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Early Pleistocene human hand phalanx from the Sima del Elefante (TE) cave site in Sierra de Atapuerca (Spain)

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ABSTRACT

In this study, a new Early Pleistocene proximal hand phalanx (ATE9-2) from the Sima del Elefante cave site (TE – Sierra de Atapuerca, Spain), ascribed to *Homo* sp., is presented and comparatively described in the context of the evolution of the genus *Homo*. The ATE9-2 specimen is especially important because of the paucity of hand bones in the human fossil record during the Early Pleistocene. The morphological and metrical analyses of the phalanx ATE9-2 indicate that there are no essential differences between it and comparator fossil specimens for the genus *Homo* after 1.3 Ma (millions of years ago). Similar to Sima de los Huesos and Neandertal specimens, ATE9-2 is a robust proximal hand phalanx, probably reflecting greater overall body robusticity in these populations or a higher gracility in modern humans. The age of level TE9 from Sima del Elefante and morphological and metrical studies of ATE9-2 suggest that the morphology of the proximal hand phalanges and, thus, the morphology of the hand could have remained stable over the last 1.2–1.3 Ma. Taking into account the evidence recently provided by a metacarpal from Kaitio (Kenya) from around 1.42 Ma, we argue that modern hand morphology is present in the genus *Homo* subsequent to *Homo habilis*.

Introduction

Study of the hominin hand provides important information about tool use (Susman, 1994; Ward et al., 2014 and references therein) as well as phylogeny and taxonomy. Analysis of a third metacarpal from Kaitio dated to around 1.42 Ma (millions of years ago) indicates a styloid process morphology similar to that of modern humans (Ward et al., 2014). This suggests that this early *Homo* individual was potentially able to manufacture lithic tools, as later *Homo* individuals did (Marzke and Marzke, 2000). However, the scarcity of hand bones in the human fossil record complicates investigation of the evolution of this anatomical region in the genus *Homo* and consequently when modern-like hand morphology appeared in the fossil record. In particular, little is known about the morphology of hand phalanges in the genus *Homo*, especially from the Early to Middle Pleistocene. Only a small number of *Homo* proximal hand phalanges have been described (Leakey et al., 1964; Lorenzo et al., 1999; Susman et al., 2001; Moyá-Solá et al., 2008). Furthermore, in the case of the Early Pleistocene African fossils, it may be difficult to determine whether they belong to the genus *Homo*, *Australopithecus* or *Paranthropus* (Susman et al., 2001; Moyá-Solá et al., 2008).

Some morphological traits of the hominin hand seem to have been in stasis for over a million years (Lorenzo et al., 1999; Ward et al., 2014), although verifying evolutionary trends in hand phalanges through the late Early and early Middle Pleistocene is thwarted by the paucity of fossil remains from early *Homo* and Middle Pleistocene hominins. The ATE9-2 specimen (a hominin

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adult left hand phalanx, probably of the fifth finger, Fig. 1) from Sima del Elefante described and compared here thus represents an important contribution in the understanding of the evolution of the hand phalanges in the Early and Middle Pleistocene. The best evidence for the evolution of the Pleistocene hominin hand comes from comparisons of Neandertals and modern humans. Although there are no key differences in the morphology of the hand between these two taxa, the proximal hand phalanges of Neandertals display broader diaphyses and trochleas (Musgrave, 1970; Trinkaus, 1983; Villemeur, 1994) compared with the more gracile form evident in modern human populations. These traits observed in Neandertals have been related to corporal robusticity (Trinkaus, 1983). Alternatively, they could represent the primitive morphological pattern, since relatively broad trochleas in proximal hand phalanges are evident in *Homo antecessor* (Lorenzo et al., 1999; Carretero et al., 2001). Nonetheless, the *H. antecessor* hand phalanges from the Early Pleistocene site of TD6, dated to around 900–950 ka (thousands of years ago) (Berger et al., 2008), are very similar to modern humans and Neandertals (Lorenzo et al., 1999).

