

OH 7, THE CURIOUS CASE OF THE ORIGINAL HANDY MAN?

OH 7, el curioso caso del primer hombre hábil?

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ABSTRACT

The phalanges from the Olduvai Hominid 7 (OH 7) partial hand are evaluated from a morphological and morphometric viewpoint, with special emphasis on the distal phalanges. These remains have been traditionally attributed to the holotype of *Homo habilis*, but recently Moyà-Solà *et al.*, (2008) concluded that, given their similarities with the remains of *Paranthropus robustus*, an attribution to the robust australopith *P. boisei* appears much more likely. The results of the present study confirm this conclusion, further indicating that the pattern of robusticity of the pollical and middle finger distal phalanges in OH 7 differs from the pattern displayed by modern and fossil humans, as well as by the great apes, much more closely resembling the pattern displayed by quadrupedal monkeys and the genus *Paranthropus*.

Keywords: *H. habilis*, *Paranthropus*, early *Homo*, hand, phalanges, evolution.

RESUMEN

Se evalúan las falanges de la mano parcial del Homínido de Olduvai 7 (OH 7), desde un punto de vista morfológico y morfométrico, con especial énfasis en las falanges distales. Estos restos se han incluido tradicionalmente en el holotipo de *Homo habilis*, pero recientemente Moyà-Solà *et al.*, (2008) han concluido que, debido a sus semejanzas con los restos de *Paranthropus robustus*, una atribución al australopiteco robusto *P. boisei* parece mucho más probable. Los resultados de este estudio confirman esta conclusión, poniendo además de manifiesto que el patrón de robustez de las falanges distales del pulgar y del dedo medio en OH 7 es distinto al patrón que muestran los humanos actuales y fósiles, así como los grandes antropomorfos, siendo mucho más parecido al patrón que muestran los monos cuadrúpedos y el género *Paranthropus*.

Palabras clave: *H. habilis*, *Paranthropus*, primeros *Homo*, mano, falanges, evolución.

INTRODUCTION

The hands of humans differ from those of apes by being considerably shorter relative to body mass, so that the former display relatively longer thumbs (Alba *et al.*, 2003). From a functional viewpoint, this can be easily explained by the striking differences in locomotor behaviors between apes and humans: while the former need long hands for arboreal behaviors, such as vertical climbing and below-branch suspension, the acquisition of habitual terrestrial bipedalism in the human lineage (and the concomitant loss of locomotor function by the hands) permitted the optimization of manual proportions for manipulative purposes (Alba *et al.*, 2003, 2005). As such, australopiths (*Australopithecus*) already display human-like manual proportions, i.e. short hands with a relatively long thumb (Alba *et al.*, 2003, 2005; Green & Gordon, 2008). In this sense, human hands are more similar to the hands of stem hominoids such as *Proconsul* (Begun *et al.*, 1994), which were essentially generalized arboreal primates with powerful-grasping capabilities with no suspensory adaptations. Whether the short hands of humans evolved from a long-handed condition similar to that of chimpanzees (our living closest relative, according to molecular studies) remains to be tested by fossil evidence. Nonetheless, given the short-handed condition of australopithecines, there seems to be no doubt that this is a plesiomorphic condition for the genus *Homo*. Given the fact that the manual remains of *A. anamensis* predate by about one million years the first stone tools, it has been concluded that human-like hand proportions are not an adaptation to tool-making (Alba *et al.*, 2003, 2005).

Many other morphological features of the hand of modern humans have been identified as tool-making adaptations. Ideally, these functional hypotheses must be contrasted with the evidence provided by the fossil record. Unfortunately, however, the evidence of manual remains of fossil *Homo* species is very scarce; Neandertals (*H. neanderthalensis*) are an exception, but given their recent chronology, they cannot provide many insights on the hand of early *Homo*. Some remains are available for *H. ergaster* from Nariokotome (Walker & Leakey, 1993), and also from *Homo* sp. from Swartkrans (Susman, 1988, 1989). Albeit with

