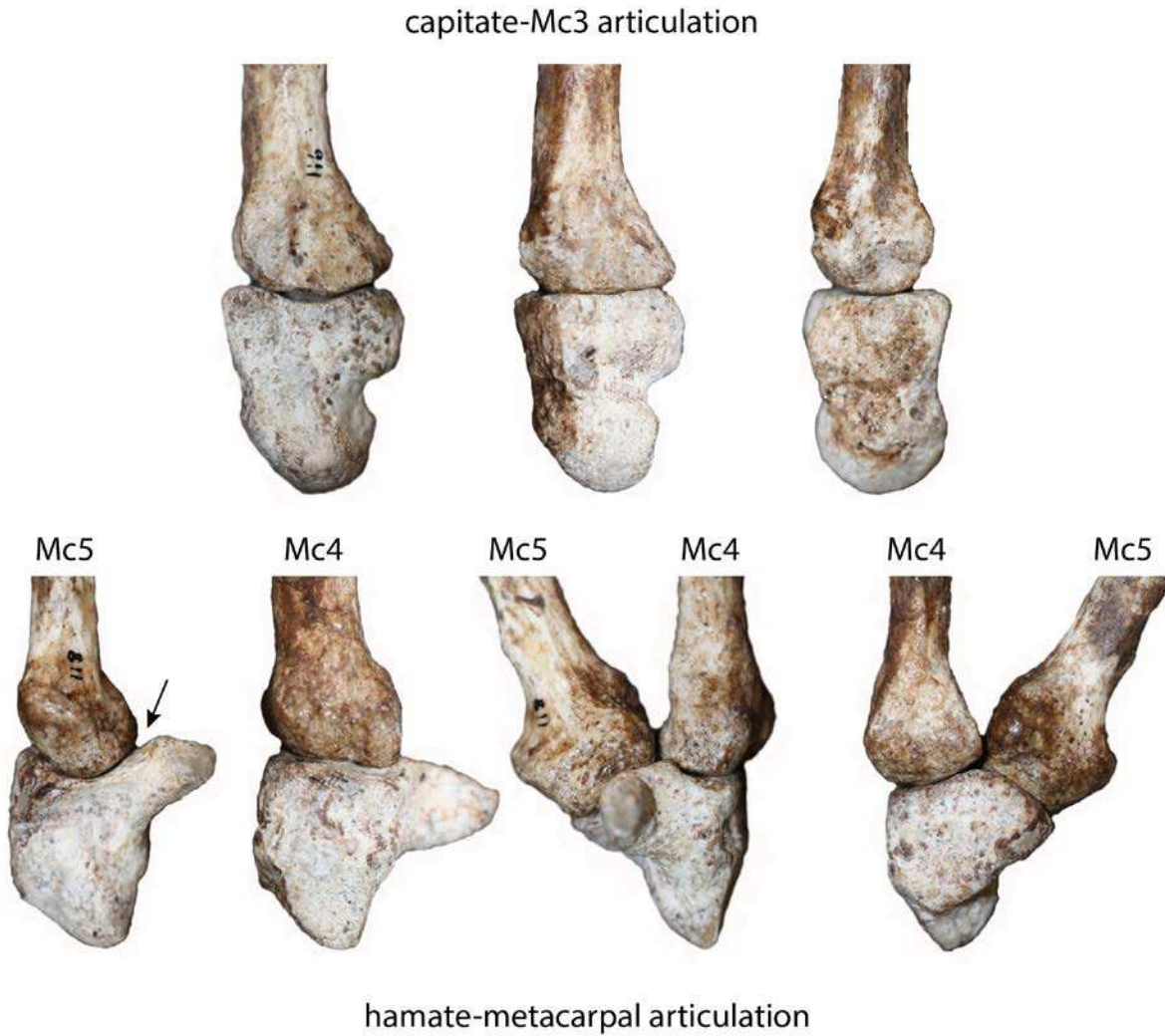
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1 *Figure 6. MH2 left (U.W. 88-105) and right (U.W. 88-156) capitates. Top, from left to right, U.W.*  
 2 *88-105 shown in lateral view of the scaphoid and second metacarpal facets, proximal view of*  
 3 *the scapholunate facet, medial view of hamate facet, palmar view of non-articular surface.*  
 4 *Bottom, U.W. 88-105 shown in distal view of third metacarpal facet (far left) and dorsal view of*  
 5 *non-articular surface (far right). In box, U.W. 88-156 shown in distal and dorsal views, missing a*  
 6 *portion of the distodorsolateral corner of the capitate body.*  
 7



8

1 *Figure 7. Carpometacarpal articulations in the MH2 right hand. Above, capitate-third metacarpal*  
 2 *(Mc3) articulation in medial (left), lateral (middle) and dorsal (right) views. Below, hamate-*  
 3 *metacarpal articulations, showing, from left to right, hamate-Mc5 in medial view, hamate-Mc4*  
 4 *articulation in lateral view, and hamate-Mc4-Mc5 articulation in palmar and dorsal views. The*  
 5 *arrow points to the space between palmar edge of the Mc5 facet and the dorsal curvature of the*  
 6 *hamulus that could accommodate the pisometacarpal ligament.*



7  
8  
9



1 *Figure 8. MH2 left (U.W. 88-106) and right (U.W. 88-95) hamates, above, shown in dorsal view*  
2 *of the non-articular surface, in which proximal is towards the top; middle, shown in medial view*  
3 *of triquetrum facet, and, below, lateral view of hamate facet, in which palmar is towards the top.*  
4



UW 88-106

UW 88-95

5

1 *Figure 9. MH2 right first metacarpal U.W. 88-119, shown in, from left to right, dorsal, palmar,*  
2 *lateral, medial, distal (far right, above) and proximal (far right, below) views. Extent of muscle*  
3 *insertions are highlighted with lines for the M. first dorsal interosseous (A) and M. opponens*  
4 *pollicis (B). Note the prominent palmar beak on the head of the Mc1 (C). Arrows highlight*  
5 *depressions flanking the palmar beak for the medial and lateral sesamoid bones.*



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1 *Figure 10. MH2 right second metacarpal U.W. 88-115 shown in, from left to right, palmar,*  
2 *medial, lateral and dorsal views.*  
3



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1 *Figure 11. MH1 U.W. 88-112 left and MH2 U.W. 88-116 right third metacarpals, both shown in,*  
2 *from left to right, lateral, palmar, medial, and dorsal views. At the far right, distal view of*  
3 *epiphyseal surface in U.W. 88-112 (top) and proximal view of base (bottom).*

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1 *Figure 12. MH2 right fourth metacarpal U.W. 88-117 shown in, from left to right, palmar, medial,*  
2 *lateral and dorsal views.*  
3



1 *Figure 13. MH2 right fifth metacarpal U.W. 88-118 shown in, from left to right, palmar, medial,*  
2 *lateral, dorsal, distal (far right, above) and proximal (far right, below) views. The extent of the M.*  
3 *opponens digiti minimii insertion is highlighted in the palmar view and the arrow points to a crest*  
4 *along the dorsal surface for the fourth M. dorsal interosseous insertion.*



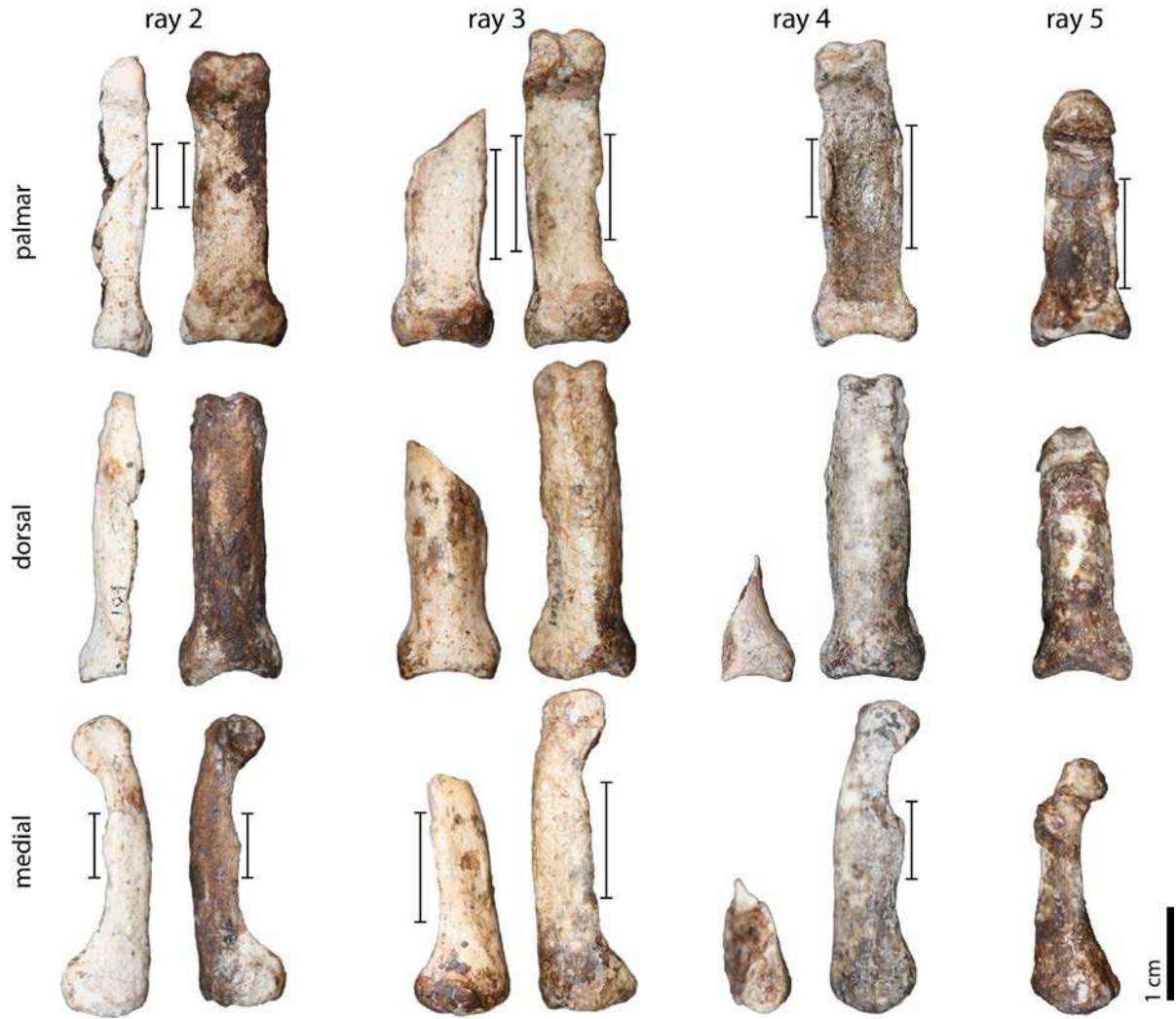
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1 *Figure 14. MH2 left (U.W. 88-91) and right (U.W. 88-160) pollical proximal phalanges shown in*  
2 *palmar (top, left), dorsal (top, right), lateral (middle, left), medial (middle, right), and proximal*  
3 *(bottom) views. The left first proximal phalanx (left side of each set of images) is better*  
4 *preserved than the right, particularly at the articular ends.*  
5



6

1 *Figure 15. MH2 non-pollical proximal phalanges, including U.W. 88-109 left PP2, U.W. 88-164*  
 2 *right PP2, U.W. 88-182 left PP3, U.W. 88-120 right PP3, U.W. 88-110 left PP4, U.W. 88-108*  
 3 *right PP4, and U.W. 88-121 right PP5. Extent of complete flexor sheath ridges are highlighted*  
 4 *by black lines in palmar and medial views.*



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1 *Figure 16. MH2 intermediate phalanges, shown in palmar (above) and medial (below) views,*  
 2 *except for U.W. 88-123, which is shown in lateral view due to matrix. Extent of complete flexor*  
 3 *sheath ridges are highlighted by black lines in palmar and medial views.*