During the 2008 field season, the ATE9-2 specimen was recovered from square I-28 of the TE9c level of the Sima del Elefante cave site (Sierra de Atapuerca, Burgos, northern Spain). It was found at the same depth and less than 2 m from the hominin mandible ATE9-1 (Carbonell et al., 2008) that has been referred to *Homo* sp. (Bermúdez de Castro et al., 2011). The Sima del Elefante cave site (TE) is located in the Railway Trench, 100 m from the entrance and about 200 m away from the Gran Dolina cave site (Bermúdez de Castro et al., 1999; Fig. 2). The TE site corresponds to a sedimentary karstic infilling stopping up the entrance to the so-called 'Galería Baja', which belongs to the Cueva Mayor-Cueva del Silo complex where the Sima de los Huesos site is also located (Arsuaga et al., 1997a; Fig. 2).

The Sima del Elefante cave is about 15 m wide and the railway outcrop exposed a sedimentary thickness of about 25 m. The section is formed by 16 lithostratigraphic units mostly composed of debris flow deposits and defined by major unconformities, (TE7–TE21) (Rosas et al., 2006; Fig. 2). Starting in 1996, the entire TE sequence was cleaned, and a vertical profile of the infilling has been undertaken. Samples were taken mainly for biostratigraphic and geochronological studies. Furthermore, starting in 2005, an excavation of the TE9 level was conducted on an area of more than 30 m^2. A complete and detailed biostratigraphical study was done by Cuenca-Bescós et al. (2010, 2013) and Rofes and Cuenca-Bescós (2013). The climatic conditions and environment at the time of formation of the TE7–TE16 levels (the so-called Sima del Elefante Lower Red Unit) was researched by Blain et al. (2010), whose findings were based on the amphibian and squamate reptile assemblages.

Paleomagnetic study of TE reveals that stratigraphic layers TE7–TE16 have reverse magnetization directions only (Parés et al., 2006; Fig. 1). These results are consistent with a Matuyama age of the sediments (1.78–0.78 Ma) and with the mammal assemblage (Carbonell et al., 2008; García et al., 2008; Cuenca-Bescós et al., 2013). Two dates based on the radioactive decay of cosmogenic ^{26}Al and ^{10}Be obtained in the TE9 and TE7 (Fig. 1) suggest a range of 0.95–1.38 Ma for these levels (Carbonell et al., 2008). Thus, based on a combination of paleomagnetism, cosmogenic nuclides, and biostratigraphical data, the TE9 level has been dated to the Early Pleistocene (about 1.2 Ma) or possibly even older (1.3 Ma).

The objective of this report is to present and comparatively describe the ATE9-2 specimen, which together with the mandible ATE9-1 (Carbonell et al., 2008) and the Barranco León deciduous molar (Toro-Moyano et al., 2013), represents one of the oldest hominin fossils found in Europe. We also carry out a study of proximal hand phalanges in fossil humans in comparison with ATE9-2 in order to test when the modern hand morphology appeared and establish the polarity of the ATE9-2 morphology.

Material and methods

Our comparative sample comprised original fossils of proximal hand phalanges of the fifth finger (PHP5) from Kebara 2, La