some differences, these remains can be identified as belonging to *Homo*, a situation that strikingly contrasts with the OH 7 partial hand from bed I locality FLK NN (Napier, 1962), which in the past has been attributed to *H. habilis* ('handy man') by most researchers. This hand is of topmost significance, not only because its chronology (ca. 1.75 Ma) postdates the appearance of lithic remains in the record, but especially because it has been attributed to one of the earliest *Homo* species (the other being *H. rudolfensis*). In the original description of *H. habilis*, Leakey *et al.* (1964) included the manual remains, together with craniodental remains from the same locality, into the holotype of the species (OH 7)—mainly on the basis that they all belonged to a subadult individual and with no clear taphonomic association. Most researchers have subsequently accepted the attribution of all these remains to a single individual, albeit with some notorious exceptions (Robinson, 1972). Most recently, Moyà-Solà *et al.* (2008) evaluated this taxonomic attribution and noted that, on morphological and morphometrical grounds, the phalanges of OH 7 most closely resemble those of robust australopiths (*Paranthropus*), thereby concluding that an attribution to *P. boisei*, also documented at the same site, seemed more likely. Interestingly, a similar conclusion was recently reached regarding the foot OH 8 (Gebo & Schwartz, 2006), also included by Leakey *et al.* (1964) into the hypodigm of *H. habilis* as a paratype.

In particular, Moyà-Solà *et al.* (2008) mainly focused on middle phalanges. They found that the OH 7 middle phalanges displayed trochleae with primitive (australopith-like) proportions, while at the same being derived by displaying mediolaterally expanded shafts. To sum up, the proportions of these phalanges do not fit a human-like pattern (either fossil or extant), most closely resembling the phalanges of the South-African robust australopith, *P. robustus*. Moyà-Solà *et al.* (2008) devoted relatively little attention to the OH 7 distal phalanges, concentrating only on the pollical one. They investigated the mediolateral robusticity at the tuft and the shaft, showing that, like *P. robustus* and Neandertals, the OH 7 pollical distal phalanx (PDP) departed from the modern human condition by displaying a stouter phalanx both at

the tuft and at midshaft. In this communication, we review the morphological evidence provided by the OH 7 manual phalanges, and provide further morphometrical evidence regarding the robusticity of the distal phalanges by comparing the first with the third manual ray.

MATERIALS AND METHODS

Regarding the morphometric comparisons, phalangeal robusticity was computed by means of a logarithmically transformed bivariate index, following the formula: $DPR = \ln(MLT/L)$, where DPR means 'distal phalanx robusticity', MLT 'mediolateral tuft width' and L 'total phalanx length'. The use of ratios has been criticized by some morphometricians, with statistical difficulties arising because a quotient of two variables (X/Y) is not a linear function of the variables X and Y . However, as noted by Hills (1978) these difficulties disappear by applying logarithms, because the $\log(X/Y) = \log X - \log Y$, i.e. the log-transformed ratio is a linear function of $\log X$ and $\log Y$ (see also Smith, 1999), so that the assumption that the variable analyzed displays a normal distribution is much more rarely disturbed. The resulting log-transformed index, DPR, was then investigated by means of analysis of variance (ANOVA). The mean values of extant

taxa were compared with one another by means of post-hoc multiple comparisons (Bonferroni method), whereas the values for individual fossil specimens were compared with extant taxa on the basis of their respective 95% confidence intervals. Statistical calculations were carried out by means of the statistical package SPSS 16.0. Besides the OH 7 distal phalanges I and III (specimens A and B, respectively), the fossil sample included the pollical and middle finger distal phalanges of *P. robustus* from Swartkrans (respectively, SKX 5016 and SKX 27504) and *H. neanderthalensis* from La Ferrassie I and Shanidar 3, 4 and 5; measurements were taken from good quality casts or from the literature (Trinkaus, 1983; Susman, 1989). The comparative extant sample includes the extant ape genera, i.e. chimpanzees and bonobos (*Pan*), gorillas (*Gorilla*) and orangutans (*Pongo*), as well as pronograde monkeys such as baboons (*Papio*, *Mandrillus* and *Theropithecus*) and macaques (*Macaca*), and modern humans (*H. sapiens*).