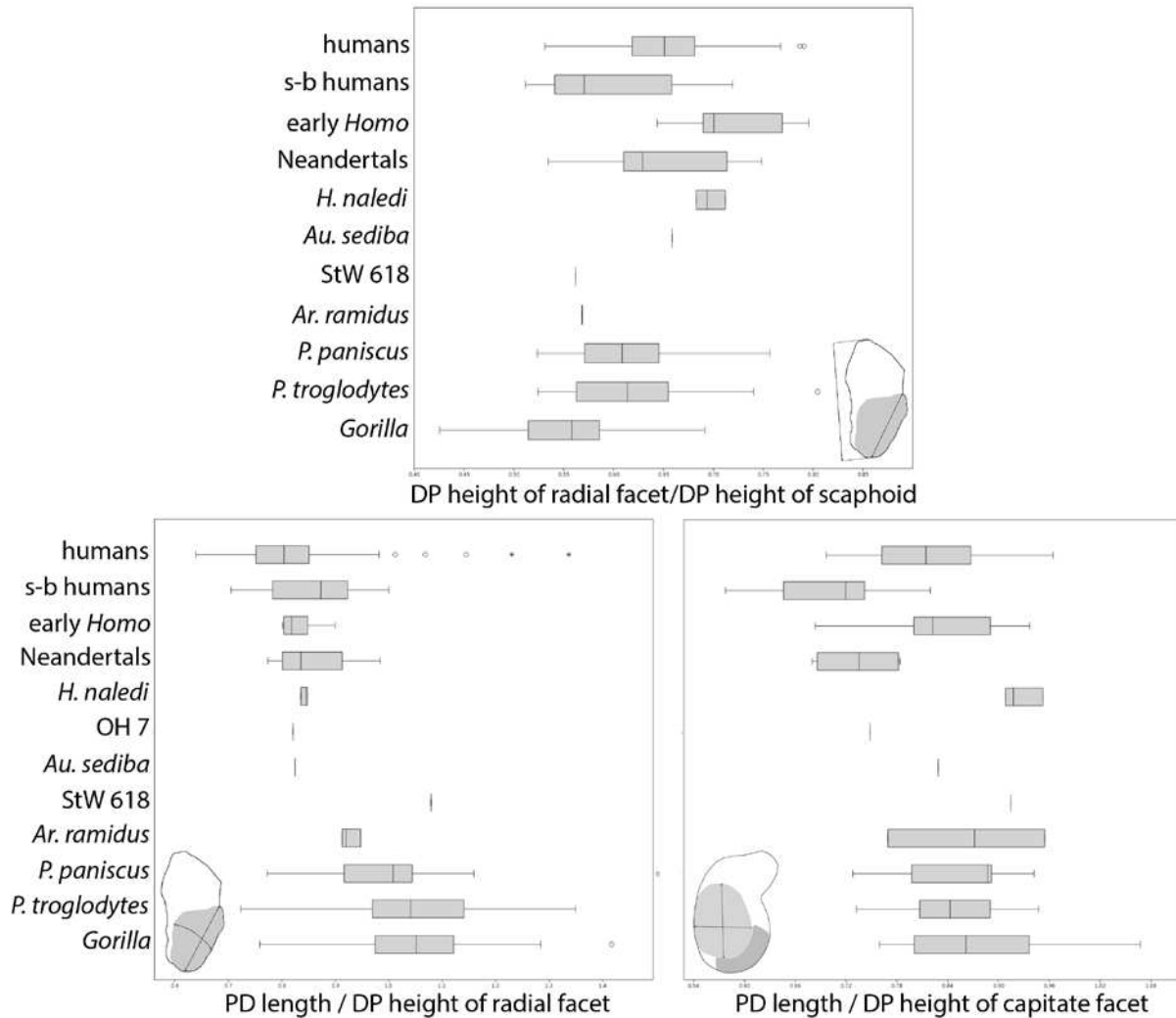
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1 *Figure 17. MH2 right distal pollical phalanx U.W. 88-124, shown in, from left to right, medial,*  
2 *dorsal, lateral and palmar views. Morphological features highlighted by arrows are the ridge for*  
3 *the attachment of the M. flexor pollicis longus (A), the proximal fossa (B), and the distal or*  
4 *ungual fossa (C).*



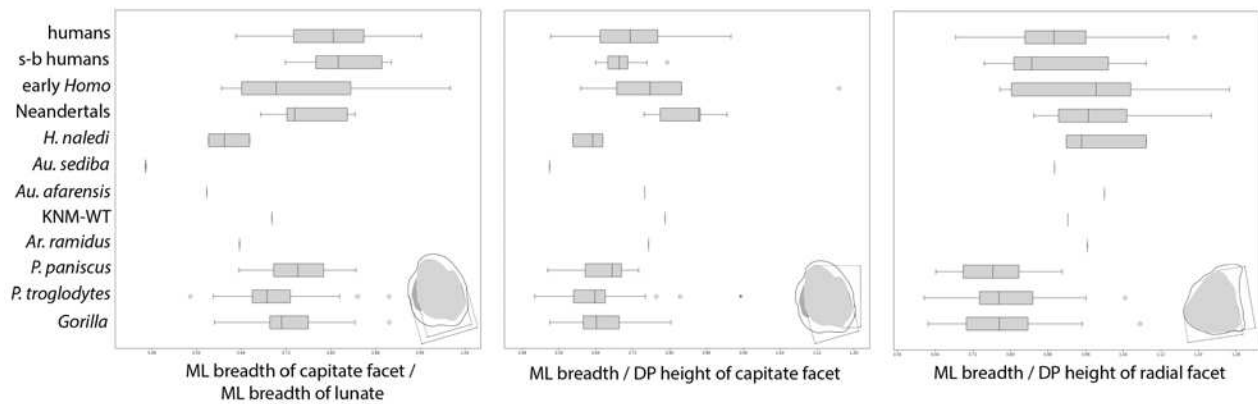
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1 Figure 18. Comparative analysis of the MH2 U.W. 88-158 scaphoid morphology. Box-and-  
 2 whisker plots of scaphoid shape showing dorsopalmar (DP) height of the radial facet relative to  
 3 DP height of the scaphoid body (top), proximodistal (PD) length relative to DP height of the  
 4 radial facet (bottom left) and capitulate facet (bottom right). Comparative extant sample includes  
 5 Gorilla sp. (n=56), *P. troglodytes* ssp. (n=46), *P. paniscus* (n=23), recent small-bodied (s-b)  
 6 Khoisan humans (n=16), recent humans (n=142). Comparative fossil sample composed of in Ar.  
 7 *ramidus* (n=2, ARA-VP-6/500-085 and -062), *Australopithecus* sp. StW 618, *H. habilis* FLK NN-  
 8 P of OH 7 hand, *H. naledi* (n=3, including U.W. 101-807, -1639 and -1726), Neandertals (n=8,  
 9 including Shanidar 3, 4, 6 and 8, Kebara 2, Tabun 1-152, La Ferrassie 1, and Regourdou 1) and  
 10 early *H. sapiens* ('early Homo') (n=7, including Dolní Věstonice 3, 14 and 16, Qafzeh 9, Ohalo  
 11 II, Barma Grande 2 and Arene Candide 2). Inset image shows how measurements were taken,  
 12 with palmar surface of scaphoid oriented towards the top of the page. For Ar. *ramidus*  
 13 specimens, all data were measured on original fossils by TLK, apart from the published data on  
 14 the DP height and PD length of the radial facet on ARA-VP-6/500-085 from Lovejoy et al.  
 15 (2009).



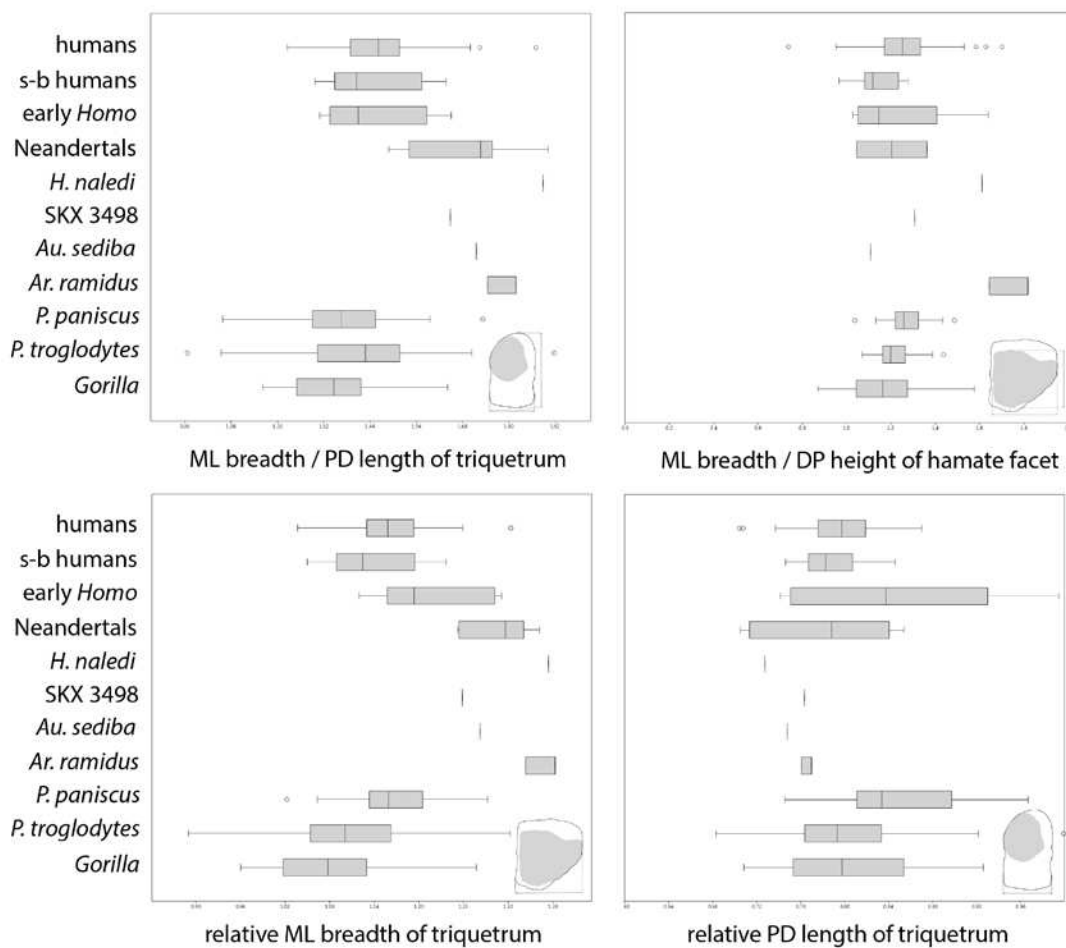
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1 Figure 19. Comparative analysis of the MH2 U.W. 88-159 lunate morphology. Box-and-whisker  
 2 plots of lunate shape, showing mediolateral (ML) breadth of the capitate facet relative to the ML  
 3 breadth of the lunate body (left), ML breadth relative to dorsopalmar (DP) height of capitate  
 4 facet (middle) and radial facet (right). Comparative extant sample includes Gorilla sp. (n=51), P.  
 5 troglodytes ssp. (n=38), P. paniscus (n=22), recent small-bodied (s-b) Khoisan humans (n=16),  
 6 recent humans (n=136). Comparative fossil sample composed of Ar. ramidus ARA-VP-6/500-  
 7 034, cf. Au. afarensis KNM-WT 22944-J, Au. afarensis A.L. 444-3, H. naledi (n=3, including  
 8 U.W. 101-418B, -1546, and -1732), Neandertals (n=6, including Shanidar 3 and 4, Kebara 2,  
 9 Tabun 1-162, Amud 1, and Neandertal 1), and early H. sapiens ('early Homo') (n=9, including  
 10 Dolní Věstonice 3, 14, 15 and 16, Qafzeh 9, Ohalo II, Barma Grande 2, Arene Candide 2, and  
 11 Tianyuan 1). Inset images show how measurements were taken, with palmar surface of lunate  
 12 oriented towards the top of the page. For Ar. ramidus ARA-VP-6/500-034, all data were  
 13 measured on original fossils by TLK, and DP height (13.7mm) and ML breadth (13.2mm) of the  
 14 radial facet values are adjusted from data reported from casts in Lovejoy et al. (2009).



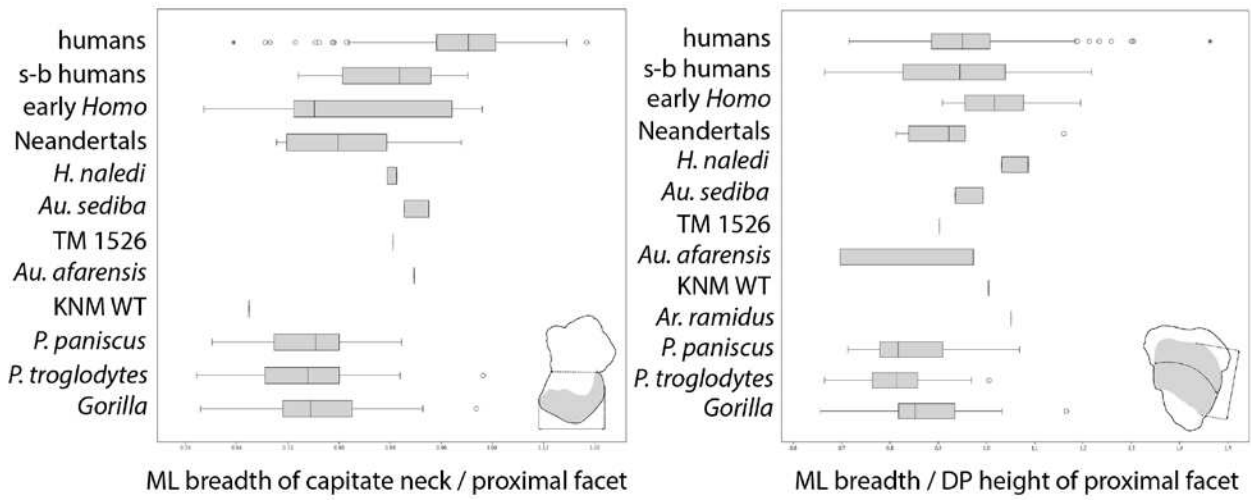
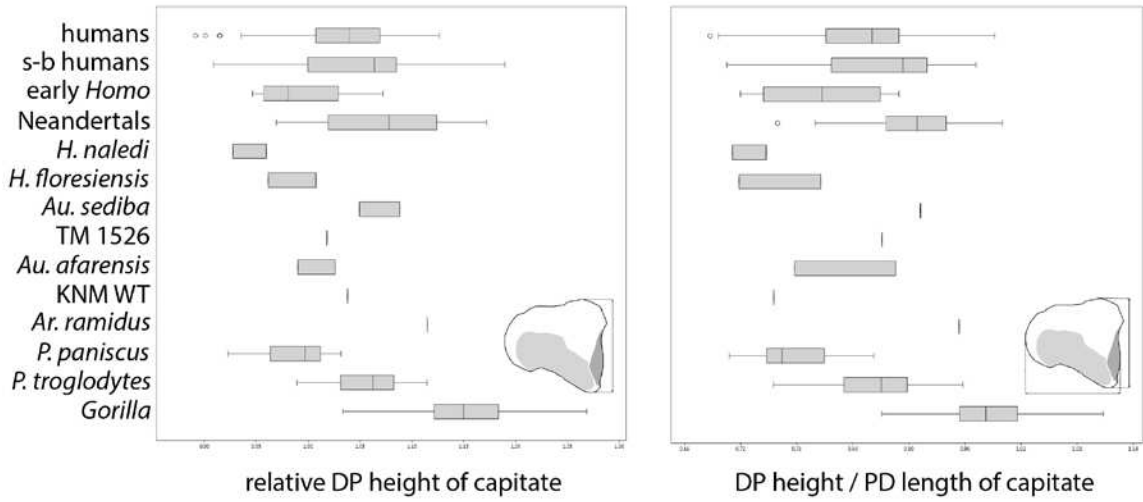
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1 *Figure 20. Comparative analysis of the MH2 U.W. 88-157 triquetrum morphology. Box-and-*  
 2 *whisker plots of triquetrum shape, showing mediolateral (ML) breadth relative to proximodistal*  
 3 *(PD) length of the triquetrum (top, left), ML breadth relative to dorsopalmar (DP) height of the*  
 4 *hamate facet (top, right), and relative (i.e. divided by a geometric mean) ML breadth and PD*  
 5 *length of the triquetrum body. Comparative extant sample includes Gorilla sp. (n=56), P.*  
 6 *troglodytes ssp. (n=45), P. paniscus (n=22), recent small-bodied (s-b) Khoisan humans (n=16),*  
 7 *recent humans (n=135). Comparative fossil sample composed of Ar. ramidus (n=2, ARA-VP-*  
 8 *6/500-029 and -068), Swartkrans Au. robustus or early Homo SKX 3498, H. naledi U.W. 101-*  
 9 *1727, Neandertals (n=5, including Kebara 2, Tabun 1-154, Amud 1, Regourdou 1, and La*  
 10 *Ferrassie 1), and early H. sapiens ('early Homo') (n=7, including Skhul IV and V, Qafzeh 8 and*  
 11 *9, Ohalo II, Barma Grande 2 and Arene Candide 2). For Ar. ramidus specimens, all data were*  
 12 *measured on original fossils by TLK. Inset images show how measurements were taken.*