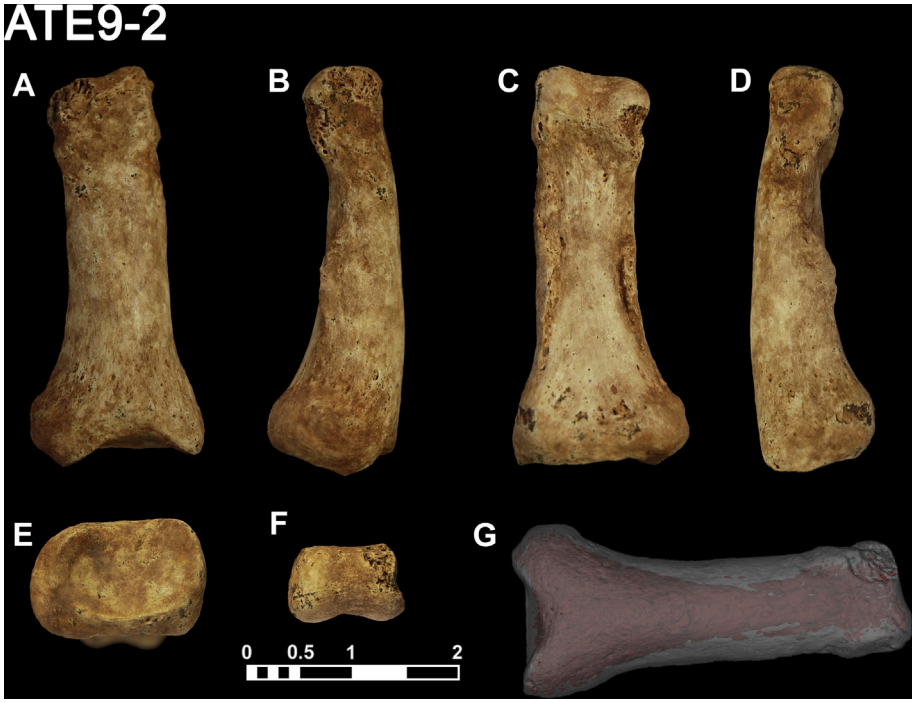

Figure 1. ATE9-2. Fifth proximal hand phalanx. Views: A) dorsal, B) lateral, C) plantar, D) medial, E) proximal, F) distal, G) 3D reconstruction from CT images. Scale in cm.