RESULTS

Morphological comparisons

A comparison of middle phalanx morphology between OH 7 and selected hominid taxa can be seen in Figure 1. The OH7 middle phalanges display

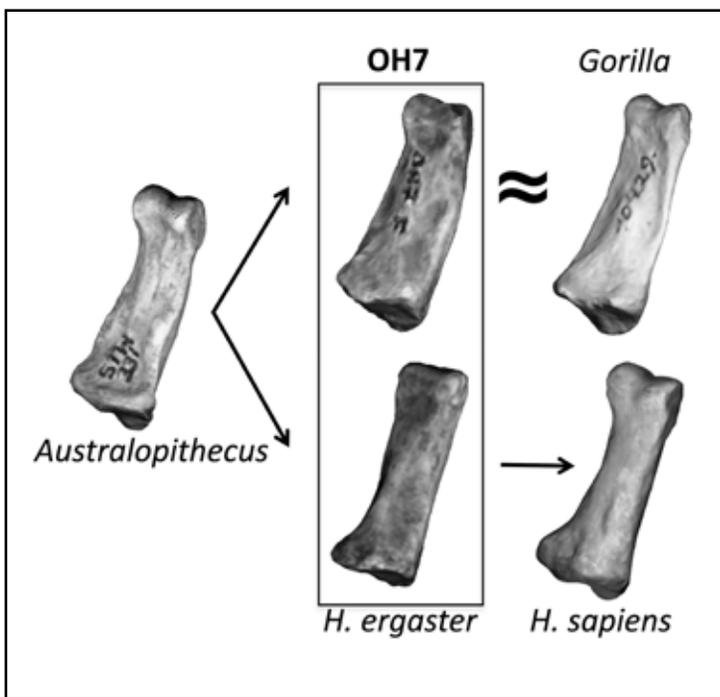


Figure 1. Composition showing a virtual model of the middle phalanx in different fossil and extant hominid taxa: *Australopithecus africanus* (Stw 331), OH 7 F, *Homo ergaster* (KNM-WT 15000-BO), *Gorilla gorilla* and *Homo sapiens*. All them are represented in oblique-palmar view and scaled to the same size in order to easily visualize the morphological differences. Even though both OH7 and *H.ergaster* are nearly contemporaneous and are represented by subadult individuals (note the lack of epiphysis in middle phalanges), they differ considerably in morphology. See text for further details.

mediolaterally-expanded shafts, especially in the proximal two thirds. Distally, the margins of the shaft converge abruptly just before the trochlea, giving them their characteristic ‘bottle-shaped’ appearance. Furthermore, these phalanges show a slightly curved shaft and relatively small trochleae (Moyà-Solà *et al.* 2008). These latter features of the OH 7 middle phalanges closely resemble those of *Australopithecus*, and must be thus interpreted as symplesiomorphic; only the increased shaft robusticity would be a derived condition as compared to *Australopithecus*. On the contrary, the dorsopalmar diameter of these phalanges is relatively small, giving them a roughly flat appearance, most similar to the morphology found among living gorillas, which display robust hand bones due to their huge body mass. The middle phalanges of *P.*

robustus (not shown) display an overall stouter appearance due to their shorter and wider shafts (both dorsopalmarly and mediolaterally), lacking any trace of curvature. The morphology of the OH 7 middle phalanges thus strikingly differs from that of the phalanges of *H. ergaster* (KNM-WT 15000-BO; Walker & Leakey, 1993), which is only slightly younger than OH 7, and which similarly correspond to a subadult individual (as shown by the lack of epiphyses). The basal morphology of the phalanges cannot be evaluated due to the unfused epiphyses, but the shaft of KNM-WT 15000-BO is already straight, as in modern humans, further resembling the latter by the lack of the very deep fossae that are associated with a prominent palmar keel and protruding ridges, and which would be indicative of powerful flexor muscles. Further resemblances