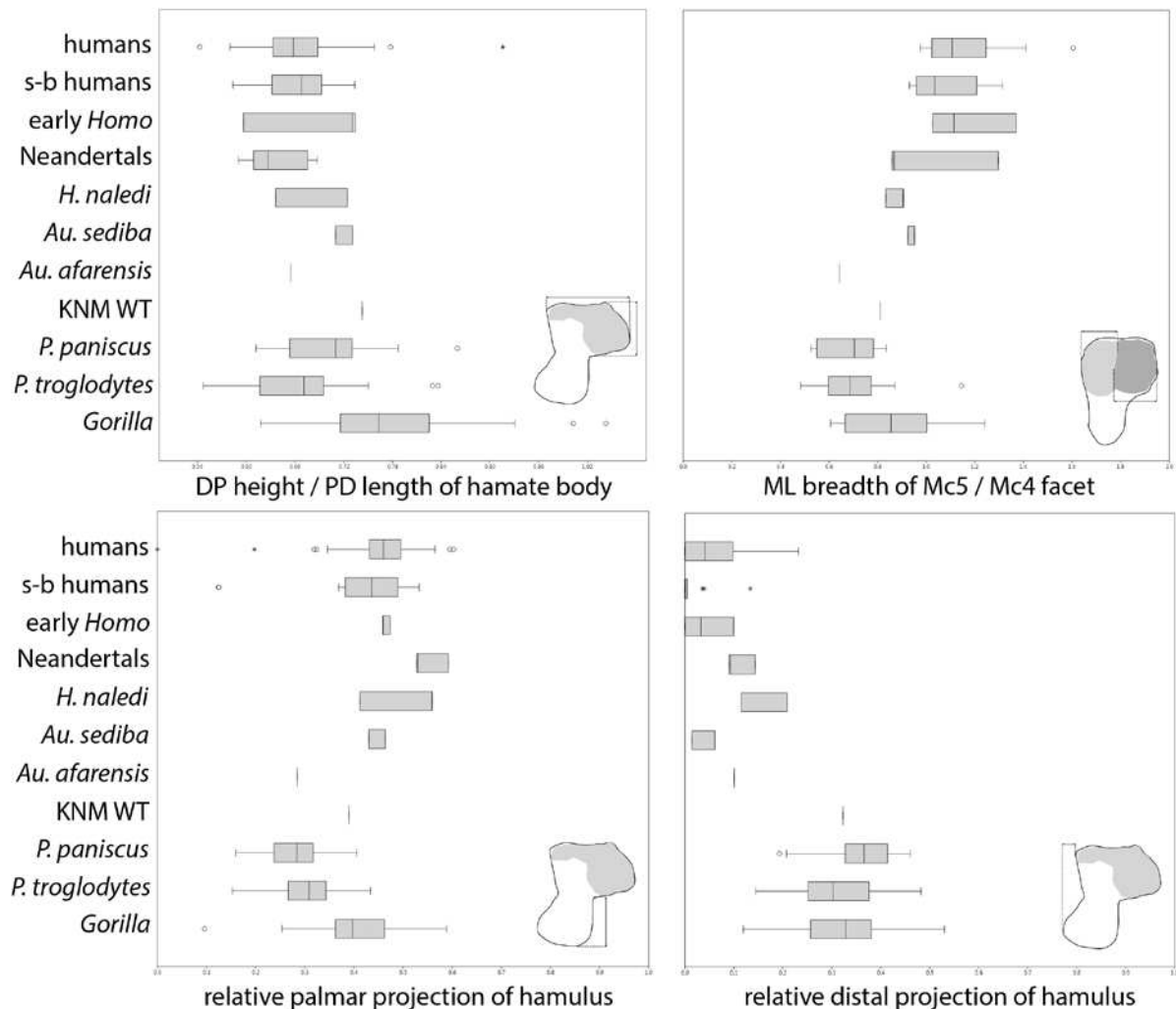
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 14 *Figure 21. Comparative analysis of the MH2 U.W. 88-105 and -156 capitate morphology. Box-*  
 15 *and-whisker plots of capitate shape, showing relative (i.e. divided by a geometric mean)*  
 16 *dorsopalmar (DP) height of capitate body (top, left), DP height relative to proximodistal (PD)*  
 17 *length of capitate body (top, right), capitate “waisting” measured as mediolateral (ML) breadth of*  
 18 *the capitate neck relative to ML breadth of the proximal facet (bottom, left), ML breadth relative*  
 19 *to DP height of proximal facet. Comparative extant sample includes Gorilla sp. (n=52), P.*

1 troglodytes ssp. ( $n=46$ ), *P. paniscus* ( $n=21$ ), recent small-bodied (*s-b*) Khoisan humans ( $n=25$ ),  
 2 recent humans ( $n=167$ ). Comparative fossil sample composed of *Ar. ramidus* ARA-VP-6/500-  
 3 058 [using published values from Lovejoy et al. (2009)], cf. *Au. afarensis* KNM-WT 22944-H, *Au.*  
 4 *afarensis* ( $n=2$ , A.L. 288-1w and 333-40, *Au. africanus* TM 1526, *H. floresiensis* ( $n=2$ , LB1-45  
 5 and LB 20), *H. naledi* ( $n=2$ , U.W. 101-930 and -1730, Neandertals ( $n=10$ , including Shanidar 4,  
 6 Kebara 2, Tabun 1, Amud 1, La Ferrassie 1 and 2, Moula Guercy M-F1-461, La Chapelle,  
 7 Krapina 200, and Neandertal 1), and early *H. sapiens* ('early Homo') ( $n=7$ , including Dolní  
 8 Věstonice 15 and 16, Qafzeh 9, Ohalo II, Tianyuan 1, Barma Grande 2 and Arene Candide 2).  
 9 Inset images show how measurements were taken.



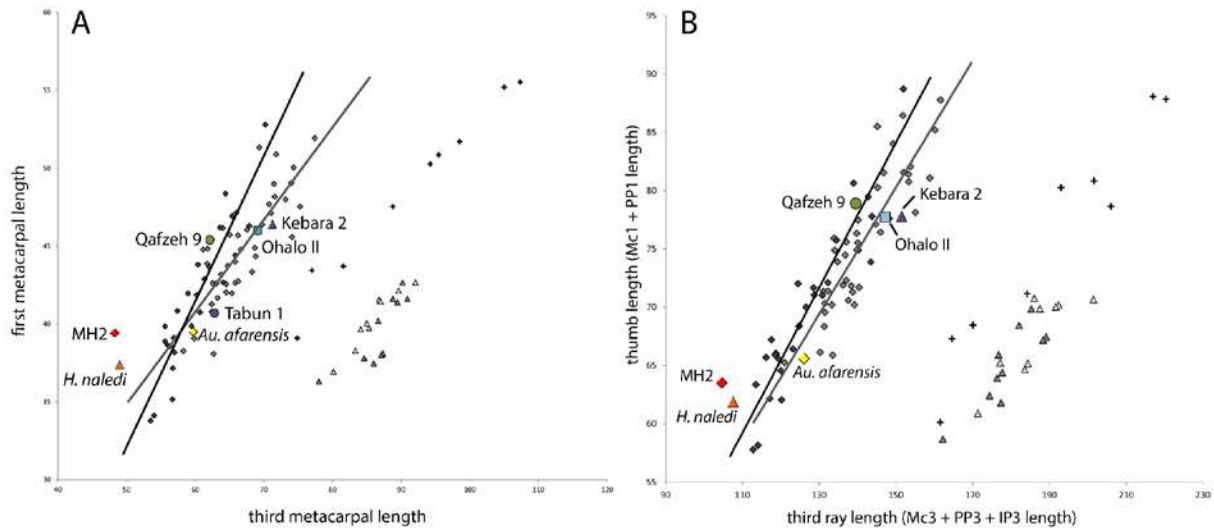
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1 Figure 22. Comparative analysis of the MH2 U.W. 88-106 (left) and -95 (right) hamate  
 2 morphology. Box-and-whisker plots of hamate shape, showing dorsopalmar (DP) height relative  
 3 to proximodistal (PD) length of hamate body (excluding hamulus; top, left), mediolateral (ML)  
 4 breadth of the fifth relative to the fourth metacarpal facets (top, right), relative (i.e. divided by  
 5 geometric mean) palmar projection (bottom, left) and distal projection (bottom, right) of the  
 6 hamulus. For the latter, several *H. sapiens* specimens show no distal projection of the hamulus.  
 7 Comparative extant sample includes *Gorilla* sp. ( $n=51$ ), *P. troglodytes* ssp. ( $n=42$ ), *P. paniscus*  
 8 ( $n=23$ ), recent small-bodied (s-b) Khoisan humans ( $n=16$ ), recent humans ( $n=138$ ).  
 9 Comparative fossil sample composed of *cf. Au. afarensis* KNM-WT 22944-I, *Au. afarensis* A.L.  
 10 333-50, *H. naledi* ( $n=2$ , including U.W. 101-1640 and -1729, Neandertals ( $n=5$ , including  
 11 Shanidar 3, Kebara 2, Regourdou 1, Tabun 1-154 and Tabun 3), and early *H. sapiens* ('early  
 12 Homo') ( $n=4$ , including Dolní Věstonice 3, Qafzeh 9, Ohalo II, and Arene Candide 2). Inset  
 13 images show how measurements were taken.