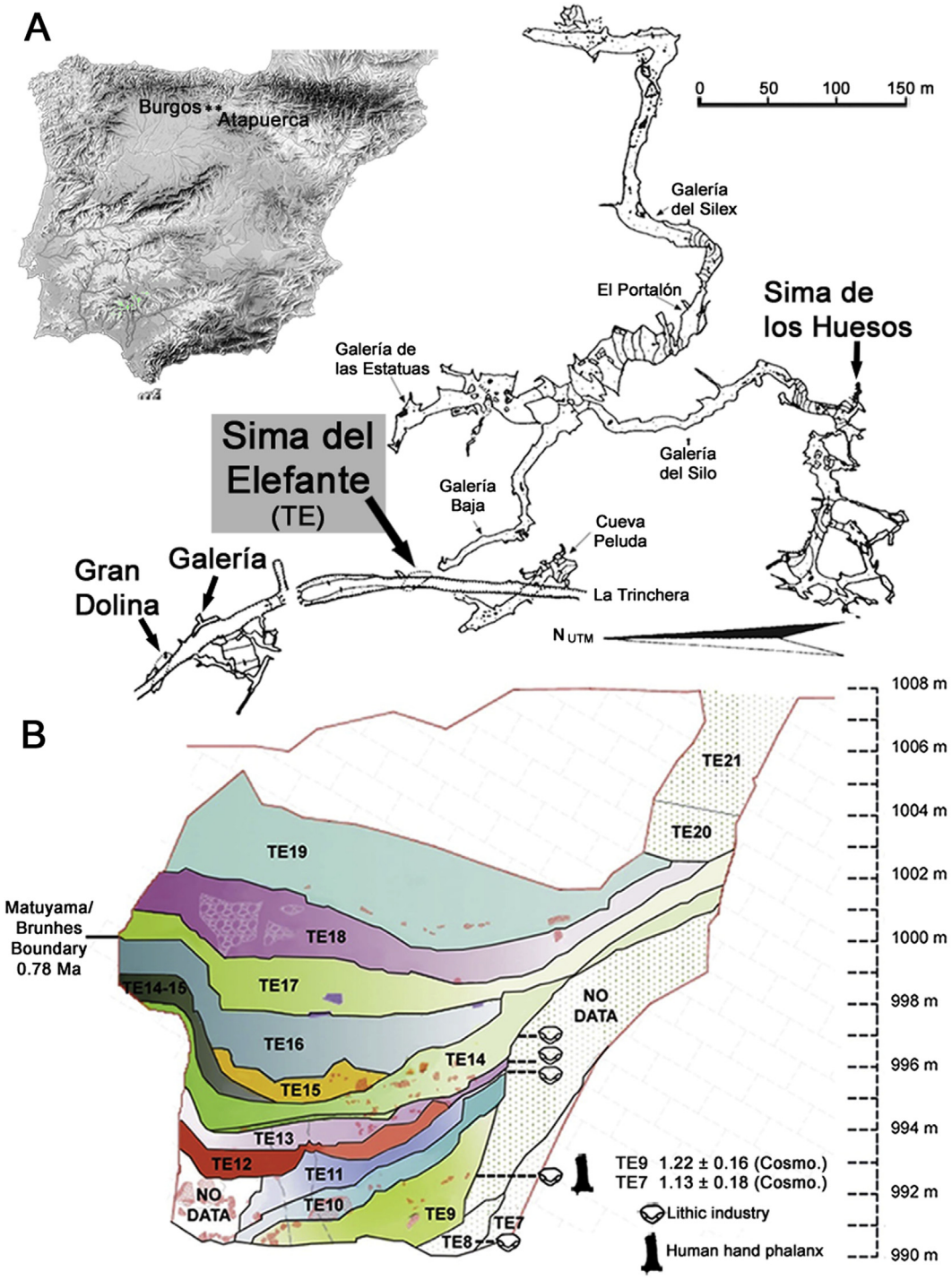

Figure 2. A) Location of the Sima del Elefante site in relation to other sites in the Railway Trench at Atapuerca (Burgos, Spain). B): Stratigraphic profile of the Sima del Elefante cave site. Cosmogenic burial ages in TE7 and TE9 are also shown, with the standard error given at the 68% confidence interval.
Modified from Pérez-Martínez in Huguet (2007).

Ferrassie 1 and 2 and Middle Pleistocene material from Sima de los Huesos (SH) in Atapuerca (Lorenzo et al., 2012), as well as previously published raw data from Shanidar 4 and 5 (Trinkaus, 1983), El Sidrón SDR-083 (Sierra Gómez, 2000), Dolní Věstonice 3, 14, 15 and 16 (Trinkaus and Jelínek, 1997; Sládek et al., 2000), Qafzeh 7, 8 and 9 (Vandermeersch, 1981), Skhul 4 (McCown and Keith, 1939) Pavlov 31p (Trinkaus et al., 2010), and UW.88.121 (*Australopithecus sediba*) from Malapa (Kivell et al., 2011). We also included our own measurements of the Stw 28 cast (early *Homo* or *Australopithecus*) from Sterkfontein Member 4. The modern human sample was drawn from the Hamann-Todd collection (composed of 96 individuals consisting of 48 Euro-Americans and 48 Afro-Americans) housed in the Cleveland Museum of Natural History (Ohio, USA), as well as a further recent human sample of 38 Europeans (Musgrave, 1970). In addition, published phalangeal curvature data from Plio-Pleistocene southern African hominin specimens, and Pliocene

Hadar specimens (Susman et al., 1984, 2001; Susman, 1989) were used in comparisons.