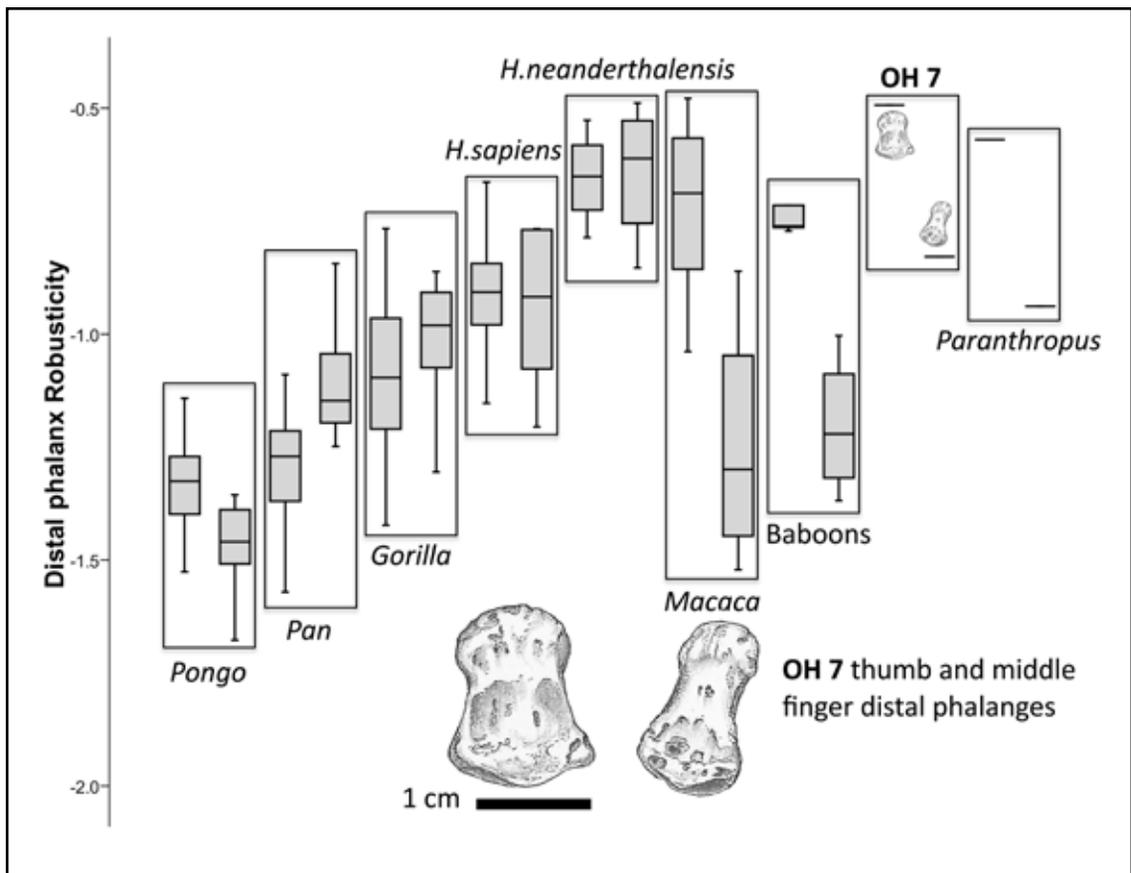


Figure 2. Boxplot showing the robusticity of the distal phalanges in selected extant taxa, Neandertals, OH 7 and *Paranthropus robustus*. The robusticity refers to the distal end in relation to the maximum length of the phalanx (see Materials and Methods for further details). In each taxa, the robusticity for the pollical and middle finger distal phalanges is represented (left/right respectively). Horizontal lines represent the median values, whereas the boxes represent the 25% and 75% percentiles, and the whiskers the maximum-minimum ranges. Depictions from OH 7 phalanges are modified from Moyà-Solà *et al.* (2008).