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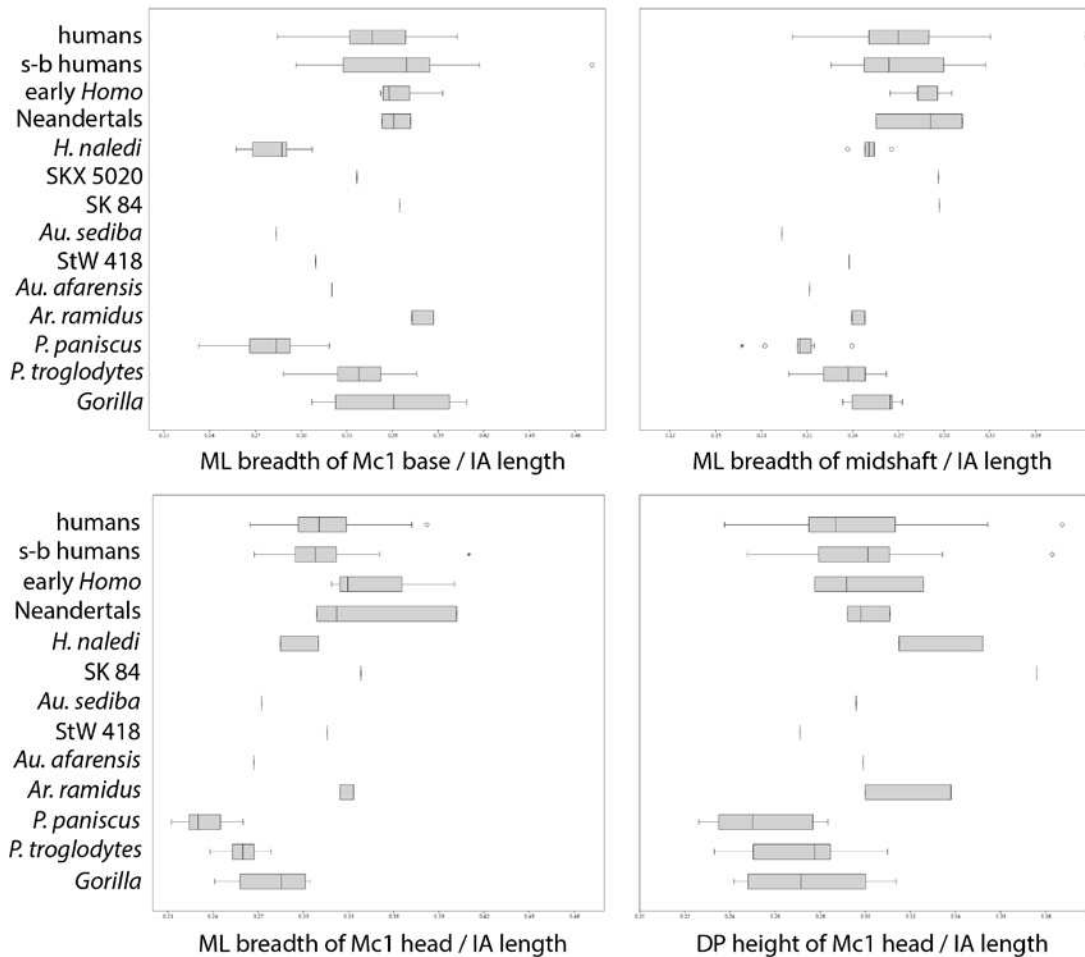
1 Figure 23. Relative thumb length in MH2. (A) First metacarpal (Mc1) length against third  
 2 metacarpal (Mc3) length and (B) thumb length (Mc1 length + proximal phalanx (PP) 1 length)  
 3 against third ray length (Mc3 length + PP3 length + intermediate phalanx (IP) 3 length), in  
 4 comparison to recent humans (gray diamonds), small-bodied recent humans (black diamonds),  
 5 *P. paniscus* (dark triangles), *P. troglodytes* ssp. (light triangles), and Gorilla ssp. (crosses). All  
 6 fossil values are derived from hand bones associated with a single individual apart from the *Au.*  
 7 *afarensis*, which is a composite of several individuals (Marzke 1983; Alba et al. 2003). Linear  
 8 regression lines shown for recent humans (gray) and small-bodied humans (black). The *Au.*  
 9 *sediba* MH2 hand has a relatively long Mc1 and thumb for its small hand size, falling outside the  
 10 range of variation of recent humans, and is most similar to Hand 1 of *H. naledi*.



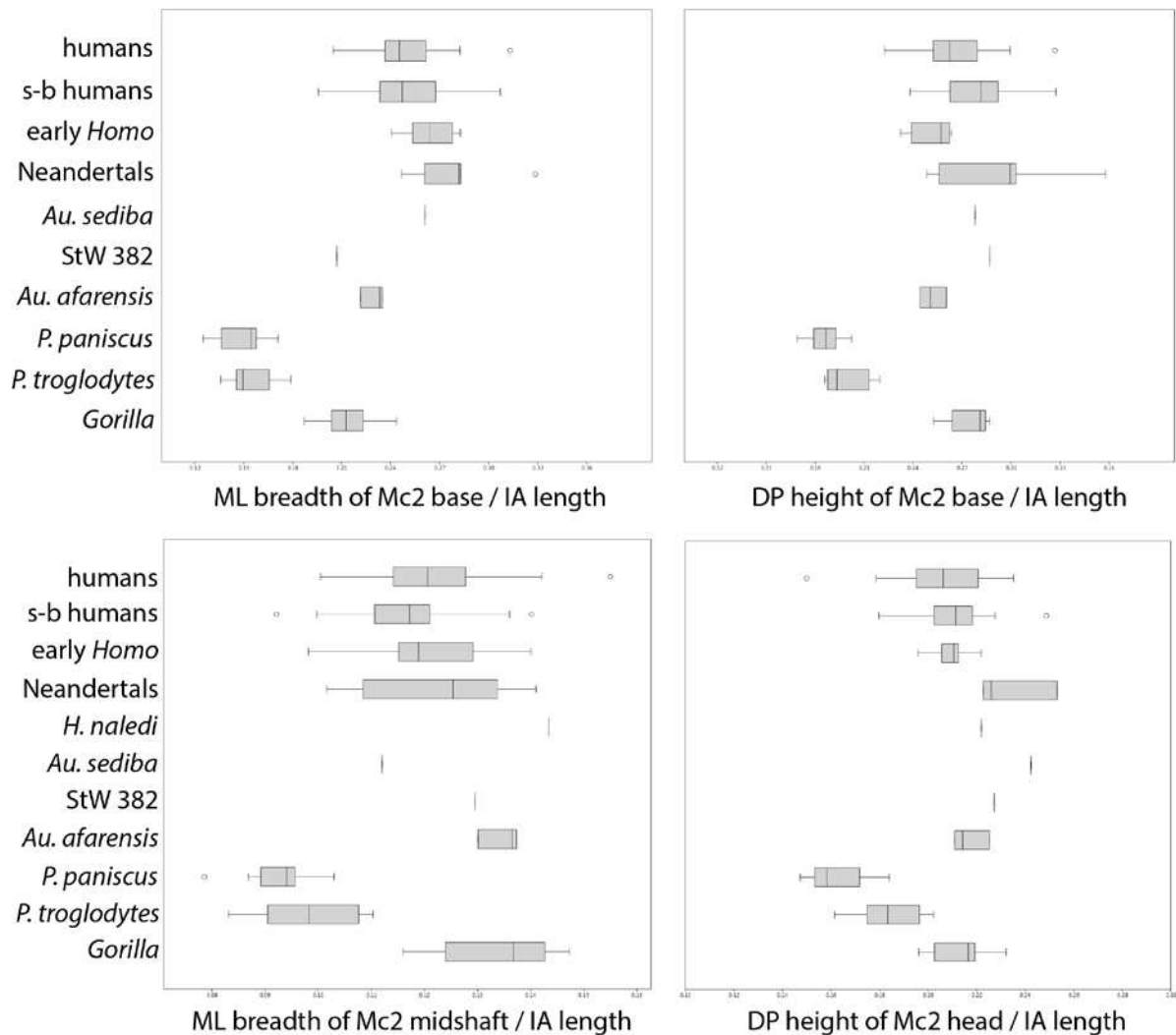
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1 Figure 24. Comparative analysis of the MH2 U.W. 88-119 first metacarpal morphology. Box-  
 2 and-whisker plots of first metacarpal (Mc1) shape, in which each variable is shown as a ratio of  
 3 interarticular (IA) length: mediolateral (ML) breadth of the Mc1 base (top, left), midshaft (top,  
 4 right) and Mc1 head (bottom left), as well as the dorsopalmar (DP) height of the Mc1 head  
 5 (bottom, right). Comparative extant sample includes Gorilla sp. (n=9), P. troglodytes ssp.  
 6 (n=10), P. paniscus (n=11), recent small-bodied (s-b) Khoisan humans (n=25), recent humans  
 7 (n=43). Comparative fossil sample composed of Ar. ramidus (n=2, ARA-VP-6/500-015 and  
 8 ARA-VP-6/1638), Au. afarensis A.L. 333w-39, Au. africanus StW 418, Au. robustus/early Homo  
 9 SK 84 and SKX 5020, H. naledi (n=6, including U.W. 101-007, -270, -917, -1282, -1321, and  
 10 1641), Neandertals (n=4, including Shanidar 4, Kebara 2, Amud 1 and Tabun 1), and early H.  
 11 sapiens ('early Homo') (n=5, including Dolní Věstonice 16, Qafzeh 9, Ohalo II, Barma Grande 2  
 12 and Arene Candide 2). Note that interarticular length is estimated for SKX 5020, as the proximal  
 13 end is not preserved and thus results should be interpreted with caution. Regarding Ar. ramidus  
 14 specimens, all data are taken published values in Lovejoy et al. (2009) apart from values for DP  
 15 height of the base ([12mm] and midshaft (6.3mm) and ML breadth of the head (11mm) in ARA-  
 16 VP-6/500-015 and DP height of head (12.4mm) in ARA-VP-6/1638, which have been adjusted  
 17 after re-measurement on original fossils. Interarticular length of both Ar. ramidus specimens was  
 18 measured directly on the original fossils by TLK.

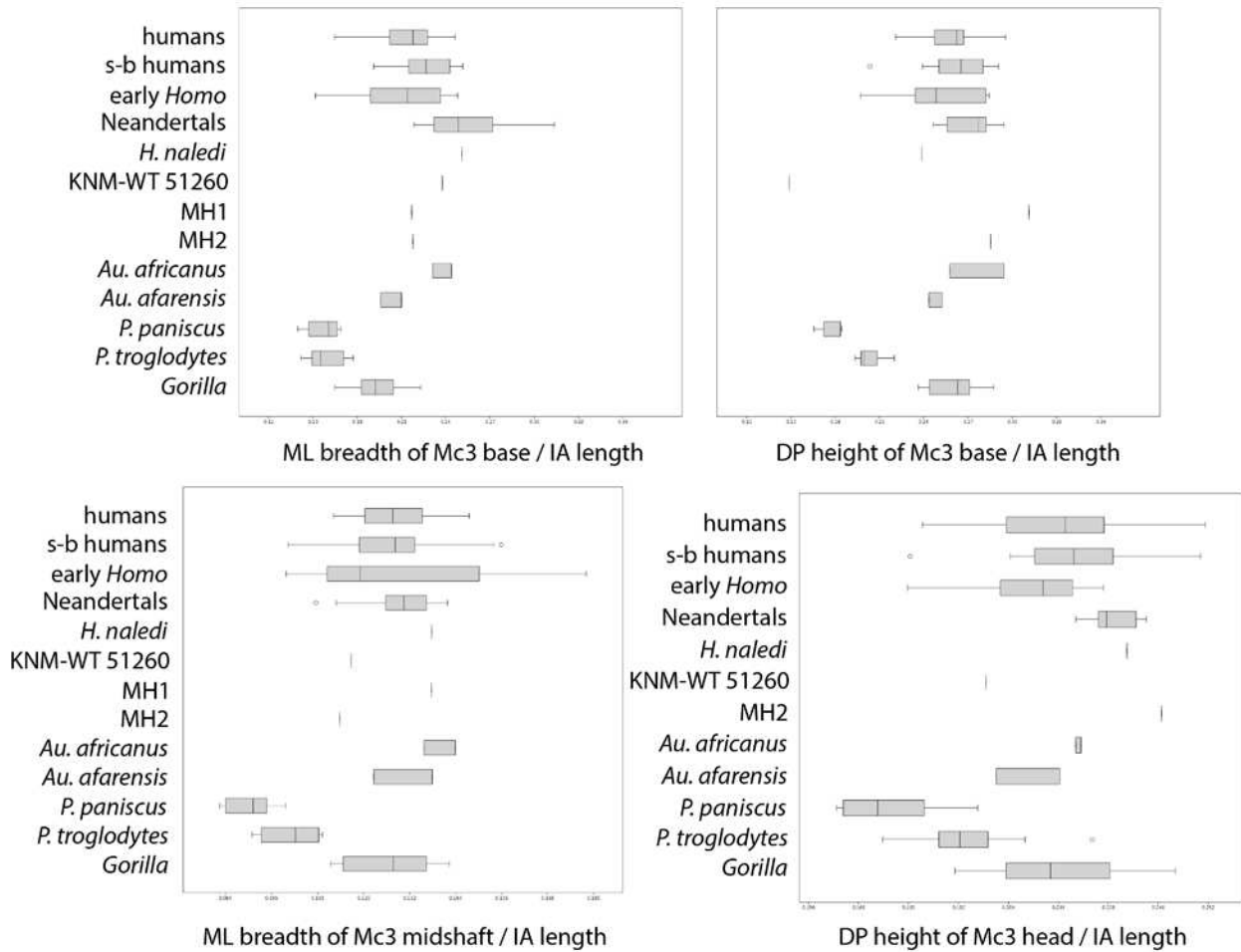


1 Figure 25. Comparative analysis of the MH2 U.W. 88-115 second metacarpal morphology. Box-  
 2 and-whisker plots of second metacarpal (Mc2) shape, in which each variable is shown as a ratio  
 3 of interarticular (IA) length: mediolateral (ML) breadth (top, left) and dorsopalmar (DP) height  
 4 (top, right) of the Mc2 base, ML breadth at midshaft (bottom, left) and DP height of the head  
 5 (bottom, right). Comparative extant sample includes Gorilla sp. (n=10), P. troglodytes ssp.  
 6 (n=11), P. paniscus (n=11), recent small-bodied (s-b) Khoisan humans (n=25), recent humans  
 7 (n=45). Comparative fossil sample composed of Au. afarensis (n=3, A.L. 333-48, A.L. 438-If and  
 8 -Ie, Au. africanus StW 382, H. naledi U.W. 101-1320, Neandertals (n=11, La Chapelle, La  
 9 Ferrassie 1 and 2, Regourdou 1, Shandiar 4 and 5, Spy 2 and 21A, Tabun 1-160, Kebara 2, and  
 10 Moula-Guercy M-G2-648), and early H. sapiens ('early Homo') (n=8, Dolní Věstonice 13, 15, 16  
 11 and 59, Pavlov 31, Qafzeh 9, Ohalo II, and Arene Candide 2).