The morphological variables used in our analyses are as described in Bräuer (1988), detailed in Appendix A, Supplementary Online Material (SOM Table SI.1 and Figure SI.1). We used standard anthropometric techniques and instruments to take all measurements (digital calipers to the nearest 0.1 mm). In order to describe the size, relative proportions and articular dimensions of the proximal hand phalanx ATE9-2, ten linear variables (total length, articular length, proximal maximum height, proximal maximum breadth, proximal articular height, proximal articular breadth, midshaft height, midshaft breadth, distal height and distal breadth) and five indices (Table 1) were used, along with qualitative morphological descriptions. In order to test to which finger the phalanx ATE9-2 belongs, a discriminant function analysis (DFA) was carried out on our modern human sample of known rays, and the fossil ATE9-2 classified into one of the phalanx groups.

Phalanx curvature was assessed through examining the included angle (θ). One of several methods proposed to quantify the curvature of the phalanges (Stern et al., 1995; and references therein), θ has been demonstrated to be highly correlated with the normalized curvature moment arm and can be obtained from phalangeal landmarks and distances (Susman et al., 1984; Jungers et al., 1997; see Table 2 for measurement protocol).

A comparative univariate analysis of all of the variables was undertaken. To compare individual values from ATE9-2 with the averages from the fossil and modern samples, Z-scores were calculated, and a value of 1.96 was considered significant ($p < 0.05$,

Table 1
Comparisons of ATE9-2 fifth proximal hand phalanx measurements (in mm).