	DPR (manual ray I)						
Taxon	N	Mean	SD	95% CI		Range	
Orangutans	12	-1.33	0.10	-1.39	-1.26	-1.53	-1.14
Chimpanzees	23	-1.29	0.12	-1.34	-1.24	-1.57	-1.09
Gorillas	16	-1.12	0.26	-1.26	-0.98	-1.83	-0.77
Modern humans	20	-0.87	0.20	-0.97	-0.78	-1.15	-0.19
Neandertals	4	-0.65	0.11	-0.82	-0.48	-0.79	-0.53
Macaques	18	-0.72	0.17	-0.80	-0.63	-1.04	-0.48
Baboons	5	-0.72	0.07	-0.81	-0.64	-0.77	-0.61
OH 7	1	-0.49				-0.49	-0.49
<i>P. robustus</i>	1	-0.57				-0.57	-0.57
	DPR (manual ray III)						
Taxon	N	Mean	SD	95% CI		Range	
Orangutans	11	-1.46	0.10	-1.53	-1.40	-1.68	-1.36
Chimpanzees	23	-1.13	0.15	-1.20	-1.07	-1.57	-0.84
Gorillas	15	-1.00	0.12	-1.07	-0.93	-1.31	-0.86
Modern humans	6	-0.94	0.17	-1.12	-0.76	-1.21	-0.77
Neandertals	4	-0.64	0.16	-0.89	-0.39	-0.85	-0.49
Macaques	14	-1.25	0.22	-1.38	-1.12	-1.52	-0.86
Baboons	4	-1.20	0.16	-1.45	-0.96	-1.37	-1.00
OH 7	1	-0.83				-0.83	-0.83
<i>P. robustus</i>	1	-0.94				-0.94	-0.94

Table 1. Descriptive statistics for distal phalanx robusticity (DPR); see Materials and Methods for further details.

with modern humans can be found at the trochlear region; thus, although the trochlea in KNM-WT 15000-BO is not completely developed (due to its subadult ontogenetic status), unlike the OH 7 specimens, it most closely resembles the trochlear region of a subadult *H. sapiens*.

Like the middle phalanges, the distal phalanges of OH 7 further depart from the human condition by being exceptionally robust, especially at the level of the shaft, which is mediolaterally expanded, as in the middle phalanges (see figure 2). The OH 7 PDP is exceptionally wide, which gives to it an overall flat appearance. In palmar view, it shows a huge fossa, which is even larger (in absolute and relative terms) than in extant humans. A remarkable

difference with respect to the human PDP is the lack of ungual spines on the lateral borders of the apical tuft. The overall morphology is very similar to that of the PDP SKX 5016, attributed to *P. robustus* (see Susman, 1989: his Figure 1).

Morphometric comparisons

The descriptive statistics for DPR has been reported in Table 1; see Figure 2 for a comparison of the numerical results between OH 7 and the other taxa included in the morphometric analysis. With regard to the extant taxa, ANOVA comparisons indicate that significant differences exist for both the pollical ($F=34.7$, $p<0.001$) and the third ($F=14.7$, $p<0.001$) distal phalanges. Post-

hoc multiple comparisons further show that there are more differences between the several pairs of groups regarding the pollical than the third distal phalanx. In particular, with regard to the PDP, all pair comparisons display significant differences (at least $p < 0.05$), except for chimpanzees as compared to gorillas and orangutans, and for humans as compared to macaques and baboons. In other words, extant apes differ from humans and quadrupedal monkeys by displaying low (chimpanzees and orangutans) to moderate (gorillas) degrees of distal pollical phalanx robusticity, whereas humans and monkeys display, respectively, high to very high degrees (see Figure 2). The degree of distal pollical phalanx robusticity displayed by Neandertals overlaps with that of modern humans, although being more similar (even higher) on average to that of macaques and baboons. The degree of robusticity displayed by OH 7 is clearly above the 95% confidence interval of all these taxa and only minimally overlaps with the maximum range displayed by macaques, being most comparable (albeit higher) to the figure displayed by *P. robustus*. When the robusticity of the third distal phalanx is taken into account, it emerges that Neandertals, despite their higher robusticity, resemble modern humans and extant great apes by displaying a similar degree of robusticity for both distal phalanges. OH 7 and *P. robustus*, on the contrary, appear more similar to the condition displayed by monkeys, in which there is a great disparity in the degree of robusticity displayed by both phalanges, with the pollical one being much more robust than that from the third manual ray.