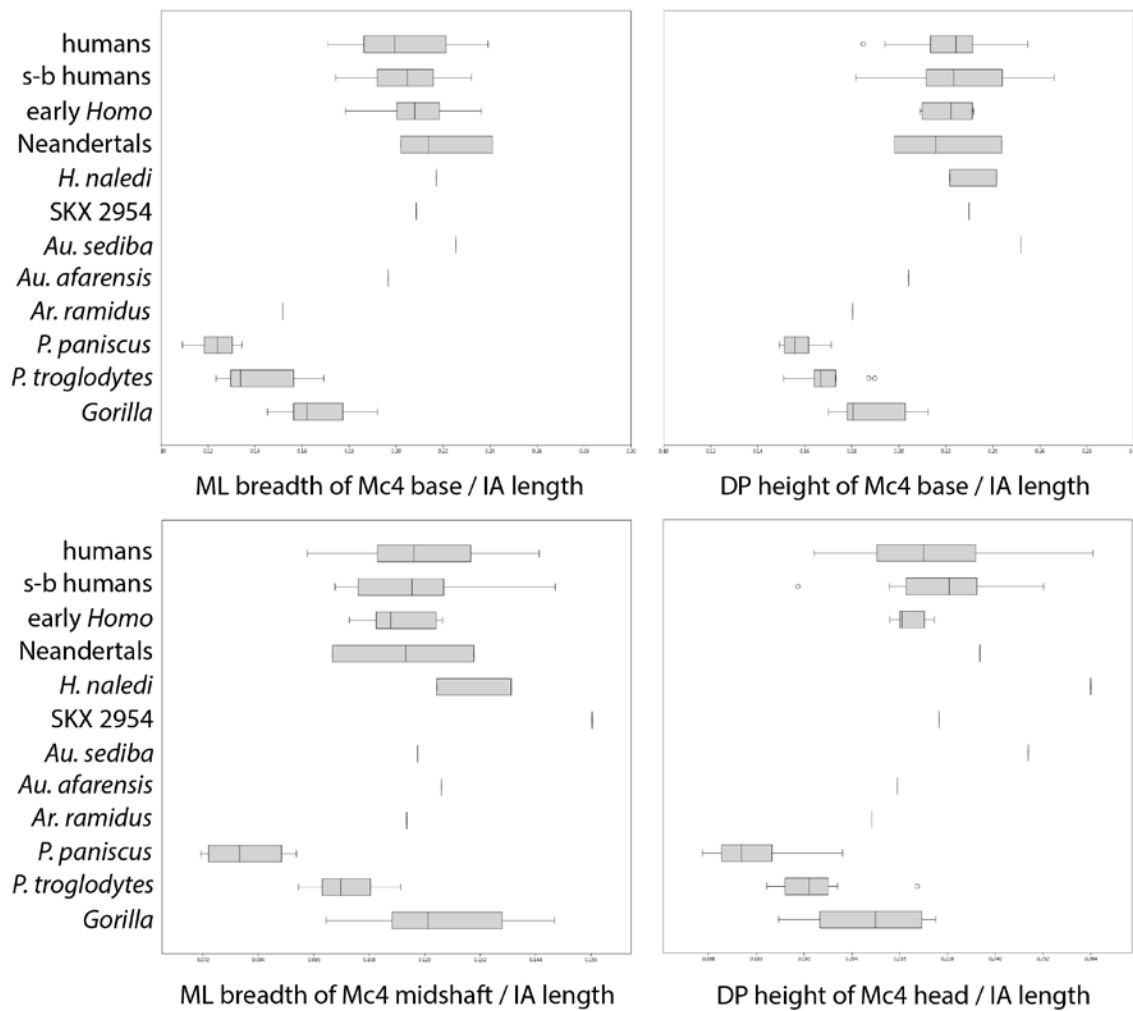
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1 Figure 26. Comparative analysis of the MH1 U.W. 88-112 and MH2 U.W. 88-116 third  
 2 metacarpal morphology. Box-and-whisker plots of third metacarpal (Mc3) shape, in which each  
 3 variable is shown as a ratio of interarticular (IA) length: mediolateral (ML) breadth (top, left) and  
 4 dorsopalmar (DP) height (top, right) of the Mc3 base (top, left), ML breadth at midshaft (bottom,  
 5 left) and DP height of the head (bottom, right). Comparative extant sample includes Gorilla sp.  
 6 ( $n=11$ ), *P. troglodytes* ssp. ( $n=12$ ), *P. paniscus* ( $n=11$ ), recent small-bodied (s-b) Khoisan  
 7 humans ( $n=25$ ), recent humans ( $n=42$ ). Comparative fossil sample composed of *Au. afarensis*  
 8 ( $n=2$ , A.L. 333-16 and A.L. 438-1d), *Au. africanus* ( $n=2$ , StW 64 and 68), probable *H. erectus*  
 9 KNM-WT 51260 (Ward et al. 2013), *H. naledi* U.W. 101-1319, Neandertals ( $n=11$ , La Chapelle,  
 10 La Ferrassie 1 and 2, Regourdou 1, Shanidar 4 and 6, Kebara 2, Amud 1, Moula-Guercy M-D3-  
 11 768, Spy 22A and Tabun 1-151), and early *H. sapiens* ('early Homo') ( $n=8$ , Dolní Věstonice 13,  
 12 16 and 58, Qafzeh 8 and 9, Ohalo II, Barma Grande 2 and Arene Candide 2). Note that  
 13 interarticular length was estimated for La Chapelle and Amud 1 (Niewoehner et al. 1997), and,  
 14 importantly, for MH1 U.W. 88-112, which is missing its proximal epiphysis. All variables were  
 15 also analysed using total length that includes the Mc3 styloid process in *H. sapiens* and  
 16 Neandertals and relative relationships among taxa did not change.



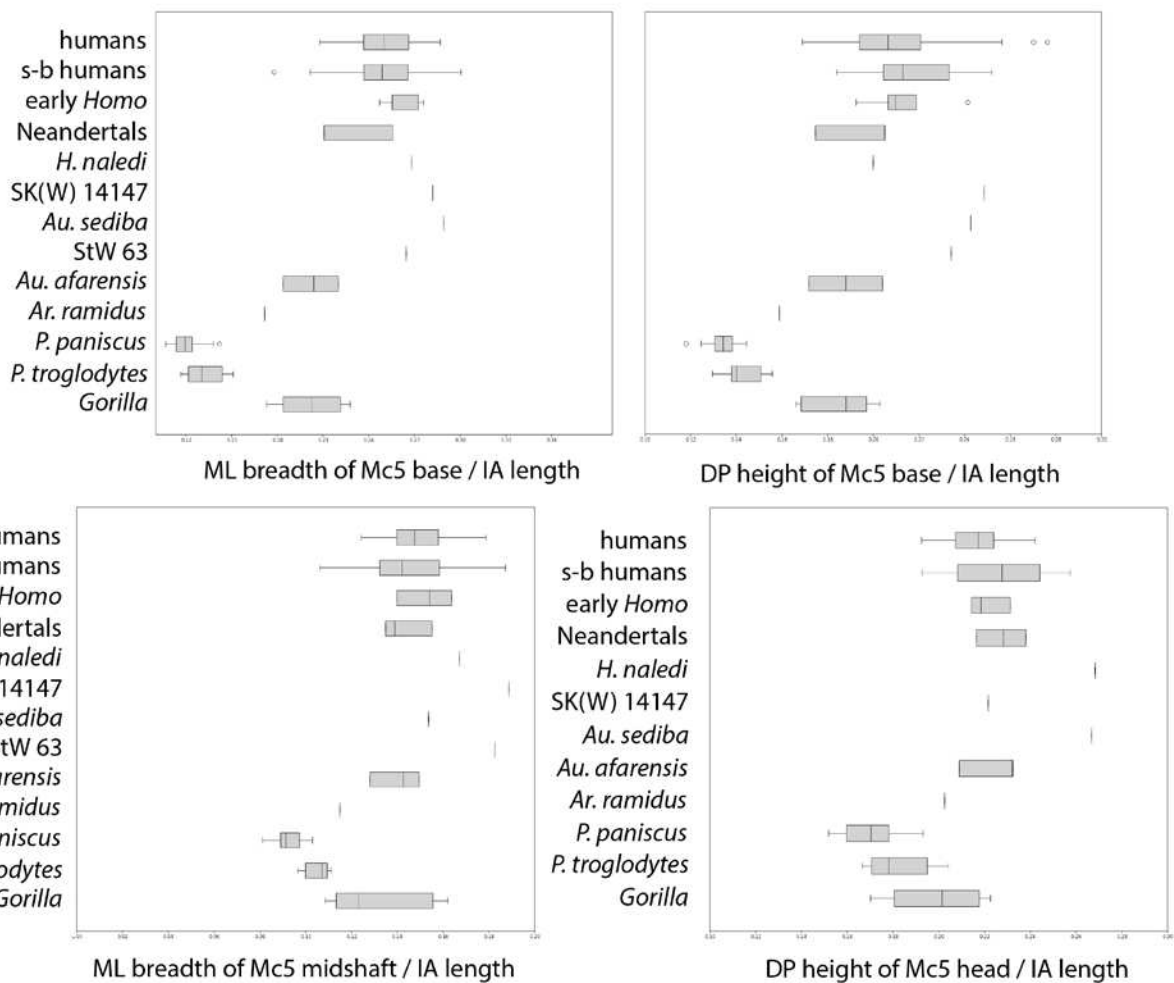
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1 Figure 27. Comparative analysis of the MH2 U.W. 88-117 fourth metacarpal morphology. Box-  
 2 and-whisker plots of fourth metacarpal (Mc4) shape, in which each variable is shown as a ratio  
 3 of interarticular (IA) length: mediolateral (ML) breadth (top, left) and dorsopalmar (DP) height  
 4 (top, right) of the Mc4 base (top, left), ML breadth at midshaft (bottom, left) and DP height of the  
 5 head (bottom, right). Comparative extant sample includes Gorilla sp. (n=11), P. troglodytes ssp.  
 6 (n=12), P. paniscus (n=11), recent small-bodied (s-b) Khoisan humans (n=25), recent humans  
 7 (n=40). Comparative fossil sample composed of Ar. ramidus ARA-VP-7/2G, Au. afarensis A.L.  
 8 333-56, Au. robustus/early Homo SKX 2954, H. naledi U.W. 101-1318 and U.W. 102-028,  
 9 Neandertals (n=4, Shanidar 4 and 5, Spy 22C, and Tabun 1-166), and early H. sapiens ('early  
 10 Homo') (n=5, Dolní Věstonice 16, Qafzeh 9, Ohalo II, Barma Grande 2 and Arene Candide 2).  
 11 Regarding Ar. ramidus ARA-VP-7/2G, all data are taken published values in Lovejoy et al.  
 12 (2009) apart from DP height of the base (10.1mm), which has been adjusted from the published  
 13 value after re-measurement on the original fossil, and interarticular length (56mm), which was  
 14 measured on the original fossil by TLK and G. Suwa.



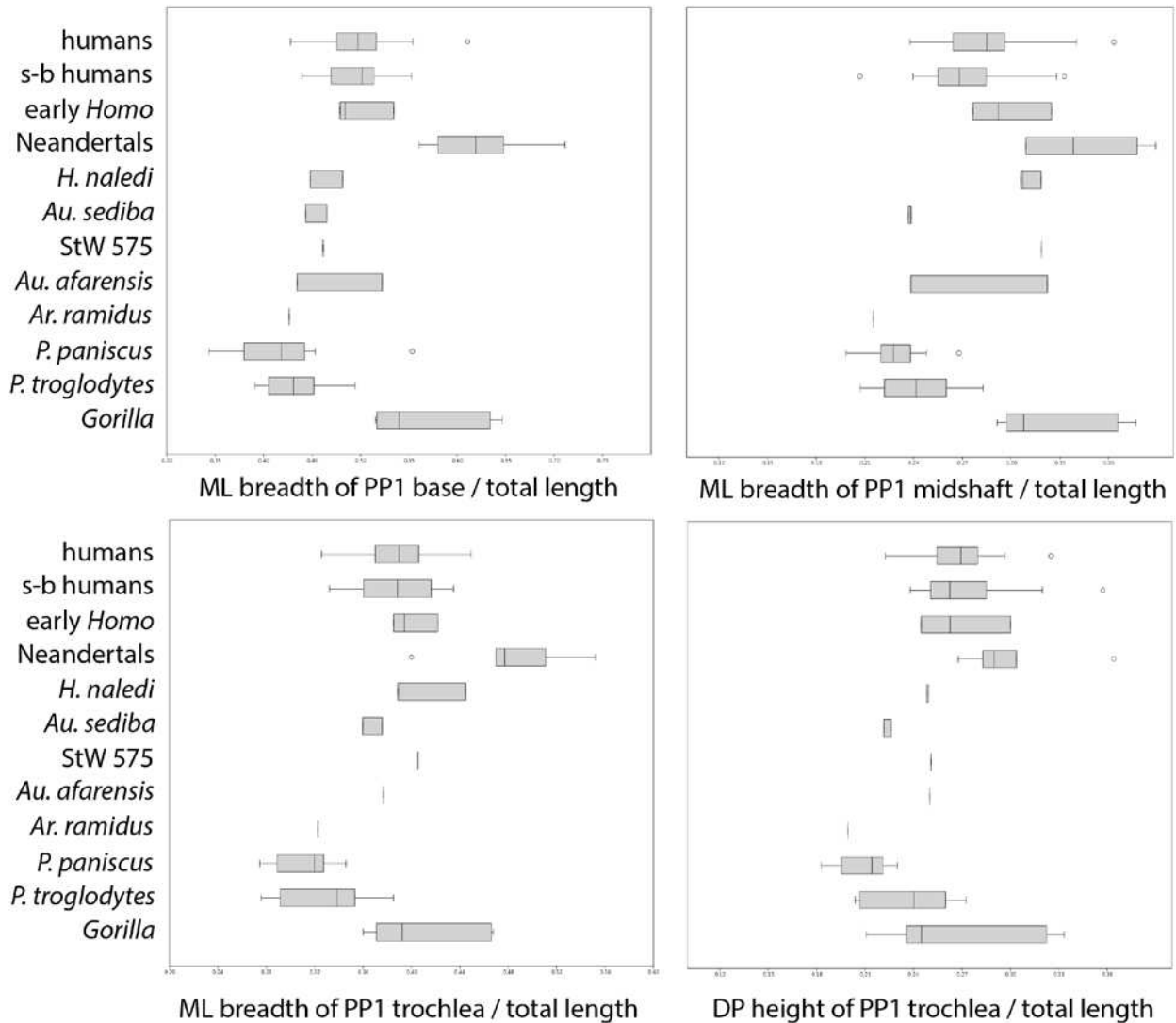
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1 Figure 28. Comparative analysis of the MH2 U.W. 88-118 fifth metacarpal morphology. Box-  
 2 and-whisker plots of fifth metacarpal (Mc5) shape, in which each variable is shown as a ratio of  
 3 interarticular (IA) length: mediolateral (ML) breadth (top, left) and dorsopalmar (DP) height (top,  
 4 right) of the Mc5 base, ML breadth at midshaft (bottom, left) and DP height of the head (bottom,  
 5 right). Comparative extant sample includes Gorilla sp. (n=9), P. troglodytes ssp. (n=11), P.  
 6 paniscus (n=11), recent small-bodied (s-b) Khoisan humans (n=25), recent humans (n=37).  
 7 Comparative fossil sample composed of Ar. ramidus ARA-VP-6/500-036, Au. afarensis (n=3,  
 8 A.L. 333-14, -89 and -141), Au. africanus StW 63, Au. robustus/early Homo SK(W) 14147 (SKW  
 9 27), H. naledi U.W. 101-1309, Neandertals (n=3, Shandiar 4 and 5, and Tabun 1-164), and  
 10 early H. sapiens ('early Homo') (n=5, Dolní Věstonice 16, Qafzeh 9, Ohalo II, Barma Grande 2,  
 11 and Arene Candide 2). Regarding Ar. ramidus, all data are derived from published values in  
 12 Lovejoy et al. (2009).