	ATE9-2	Stw 28	*A. sediba* (UW.88.121)	SH	Neandertals	LP H.sap	MH–HTH	MH–Mus
Total length (TL)	34.7	32.4	**27.2**^{1,2,3}	33.7 ± 1.5 [31.8–35.0] ($n = 5$)	33.5 ± 2.6 [30.2–37.2] ($n = 7$)	35.4 ± 3.4 [29.8–38.4] ($n = 5$)	34.0 ± 2.7 [29.3–41.6] ($n = 96$)	–
Articular length (AL)	32.3	30.1	–	31.9 ± 1.3 [30.5–33.6] ($n = 5$)	31.8 ± 2.5 [28.9–35.4] ($n = 7$)	28.0 ($n = 1$)	32.1 ± 2.6 [27.5–39.5] ($n = 96$)	31.8 ± 2.2 [26.2–36.0] ($n = 38$)
Proximal maximum height (PMH)	10.3	11.1	**8.5**^{2,4}	**9.9**^{2} ± 0.8 [9.2–11.1] ($n = 6$)	**11.0**^{4,5} ± 0.7 [10.1–12.1] ($n = 8$)	10.1 [9.2–11.0] ($n = 2$)	10.3 ± 0.9 [8.7–12.2] ($n = 96$)	10.2 ± 0.9 [8.1–12.6] ($n = 38$)
Proximal maximum breadth (PMB)	15.1	12.7	**10.8**^{1,2,4,5}	14.7 ± 1.5 [13.0–17.0] ($n = 7$)	14.8 ± 1.7 [12.9–16.7] ($n = 8$)	13.8 [12.5–15.0] ($n = 2$)	14.1 ± 1.2 [11.7–17.1] ($n = 96$)	14.4 ± 1.0 [11.7–16.8] ($n = 38$)
Proximal articular height (PAH)	8.7	9.5	–	8.6 ± 0.8 [7.7–9.5] ($n = 5$)	9.0 ± 0.9 [7.8–10.4] ($n = 8$)	–	9.0 ± 0.9 [7.3–11.3] ($n = 96$)	–
Proximal articular breadth (PAB)	11.9	11.7	–	11.1 ± 1.0 [10.0–12.3] ($n = 6$)	11.2 ± 1.1 [9.7–12.7] ($n = 8$)	–	11.0 ± 1.1 [8.5–13.6] ($n = 96$)	–
Midshaft height (MdH)	**6.5**^{2}	**6.3**^{2}	**4.3**^{1,2,4}	6.1 ± 0.6 [5.3–6.8] ($n = 7$)	5.5 ± 0.4 [4.9–6.2] ($n = 8$)	5.3 ± 0.6 [4.4–6.0] ($n = 6$)	5.7 ± 0.7 [4.1–7.0] ($n = 96$)	5.6 ± 0.7 [4.4–7.2] ($n = 38$)
Midshaft breadth (MdB)	8.9	8.8	7.7	**9.4**^{3,4,5} ± 1.0 [8.4–10.6] ($n = 7$)	**9.5**^{4,5} ± 1.2 [7.7–10.8] ($n = 8$)	8.2 ± 1.0 6.9–9.6] ($n = 6$)	8.4 ± 1.1 [5.9–10.6] ($n = 96$)	8.3 ± 1.2 [5.6–11.0] ($n = 38$)
Distal height (DH)	6.4	7.6	**5.0**^{1,2,4,5}	6.5 ± 0.6 [5.7–7.3] ($n = 8$)	6.6 ± 0.7 [5.7–7.6] ($n = 7$)	6.5 ± 0.8 [5.6–7.5] ($n = 4$)	**6.5**^{5} ± 0.7 [5.0–8.8] ($n = 96$)	7.0 ± 0.8 [5.4–8.8] ($n = 38$)
Distal breadth (DB)	9.8	9.6	**7.7**^{1,2,5}	**10.0**^{4} ± 0.9 [8.8–11.2] ($n = 8$)	**10.7**^{4,5} ± 1.1 [9.5–12.2] ($n = 7$)	10.3 ± 1.4 [8.3–11.1] ($n = 4$)	**9.3**^{5} ± 0.9 [7.3–11.5] ($n = 96$)	9.7 ± 0.8 [8.2–11.9] ($n = 38$)
Proximal index	68.2	**87.4**^{1,4,5}	**78.7**^{1,5}	**69.0**^{3,4} ± 3.5 [63.9–72.1] ($n = 6$)	74.9 ± 6.6 [67.7–88.4] ($n = 8$)	73.5 [73.3–73.6] ($n = 2$)	**73.3**^{5} ± 3.2 [67.2–81.9] ($n = 96$)	71.0 ± 3.4 [65.3–80.0] ($n = 38$)
Articular proximal index	73.1	81.2	–	78.8 ± 3.5 [76.2–84.8] ($n = 5$)	80.4 ± 5.0 [73.6–90.5] ($n = 8$)	–	81.8 ± 5.5 [69.9–97.1] ($n = 96$)	–
Midshaft index	**73.0**^{2,3}	**71.6**^{3}	**55.8**^{3,4,5}	64.5 ± 6.2 [53.9–73.3] ($n = 7$)	**58.3**^{4,5} ± 7.4 [47.2–70.1] ($n = 8$)	64.6 ± 1.6 [62.5–66.3] ($n = 5$)	67.7 ± 5.3 [53.8–81.2] ($n = 96$)	68.2 ± 5.9 [55.4–83.9] ($n = 38$)
Distal index	**65.3**^{2}	**79.2**^{1,2,4}	**65.9**^{2}	**65.2**^{2,4,5} ± 1.4 [62.6–67.0] ($n = 8$)	**62.0**^{4,5} ± 1.5 [60.0–63.5] ($n = 7$)	65.1 [59.6–68.2] ($n = 3$)	**70.5**^{5} ± 3.4 [60.0–78.5] ($n = 96$)	72.1 ± 3.8 [63.6–82.7] ($n = 38$)
Robusticity index	23.8	25.1	–	**23.9**^{5} ± 2.0 [22.6–27.4] ($n = 5$)	23.2 ± 1.3 [21.4–24.8] ($n = 7$)	20.2 ($n = 1$)	21.9 ± 2.2 [16.9–26.6] ($n = 96$)	21.9 ± 2.1 [17.4–26.5] ($n = 38$)

Mean ± standard deviation, range [ ] and sample size (n) are shown. Bold letters and superscript indicate significant differences with some of the samples (Z-score > 1.96 in absolute terms and Mann–Whitney test; $p < 0.05$); 1 = SH, 2 = Neandertals, 3 = Late Pleistocene *H. sapiens*, 4 = Hamann-Todd Osteological Collection (HTH), 5 = Musgrave's (1970) sample (Mus). Modern Humans (MH–HTH and MH–Mus) are pooled sex samples. Data for Stw 28 from cast (AMNH); data for *A. sediba* (UW.88.121) from Kivell et al. (2011).