DISCUSSION

According to Shrewsbury *et al.* (2003), there is a set of features that characterize the human PDP, and which are functionally related to the human ability of holding objects with precision between the pads of the thumb and the others fingers: (a) A compartmentalized pad, with a more or less static distal pad, as well as a large, fatty and mobile, proximal one, which would assure an adequate friction and accommodation of the thumb and the pads of the other fingers to the shape of the surface of the object during precision grip; (b) The presence of unguis spines, with a prominent ulnar one; and (c) The marked asymmetry of the flexor pollicis

longus (FPL) attachment towards the radial side. These asymmetries are the osteological correlates of the interphalangeal joint of the human thumb, in which the flexion is accompanied by pronation, so that the pulp of the thumb faces that of the rest of the fingers during flexion. This brings the maximum contact surface with the objects manipulated during tool use and tool-making. Shrewsbury *et al.*, (2003) found that some of the features that characterize the human PDP could also be found in nonhuman primates, especially baboons. These primates, like humans, show developed unguis spines, with a more prominent ulnar one. However, only modern humans show a high frequency of asymmetry in the radial side of the FPL insertion (Shrewsbury *et al.* 2003), so that the latter feature might be a good indicator of manipulative behavior in fossil species.

It is noteworthy that the PDP of OH 7 does not even display unguis spines, as previously noted by Shrewsbury & Sonek (1986), and that its insertion for the FPL neither shows any evidence of asymmetry. The latter authors concurred with the generalized view that OH 7 would have been capable of human-like precision grasping, albeit noting that the lack of unguis spines in the PDP would be indicative of limited compartmentalization and, as such, indicative of a restricted precision grip capability. Our results further indicate that, in spite of the high (Neandertal-like) degree of tuft robusticity in the distal pollical phalanx, when non-pollical manual rays are taken into account, the pattern of robusticity of OH 7, like that of *Paranthropus*, is monkey-like and does not fit neither the great-ape nor the human pattern. In great apes, the PDP is only slightly more robust than the third distal one in orangutans, whereas in African apes the reserve condition is found. In both modern humans and Neandertals, the degree of distal phalanx tuft robusticity for the first and third manual rays is very similar, thus more closely resembling the great-ape condition. In monkeys, on the contrary, the PDP is much more robust than the third distal phalanx; the same condition is also found, albeit to some lower degree, in both OH 7 and *Paranthropus*. These differences in the pattern of distal phalangeal robusticity deserve further investigation from a functional viewpoint. It is important to note that terrestrial cercopithecines display relatively short hands like humans, even

though their hand morphology reflects a main compromise between quadrupedal locomotion in hard substrates and manipulation in fact, baboons display a high opposability index, i.e. the relationship between the first and the second ray, which in *Theropithecus gelada* is even higher than in humans (Etter, 1973). Since *Paranthropus* was a habitual terrestrial biped, strong locomotor selection pressures upon hand morphology can be discarded. As such, its morphology must be regarded in the context of manipulative adaptations. OH 7 and *P. robustus* do not show exactly the same morphology for the middle phalanges, being the former roughly flatter and slightly more curved, while in the latter they are stouter and straighter. Anyway, these subtle differences might be just attributable to specific adaptations in different species of the same genera (Moyà-Solà et al., 2008), i.e. *P. boisei* and *P. robustus*. In any case, the similarities between OH 7 and *Paranthropus* confirm the previous conclusions by Moyà-Solà et al., (2008) that the former most likely does not belong to genus *Homo*, further reinforcing the functional hypothesis proposed by the latter authors that the manual proportions of the robust australopiths, instead of being indicative of tool-making, could be related to particular feeding adaptations such as those displayed by gelada baboons.

CONCLUSIONS

The morphological and morphometric comparisons reported in this communication further reinforce the conclusions previously derived by Moyà-Solà et al., (2008), according to which the OH 7 hand remains do not fit the morphological pattern found among the several species of the genus *Homo*, including its nearly contemporary species *H. ergaster* that is similarly represented by subadult remains. Our results regarding the robusticity of distal phalangeal proportions further indicate that OH 7 neither fits a great-ape pattern to this regard: both humans and great apes display a similar robusticity on the pollical and non-pollical distal phalanges; on the contrary, OH 7 displays a monkey-like pattern, in which the pollical distal phalanx shows an exceptional robusticity at the tuft, as compared to the distal phalanges from other rays. Among fossil hominins, this pattern of robusticity

is only displayed by the genus *Paranthropus*, thus favoring the view that the OH 7 hand remains most likely belongs to a robust australopith.

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