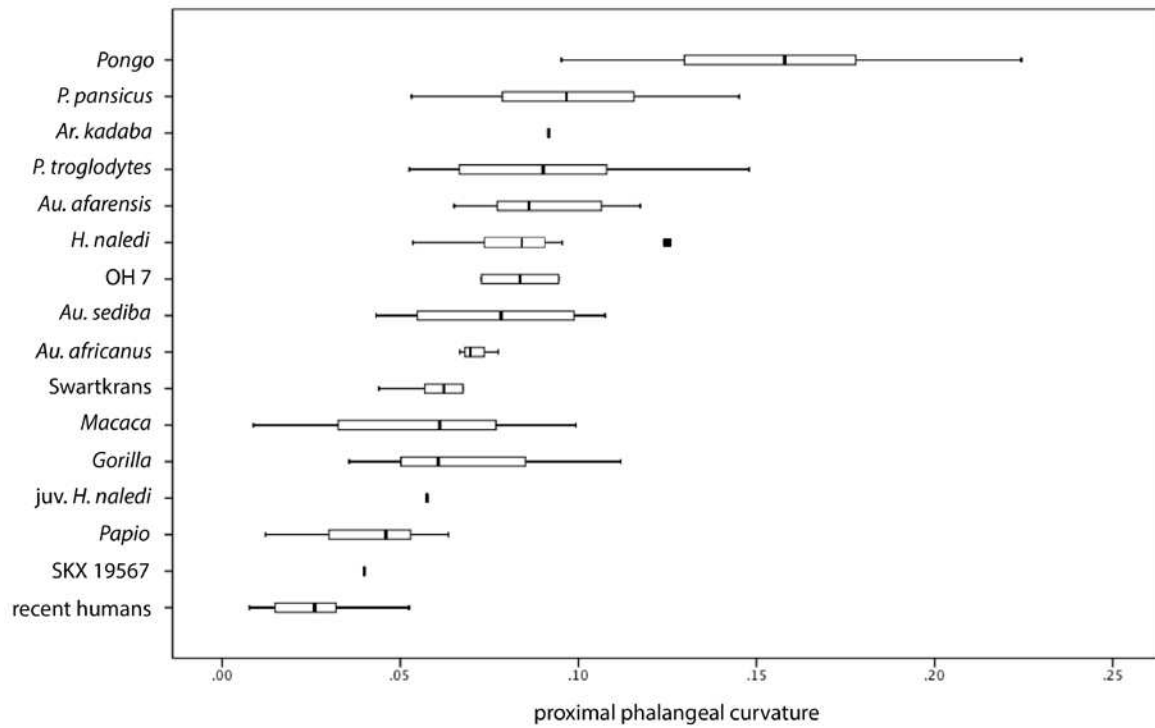
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1 Figure 29. Comparative analysis of the MH2 pollical proximal phalanx (left, U.W. 88-91 and  
 2 right, U.W. 88-160) morphology. Box-and-whisker plots of pollical proximal phalanx (PP1)  
 3 shape, in which each variable is shown as a ratio of maximum or total length: mediolateral (ML)  
 4 breadth of the PP1 base (top, left), midshaft (top, right) and distal trochlea (bottom, left) and  
 5 dorsopalmar (DP) height of the trochlea (bottom, right). Comparative extant sample includes  
 6 Gorilla sp. (n=8), P. troglodytes ssp. (n=10), P. paniscus (n=10), recent small-bodied (s-b)  
 7 Khoisan humans (n=24), recent humans (n=38). Comparative fossil sample composed of Ar.  
 8 ramidus ARA-VP-7/21, Au. afarensis (n=2, A.L. 333-69 and A.L. 438-4, total length is estimated  
 9 in the latter), Au. africanus StW 575, H. naledi (n=3, U.W. 101-428, -1055 and -1721),  
 10 Neandertals (n=7, Shandiar 4, 5 and 6, Kebara 2, Tabun 1, Moula-Guersy M-E1-123 and Spy  
 11 25H), and early H. sapiens ('early Homo') (n=4, Dolní Věstonice 14 and 16, Qafzeh 9, Ohalo II).  
 12 Ar. ramidus values derived from published values in Lovejoy et al. (2009) apart from midshaft  
 13 ML breadth (5.4mm) measured on original fossils by TLK.



14

1 *Figure 30. Phalangeal curvature of the MH2 non-pollical proximal phalanges in comparison to*  
 2 *other fossil hominins and extant catarrhines. Variation in PD curvature of the dorsal surface of*  
 3 *proximal phalanges of rays 2-4, quantified as the first polynomial coefficient using methods*  
 4 *described in Deane and Begun (2008). Although there is substantial overlap in degree of*  
 5 *curvature across taxa, Au. sediba curvature is less than the median value of Ar. ramidus, Au.*  
 6 *afarensis, H. naledi and OH 7, but greater than that of Au. africanus and hominins from*  
 7 *Swartkrans. Image adapted from Kivell et al. (2015).*  
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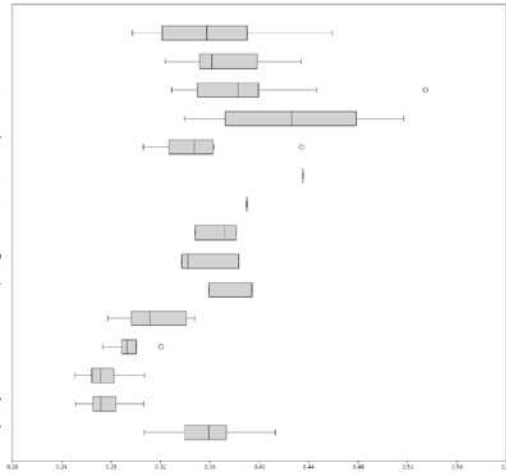


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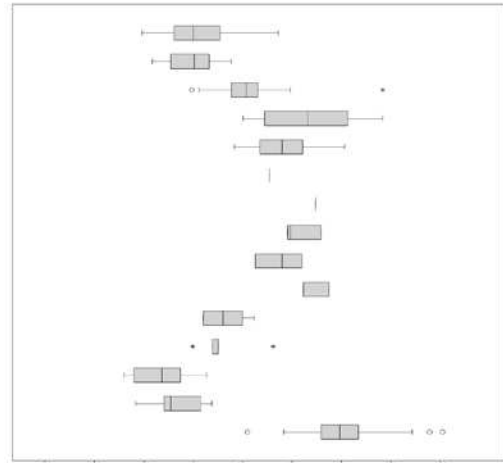
1 *Figure 31. Comparative analysis of the MH2 non-pollical proximal phalanx morphology,*  
2 *including U.W. 88-164 (PP2), -120 (PP3), -108 (PP4) and -121 (PP5). Box-and-whisker plots of*  
3 *proximal phalanx (PP) shape, in which each variable is shown as a ratio of total length:*  
4 *mediolateral (ML) breadth of the base (top, left), at midshaft (top, right) and the distal trochlea*  
5 *(bottom, left), and dorsopalmar (DP) height of the trochlea (bottom, right). Comparative extant*  
6 *sample includes Gorilla sp. (n=10 individuals), P. troglodytes ssp. (n=6), P. paniscus (n=5),*  
7 *recent small-bodied (s-b) Khoisan humans (n=6), recent humans (n=17). Comparative fossil*  
8 *sample composed of Ar. ramidus (n=5 specimens, ARA-VP-6/500-022, -030 and -069, ARA-VP-*  
9 *7/2H, and ARA-VP-6/507), Au. afarensis (n=9, A.L. 288-1x, A.L. 333-19, -57, -62, -63 and -93,*  
10 *A.L. 333w-4, A.L. 1044-1, A.L. 444-4), Au. africanus (n=2, StW 28 and -293), Au. robustus/early*  
11 *Homo (n=3, SKX 5018, -15468 and -2741), cf. H. erectus OH 86 PP5 (Domínguez-Rodrigo et*  
12 *al. 2015), Homo sp. ATE9-2 PP5 (Lorenzo et al. 2015), H. naledi (n=13, U.W. 101-558, -754, -*  
13 *923, -1025, -1326, -1327, -1328, -1454, -1460, -1643, -1644, -1645, -1725), H. floresiensis*  
14 *LB6/8 (Larson et al. 2009), Neandertals (n=5 individuals, Shandiar 4, 5 and 6, Tabun 1, Kebara*  
15 *2 in addition to Spy 24A, -24B, -24C, -426a, -748a, and -766a), and early H. sapiens ('early*  
16 *Homo') (n=8 individuals, Dolní Věstonice 3, 13, 14, 15 and 16, Qafzeh 8 and 9, Ohalo II).*  
17 *Regarding Ar. ramidus, all data derive from published values in Lovejoy et al. (2009), except for*  
18 *ML breadth at midshaft, which was measured on the original fossils by TLK, and the following*  
19 *values that have been adjusted from Lovejoy et al. (2009) following re-measurement of original*  
20 *fossils by G. Suwa: ARA-VP-6/500-069 ML breadth of base (13.8mm) and ARA-VP-6/507 DP*  
21 *height of trochlea (8.5mm).*



humans  
 s-b humans  
 early *Homo*  
 Neandertals  
*H. naledi*  
 ATE9-2  
 OH 86  
 SKX  
*Au. sediba*  
*Au. africanus*  
*Au. afarensis*  
*Ar. ramidus*  
*P. paniscus*  
*P. troglodytes*  
 Gorilla

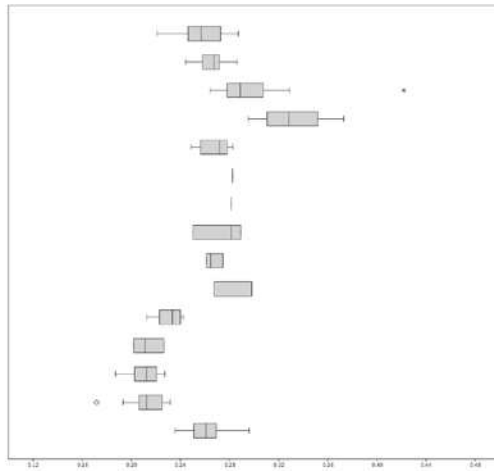


ML breadth of PP2-5 base / total length

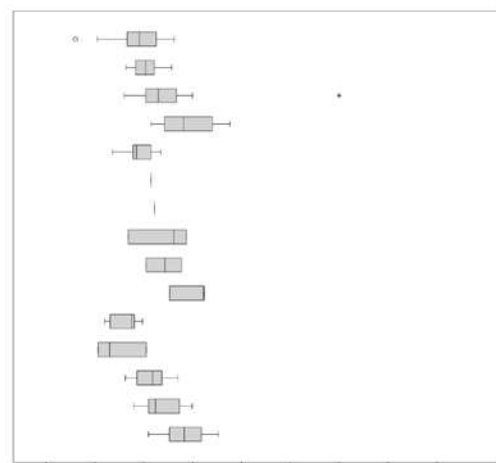


ML breadth of PP2-5 midshaft / total length

humans  
 s-b humans  
 early *Homo*  
 Neandertals  
*H. naledi*  
 ATE9-2  
 OH 86  
 SKX  
*Au. sediba*  
*Au. africanus*  
*Au. afarensis*  
*Ar. ramidus*  
*P. paniscus*  
*P. troglodytes*  
 Gorilla