Neandertal sample includes: Shanidar 4 (right and left), Shanidar 5 (right), Kebara 2 (left), La Ferrassie 1 and 2 (right and left), SDR-083 (left). Sima de los Huesos (SH) sample includes: AT-95, AT-515, AT-1326, AT-1327, AT-1390, AT-1486, AT-1827, AT-2479, AT-2831 and AT-4478. Late Pleistocene *H. sapiens* (LP H.sap) sample includes: Dolní Věstonice-DV 3 (right), DV 14 (right?), DV 15 (right?), DV 16, Qafzeh 7 (right); Qafzeh 8 (right), Qafzeh 9 (right); Skhul 4 (left) and Pavlov 31p (right?).

Proximal index = Prox. max. height/Prox. max. breadth × 100. Articular proximal index = Prox. artic. height/Prox. artic. breadth × 100. Midshaft index = Midshaft height/Midshaft breadth × 100. Distal index = Dist. height/Dist. breadth × 100. Robusticity index = (Midshaft breadth + Midshaft height) × 100/2 × (Articular length).

Table 2
Included angle of manual proximal phalanges.

Specimen	Phalangeal dorsal height (H)	Included angle	Source
ATE9-2	5.3	27.0	Present study
AL288-1	5.5	40.5	Bush et al., 1982; Susman et al., 1984
AL333-19	6.3	39.7	Bush et al., 1982; Susman et al., 1984
AL333-57	6	40.0	Bush et al., 1982; Susman et al., 1984
AL333-62	6.4	46.5	Bush et al., 1982; Susman et al., 1984
AL333-63	6.9	44.0	Bush et al., 1982; Susman et al., 1984
AL333-93	5.6	34.6	Bush et al., 1982; Susman et al., 1984
AL333-w4	6.8	32.4	Bush et al., 1982; Susman et al., 1984
SKX 5018	–	27.0	Susman, 1989
SKX 15468	5.5	30.7	Susman et al., 2001
SKX 16699	–	22.0	Susman et al., 2001
SKX 22741	–	27.0	Susman, 1989
SKX 27431	–	34.0	Susman, 1989
Stw 355	–	36.0	Susman et al., 2001
H. sapiens mean[1]	–	26.0	Susman, 1989
Chimp mean[1]	–	42.0	Susman, 1989

Measurements in mm, included angle in degrees. The phalangeal dorsal height (H) is used to calculate the included angle following the method proposed by Stern et al. (1995) [$\theta = ((H - MdH/2)^2 + (TL/2)^2)/2(H - MdH/2)$]. [1] = The mean values for modern humans (*H. sapiens*) and chimps are provided (Susman, 1989).

Sokal and Rohlf, 2003). Z-scores were only calculated in cases where the 'n' of the comparative samples was equal to or greater than five. To better understand the position of ATE9-2 in the context of human evolution, and also to characterize the comparative samples, we compared the values of the different samples/populations with a Mann–Whitney *U*-test (Mann and Whitney, 1947). For statistical analysis, we used STATISTICA 8.0 (StatSoft, 2007).