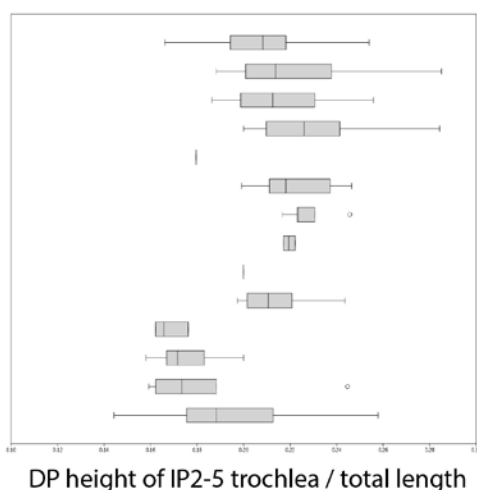
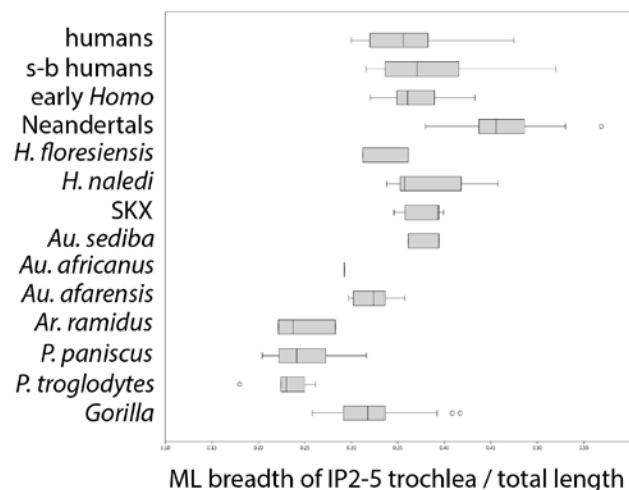
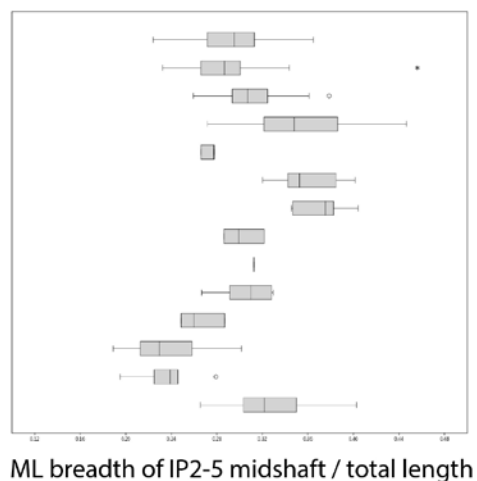
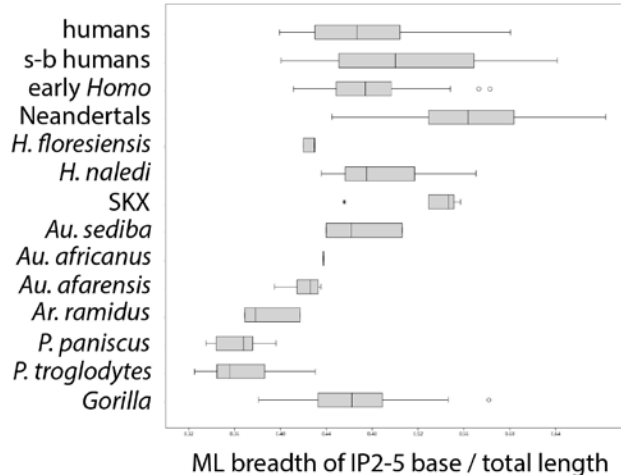
ML breadth of PP2-5 trochlea / total length



DP height of PP2-5 trochlea / total length

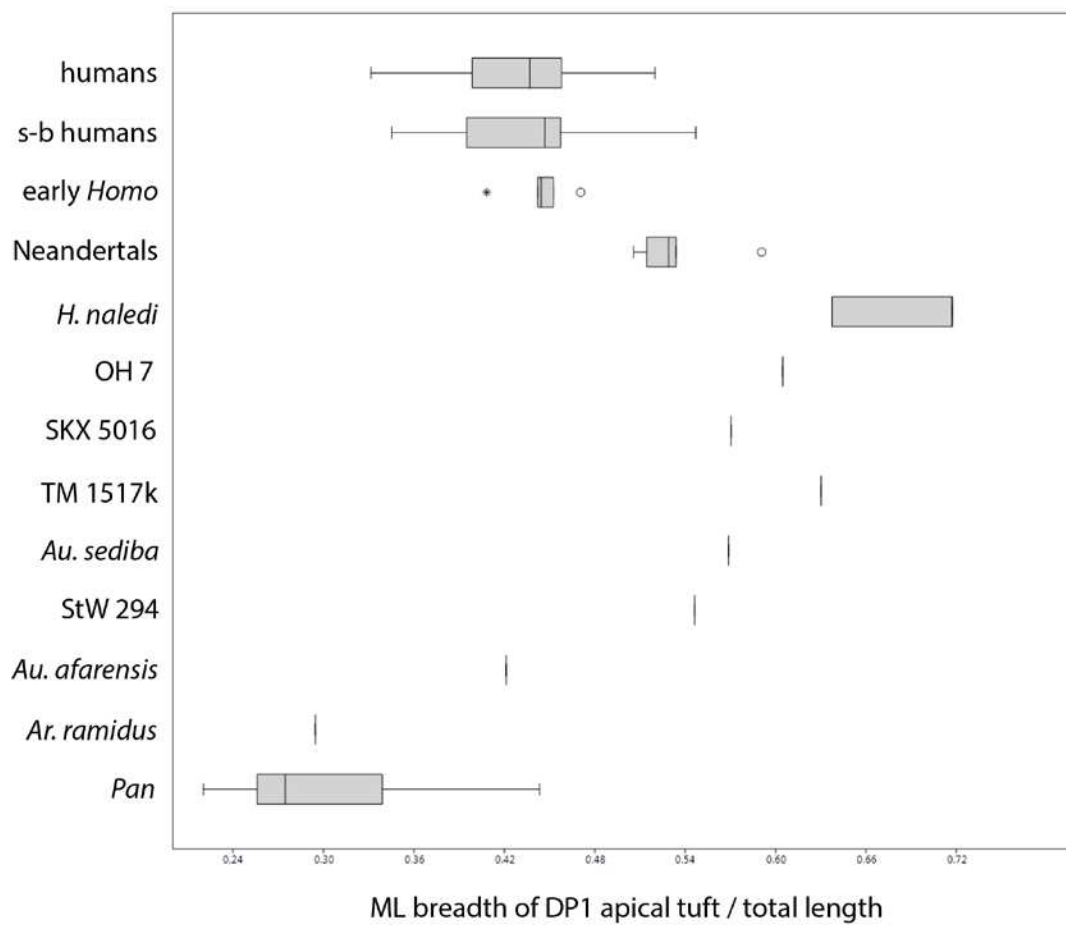
1  
 2

1 *Figure 32. Comparative analysis of the MH2 intermediate phalanx morphology, including U.W.*  
2 *88-161 (IP3), -122 (IP4) and -162 (IP5). Box-and-whisker plots of intermediate phalanx (IP)*  
3 *shape, in which each variable is shown as a ratio of total length: mediolateral (ML) breadth of*  
4 *the base (top, left), at midshaft (top, right) and the distal trochlea (bottom, left), and dorsopalmar*  
5 *(DP) height of the trochlea (bottom, right). Comparative extant sample includes Gorilla sp. (n=9*  
6 *individuals), P. troglodytes ssp. (n=4), P. paniscus (n=4), recent small-bodied (s-b) Khoisan*  
7 *humans (n=6), recent humans (n=15). Comparative fossil sample composed of Ar. ramidus*  
8 *(n=4 specimens, ARA-VP-6/500-002, -059, -078 and -092), Au. afarensis (n=7, A.L. 333-32, -*  
9 *46, -64, -88, -149 and -150, and A.L. 333x-18), Au. africanus (n=1, StW 331), Au. robustus/early*  
10 *Homo (n=6, SKX 5019, -5020, -9449, -13476, -35439, and -36712), H. naledi (n=11, U.W. 101-*  
11 *381, -777, -924, -1027, -1308, -1310, -1311, -1325, -1646, -1647, and -1648), H. floresiensis*  
12 *(n=2, LB1/48 and LB6/9; Larson et al. 2009), Neandertals (n=7 individuals, Shandiar 4, 5 and 6,*  
13 *Amud 1, Tabun 1, Kebara 2, Moula-Geursy M-G1-154 in addition to Spy 222b, -390a, 430a and*  
14 *-484a), and early H. sapiens ('early Homo') (n=10 individuals, Dolní Věstonice 3, 13, 14, 15, 16,*  
15 *34 and 53, Qafzeh 8 and 9, and Ohalo II). Regarding Ar. ramidus, all data derive from published*  
16 *values in Lovejoy et al. (2009), except for ML breadth at midshaft, which was measured on the*  
17 *original fossils by TLK, and the following values that have been adjusted from Lovejoy et al.*  
18 *(2009) following re-measurement of original fossils by G. Suwa: total length of the IP in ARA-*  
19 *VP-6/500-059 (35mm), ARA-VP-6/500-092 (37mm) and ARA-VP-6/500-002 (24.4mm) and ML*  
20 *breadth of base in ARA-VP-6/500-078 (12.9mm).*



1  
2

1 *Figure 33. Comparative analysis of the MH2 U.W. 88-124 distal pollical phalanx morphology.*  
 2 *Box-and-whisker plot of the mediolateral (ML) breadth of the distal pollical phalanx (DP1) apical*  
 3 *tuft relative to total DP1 length. Comparative extant sample includes Pan sp. (n=7), recent*  
 4 *small-bodied (s-b) Khoisan humans (n=22), and recent humans (n=34). Comparative fossil*  
 5 *sample composed of Ar. ramidus ARA-VP-6/500-049, Au. afarensis A.L. 333-159, Au. africanus*  
 6 *StW 294, Au. robustus TM 1517k, Au. robustus/early Homo SKX 5016, H. habilis OH 7 FLK-*  
 7 *NN-A, H. naledi U.W. 101-1351 and -1453, Neandertals (n=5 individuals, Shandiar 3, 4, 5 and*  
 8 *6, and Kebara 2), and early H. sapiens ('early' Homo) (n=2 individuals, Dolní Věstonice 16 and*  
 9 *Ohalo II). Ar. ramidus total DP1 length from Lovejoy et al. (2009) and ML breadth of apical*  
 10 *tuft (4.3mm) measured on original fossil by TLK. Due to preservation, both total length and apical*  
 11 *tuft breadth are estimated in U.W. 101-124 and thus results should be interpreted with caution.*



12  
 13  
 14  
 15  
 16

1 **TABLES**

2 **Table 1.** *Au. sediba* MH1 and MH2 hand bones.

3

<b>Specimen #<sup>1</sup></b>	<b>Element</b>	<b>Preservation</b>
<b>MH1 hand bone (juvenile)</b>		
U.W. 88-112	L Mc3 <sup>2</sup>	missing distal epiphysis and eroded proximal end
<b>MH2 hand bones (adult)<sup>3</sup></b>		
U.W. 88-158	R scaphoid	complete, excluding small fragment at tip of tubercle
U.W. 88-159	R lunate	complete, excluding small palmar-medial fragment of distal end
U.W. 88-157 <sup>4</sup>	R triquetrum	complete and undistorted
U.W. 88-156	R capitate	complete, excluding small fragments from dorsolateral corner and palmar beak of distal end
U.W. 88-105	L capitate	complete and undistorted
U.W. 88-95	R hamate	complete, excluding tip of hamulus
U.W. 88-106	L hamate	complete and undistorted
U.W. 88-119	R Mc1	complete and undistorted
U.W. 88-115	R Mc2	complete and undistorted
U.W. 88-116	R Mc3	complete and undistorted
U.W. 88-117	R Mc4	complete and undistorted
U.W. 88-118	R Mc5	complete and undistorted
U.W. 88-160	R PP1	complete, excluding fragments from palmar surface of base, some erosion on head
U.W. 88-91	L PP1	complete and undistorted
U.W. 88-164	R PP2	complete and undistorted
U.W. 88-109	L PP2	lateral half of bone, broken at sagittal midline
U.W. 88-120	R PP3	complete and undistorted
U.W. 88-182	L PP3	proximal half, broken just distal to the midline
U.W. 88-108	R PP4	complete, missing small fragment from palmar surface of base and palmar, lateral edge of head
U.W. 88-110	L PP4	fragment of proximal end
U.W. 88-121	R PP5	complete and undistorted
U.W. 88-123	R IP2	complete, but preserved in breccia and shaft distorted a distal end
U.W. 88-161	R IP3	complete and undistorted
U.W. 88-122	R IP4	complete, excluding small fragment from palmar surface of base
U.W. 88-162	R IP5	complete and undistorted
U.W. 88-124	R DP1	missing most of base and small fragments from medial and palmar surface side of apical tuft

4 <sup>1</sup> Abbreviations: 'L', left; 'R', right; 'Mc', metacarpal; 'PP', proximal phalanx; 'IP', intermediate  
5 phalanx; 'DP', distal phalanx.

6 <sup>2</sup>Kivell et al. (2011) reported U.W. 88-112 as a right Mc3, rather than left.

1 <sup>3</sup>Kivell et al. (2011) reported a U.W. 88-111 as a manual left DP4 or DP5 associated with the  
2 MH2 skeleton, but this bone is now considered to be a pedal distal phalanx (see DeSilva et al,  
3 this volume).

4 <sup>4</sup>This specimen was mistakenly listed as U.W. 88-163 in Kivell et al. (2011)

5

6

1 **Table 2.** Linear measurements of MH2 carpal bones.  
2

Description	Measurement (mm) <sup>1</sup>	
	MH2 right	MH2 left
<b>Scaphoid U.W. 88-158<sup>2</sup></b>		
PD <sup>3</sup> length of scaphoid body	12.2	-
DP height of scaphoid body	20.8	-
ML breadth of scaphoid body (excluding tubercle)	9.9	-
tubercle projection (following Trinkaus 1983)	11.7	-
PD length of radial facet	11.3	-
PD height of radial facet	13.7	-
DP height of lunate facet	8.9	-
PD length of lunate facet	7.9	-
DP height of capitate facet	11.1	-
PD length of capitate facet	9.2	-
DP height of trapezium-trapezoid facet	14.6	-
ML breadth of trapezium-trapezoid facet	7.6	-
<b>Lunate U.W. 88-159</b>		
PD length of lunate body	9.4	-
DP height of lunate body	12.8	-
ML breadth of lunate body	11.5	-
DP height scaphoid facet (at distal edge)	9.6	-
PD length of scaphoid facet	6.6	-
DP height of capitate facet	10	-
ML breadth of capitate facet	5.4	-
DP height radial facet	12.6	-
ML breadth of radial facet	11.2	-
DP height of triquetrum facet	6.7	-
PD length of triquetrum facet	7.6	-
<b>Triquetrum U.W. 88-157</b>		
ML breadth of triquetrum body	14.2	-
DP height of triquetrum body	11.5	-
PD length of triquetrum body	8.3	-

DP height of lunate facet	7.8	-
PD length of lunate facet	7.4	-
ML breadth of hamate facet	11.3	-
DP height of hamate facet	10.2	-
ML breadth of pisiform facet	6.1	-
PD length of pisiform facet	5.7	-

---

**Capitate U.W. 88-156 (R) and U.W. 88-105 (L)**

PD length of capitate body	17.7	17.8
DP height of capitate body	16.1	16.2
ML breadth of capitate body	[12.3]	12.8
minimum ML breadth of the capitate neck	9	9.5
ML breadth of proximal facet	10	10.1
DP height of proximal facet	10.1	10.8
DP height of hamate facet	9.3	9.4
PD length of hamate facet	15.4	15.7
PD length of Mc2 facet	4.2	4.6
DP height of Mc2 facet	8.2 pres.	11.2
ML breadth of Mc3 facet	[11]	12
DP height of Mc3 facet	11.4	12.7

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**Hamate U.W. 88-95 (R) and U.W. 88-106 (L)**

PD length of hamate	[16.6]	16.6
PD length of hamate body (excluding hamulus)	15.6	16.4
DP height of hamate	18.4	19.2
DP height of hamate body (excluding hamulus)	11.4	11.6
ML breadth of hamate body	14.1	13.6
DP height of capitate facet	8.8	9.2
PD length of capitate facet	13.9	14.2
DP height of triquetrum facet	9.2	9.6
PD length of triquetrum facet	14.3	13.7
ML breadth of Mc4 facet	8.3	8.4
DP height of Mc4 facet	10.7	11
ML breadth of Mc5 facet	7.9	7.7
DP height of Mc5 facet	8.2	8

---



1 <sup>1</sup> All measurements are the maximum of that dimension, unless otherwise noted. Additional  
2 metric data are also provided in the text for some carpal bones.

3 <sup>2</sup> Note that the PD and DP dimensions of the scaphoid follow the orientation in Figure 3.

4 <sup>3</sup> Abbreviations: 'PD', proximodistal; 'DP', dorsopalmar; 'ML', mediolateral; 'R', right; 'L', left;  
5 'pres.', preserved; [x], value estimated with confidence based on preserved morphology; '-',  
6 bone not preserved, or morphology not preserved well enough to estimate the value.

7

1 **Table 3.** Linear measurements of MH1 and MH2 metacarpals (Mc).  
 2

Description	Measurement (mm)					
	MH2 Mc1	MH2 Mc2	MH1 Mc3	MH2 Mc3	MH2 Mc4	MH2 Mc5
Specimen #: <b>U.W. 88</b>	<b>-119</b>	<b>-115</b>	<b>-112</b>	<b>-116</b>	<b>-117</b>	<b>-118</b>
Total length	39.5	53.3	44.7 pres. [53]	48.6	44.5	41.7
Interarticular length	37.7	50	-	48.4	43.9	41
DP <sup>1</sup> height of proximal base	12.7	13.9	13.9 pres. [11.5]	13.8	11.1	10
ML breadth of proximal base	10.7	13.1	10.3 pres. [16.5]	10.5	9.9	11.9
DP height of proximal facet	9.9	12.1	-	[9.3]	10.2	7.8
ML breadth of proximal facet	10.5	10.2	-	[12.2]	[7.4]	8.5
DP height at midshaft	6.3	7.4	9	7.3	6.6	5.3
ML breadth at midshaft	7.3	5.6	7.3	5.5	5.2	6.3
DP height of distal head	11.2	12.1	-	11.6	10.9	10.9
ML breadth of distal head	10.3	10.3	-	10.4	10	9.4

3 <sup>1</sup> Abbreviations the same as in Table 2.

**Table 4. Linear measurements of MH2 proximal phalanges.**

Description	Measurement (mm)									
	Ray 1 right	Ray 1 left	Ray 2 right	Ray 2 left	Ray 3 right	Ray 3 left	Ray 4 right	Ray 4 left	Ray 5 right	
<b>Specimen #: U.W. 88-</b>	<b>-160</b>	<b>-91</b>	<b>-164</b>	<b>-109</b>	<b>-120</b>	<b>-182</b>	<b>-108</b>	<b>-110</b>	<b>-121</b>	
Total length	[23.5]	24.5	31.5	31.5	34.7	26.0 pres.	[33.6]	14.3 pres.	[27.9]	
ML <sup>1</sup> breadth of proximal base	[10.6]	11.4	11.3	-	11.7	11.3	11.5	[10.3]	10.7	
DP height of proximal base	7.6 pres.	9	9.2	[9]	10.9	10.2	[9.6]	-	8.9	
DP height of proximal facet	[7.8]	7.8	7.9	[7.7]	9.1	9	[8.4]	[8.3]	7.2	
ML breadth of proximal facet	[9.6]	9.7	10	-	9.5	8.9	9.3	[8.7]	9.1	
DP height at midshaft	5.3	5.6	5.5	[5.9]	6.9	5.9	6.5	-	[4.2]	
ML breadth at midshaft	5.7	5.8	7.8	-	9.2	8.7	9.1	-	7.7	
DP height of distal trochlea	[5.3]	5.5	6.4	[6.3]	6.7	-	[6.1]	-	-	
ML breadth of distal trochea	[8.6]	[9.2]	8.7	-	9.1	-	[8.9]	-	-	

<sup>1</sup> Abbreviations the same as in Table 2.

1 **Table 5.** Linear measurements of MH2 intermediate and distal phalanges.

2

Description	Distal phalanx <sup>2</sup>		Intermediate phalanges		
	Ray 1	Ray 2	Ray 3	Ray 4	Ray 5
<b>Specimen #: U.W.88-</b>	<b>-124</b>	<b>-123</b>	<b>-161</b>	<b>-122</b>	<b>-162</b>
Total length	15.1 pres.[16]	16.6 pres. [18.3]	22.2	21.6	17.5
ML <sup>1</sup> breadth of proximal base	-	[9.8]	9.7	10	8.9
DP height of proximal base	-	-	8.7	-	-
DP height of proximal facet	-	-	6.2	-	-
ML breadth of proximal facet	-	-	8	8.4	[7.6]
DP height at midshaft	5.1	-	5	4.1	3.9
ML breadth at midshaft	5	[6.7]	6.3	6.9	5.2
DP height of apical tuft <sup>3</sup> /trochlea	4..4	-	4.9	[4.8]	[3.8]
ML breadth of apical tuft/trochlea	7.7 pres. [9.1]	[7.1]	8	7.8	6.9

3 <sup>1</sup> Abbreviations the same as in Table 2

4 <sup>2</sup> All measurements are in mm.

5 <sup>3</sup> Reference to the apical tuft applies to the distal phalanx only, while trochlea applies to the  
6 intermediate phalanges.

7

1 **Table 6.** Hand proportions in extant and fossil taxa.  
2

Taxon	Sex	n	Ratio (%) <sup>1</sup>					
			PP1:Mc1 TL	PP3:Mc3 TL	PP3:Mc3 IA	IP3:Mc3 TL	PP4:Mc4 TL	Ray 1: Ray 3
<b>EXTANT<sup>2</sup></b>								
<i>Gorilla</i>	M & F	9	56	64.3	67.5	44.9	63.8	39.7
			3.5	2.3	2.7	1.8	5.3	1.4
<i>P. troglodytes</i>	M & F	9	67.6	67.5	69.1	49.2	68.5	36.3
			3.7	1.1	1.1	1.9	1.5	1
<i>P. paniscus</i>	M & F	10	64.6	61.9	63.5	44.1	63	36.3
			3	1.9	2	1.4	1.5	0.9
<i>H. sapiens</i>	M	18	68.8	67.2	71.3	44	73.7	54
			4.4	3.4	3.8	2.2	4.5	2
	F	23	68.3	67.3	71.8	44.1	74.6	53.1
			2.6	3	3.1	1.9	3.4	1.9
s-b <i>H. sapiens</i>	M	12	67.4	67.5	71.5	43.8	74.7	55.3
			3.4	3.8	4	2.4	3	2.3
	F	13	68.1	67.4	71.3	42.8	75.8	54.5
			2.4	2.3	2.3	2	9.4	1.8
<b>FOSSILS</b>								
<b>Early <i>H. sapiens</i></b>								
Ohalo II H2			67	68.1	69.5	45.8	69	52.4
Arene Candide 2			73.7	68.5	72	45.7	74.9	56.6
Barma Grande 2			70.3	64.2	67.3	44.1	72.2	56.1
Qafzeh 9			73.8	74.7	76.6	49.9	82.3	56.6
Qafzeh 8			-	-	-	49.6	-	-
<b><i>H. neanderthalensis</i></b>								
Kebara 2			67.7	67.8	71.2	44.8	-	51.4
Shanidar 4			62.4	60.8	65.7	40.1	67 <sup>3</sup>	52.4
Tabun 1			64.4	67.4	70	-	-	-
<b>Other hominins</b>								
<i>H. naledi</i> Hand 1			65.5	73.3	73.9	46.1	77.5	57.6

<i>Au. sediba</i> MH2	62	71.4	71.7	45.7	75.5	60.7
<i>Au. afarensis</i> composite <sup>4</sup>	66	67.3	69	42.9	70	51.7
<i>Ar. ramidus</i> ARA-VP-6/500	-	-	-	-	80.3	-

1 <sup>1</sup> All values are presented as percentages, with the mean value above and standard deviation  
2 below.

3 <sup>2</sup> Abbreviations: 's-b', small-bodied, Khoisan individuals. 'TL', total length; 'IA', interarticular  
4 length

5 <sup>3</sup> ratio calculated using IA length of Mc4

6 <sup>4</sup> hand bones not associated with the same individual

1 **Table 7.** Summary of key morphological features of the *Au. sediba* hand and how they compare with other hominins.<sup>1</sup>

2

---

**Primitive or similar to (most) other australopiths and *Ardipithecus***

---

large trapezoid facet and "closed" distomedial border of scaphoid  
"waisted" capitate body  
absence of saddle-shaped hamate-Mc5 articulation  
small and relatively curved trapezium-Mc1 articulation  
gracile Mc1 shaft with poorly-developed entheses  
distally-extended first *M. dorsal interosseous* insertion on Mc1 shaft  
asymmetrical metacarpal heads  
ML narrow Mc1 head  
absence of Mc3 styloid process  
moderate curvature of proximal phalanges  
prominent flexor sheath ridges of proximal phalanges  
DP1 with ML broad apical tuft

---

**Derived or similar to (some) *Homo* species**

---

scaphoid's trapezium facet extends onto tubercle  
triquetrum morphology suggests possibly small, rather than rod-shaped, pisiform  
hamate hamulus shape with limited distal projection  
relative size of hamate's Mc4/Mc5 facets that do not extend onto the hamulus  
intrinsic thumb proportions with relatively long Mc1 and relatively short PP1 (most similar to Neandertals)  
DP1 with well-developed proximal and distal fossae and FPL tendon attachment

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**Distinct or of unknown polarity**

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triquetrum morphology with tubercle-like palmar-medial extension

ML narrow lunate (most similar to Miocene ape morphology)

extremely long length of thumb, and especially Mc1, relative to third digit

palmar beak on Mc1 head (also found only in SK 84)

poorly developed and proximally-positioned *M. opponens pollicis* insertion on Mc1 shaft

generally gracile metacarpal shafts with relatively large heads and bases (although MH1 Mc3 shaft is relatively broad)

overall shape and flexor attachment morphology of intermediate phalanges

dorsal and palmar trapezoid facets on capitate

laterally-oriented capitate-Mc2 articulation

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- 1 <sup>1</sup> Features are organised into hypothesised categories based on general similarities to all or most species within a particular genus  
2 (i.e., *Australopithecus*, *Homo*). However, given the mosaic of morphologies that are found across the hominin fossil record,  
3 particularly traditionally “derived” features in early hominins [e.g. *Orrorin* (Almécija et al. 2010)] or traditionally “primitive” features in  
4 recent hominins [e.g. *H. floresiensis* (Tocheri et al. 2007) or *H. naledi* (Kivell et al. 2015)], the polarity of any given feature is not  
5 always clear.