Results

Description and identification

The bone is complete and its dimensions are shown in Table 1. The proximal epiphysis is fused, and therefore this bone belonged to an adult individual over 16 years of age according to modern human development patterns (Scheuer and Black, 2000; Cardoso and Severino, 2010). The fossil displays a flat palmar surface and a transversally convex dorsal surface. Bilateral flexor sheath ridges are present on the palmar surface; the left ridge is slightly more developed and more projected palmarly. The proximal articular surface for the metacarpal is oval, concave and its dorsal border is slightly indented, which facilitates the hyperextension of the digit. In dorsal view, the base presents a prominent lateral tubercle for the insertion of the abductor digiti minimi muscle on the left side and the trochlea shows a right deviation. All of these traits suggest identification as a proximal hand phalanx of a left fifth finger. The distinction of proximal hand phalanges from rays 2–5 is difficult, and often can be distinguished only when all of the phalanges of the same hand are present. Given that ATE9-2 is an isolated element, to corroborate the finger assignment we performed a DFA to classify the ray of this proximal phalanx. The DFA (SOM Table SI.2 and Fig. SI.2) carried out with the proximal phalanges from ray 2–5 correctly classifies 82.6% of the modern phalanges, but specifically for the fifth finger the correct classification is much higher (97.9%). The results of the DFA indicate that ATE9-2 falls comfortably within the range of variation of ray 5 but outside the range of variation of rays 3 and 4. Although it falls just within the 95% equiprobability ellipse for ray 2, the results of our DFA classified ATE9-2 as a fifth phalanx with a posterior probability of 96.6%. Hence, we considered that ATE9-2 is a proximal hand phalanx from the fifth finger. Due to shape variability between rays, in our fossil comparative sample and further analyses we thus only used phalanges that are known to belong to the fifth finger.

Metrical comparisons

Table 1 shows the values of the different variables measured for the phalanx ATE9-2, as well as for the rest of the fossil specimens, and the main statistical parameters of the comparative samples (mean, standard deviation, range and sample size). For nearly all of the variables, ATE9-2 does not display significant differences from the comparative samples. However, ATE9-2 and Stw 28 both show a diaphysis that is absolutely and relatively higher than those of the Neandertals, as evidenced by the midshaft height (Fig. 3A) and the midshaft index (midshaft index = midshaft height/midshaft breadth × 100), with the latter significantly higher in ATE9-2 relative to Neandertals and Late Pleistocene *Homo sapiens* samples (Fig. 3D). Moreover, the distal index (distal index = dist. height/dist. breadth × 100) is also significantly higher in ATE9-2, Stw 28 and UW 88.121 compared with Neandertals (Fig. 3C). This is likely due to the broad distal articulations of the fifth proximal hand phalanges present in Neandertals (Trinkaus, 1983; Villemeur, 1994).

Although Stw 28 is similar to ATE9-2 in having a high diaphysis, Stw 28 displays high proximal and distal indices due to the small breadth of the proximal epiphysis and the high distal trochlea (Table 1). The fifth proximal hand phalanx of *A. sediba* (UW.88.121) is smaller than nearly all of the studied samples. However, its proximal index is higher than that of the SH population and modern humans. The midshaft index is lower than that of Late Pleistocene *H. sapiens* and modern humans and the distal index is higher than that of Neandertals.

The fifth proximal hand phalanges of Neandertals display absolutely thick and wide diaphyses (Fig. 3B) and broader distal articulations relative to the other samples (Musgrave, 1973; Trinkaus, 1983), except SH (Lorenzo et al., 2012). Another trait that the Neandertal and SH samples share is the low distal index compared with modern humans. ATE9-2 shares a relatively broad trochlea with SH, Neandertals and TD6, and it is different to the earlier Stw 28 phalanx (Lorenzo et al., 1999 and Fig. 3C). Moreover, the Neandertals exhibit a high base and a low midshaft index, due mainly to the broad diaphyses of their hand proximal phalanges, including the fifth finger.

The phalanx curvature value obtained for the ATE9-2 phalanx (Table 2) is identical to the value for SKX 5018 and SKX 22741, close to the modern human mean and above the value of SKX 16699 (Susman et al., 1984, 2001; Susman, 1989 and Table 2). The value of ATE9-2 is lower than that obtained for SKX 15468, SKX 27431, Stw 355 and all the Hadar fossils, which represent the highest values

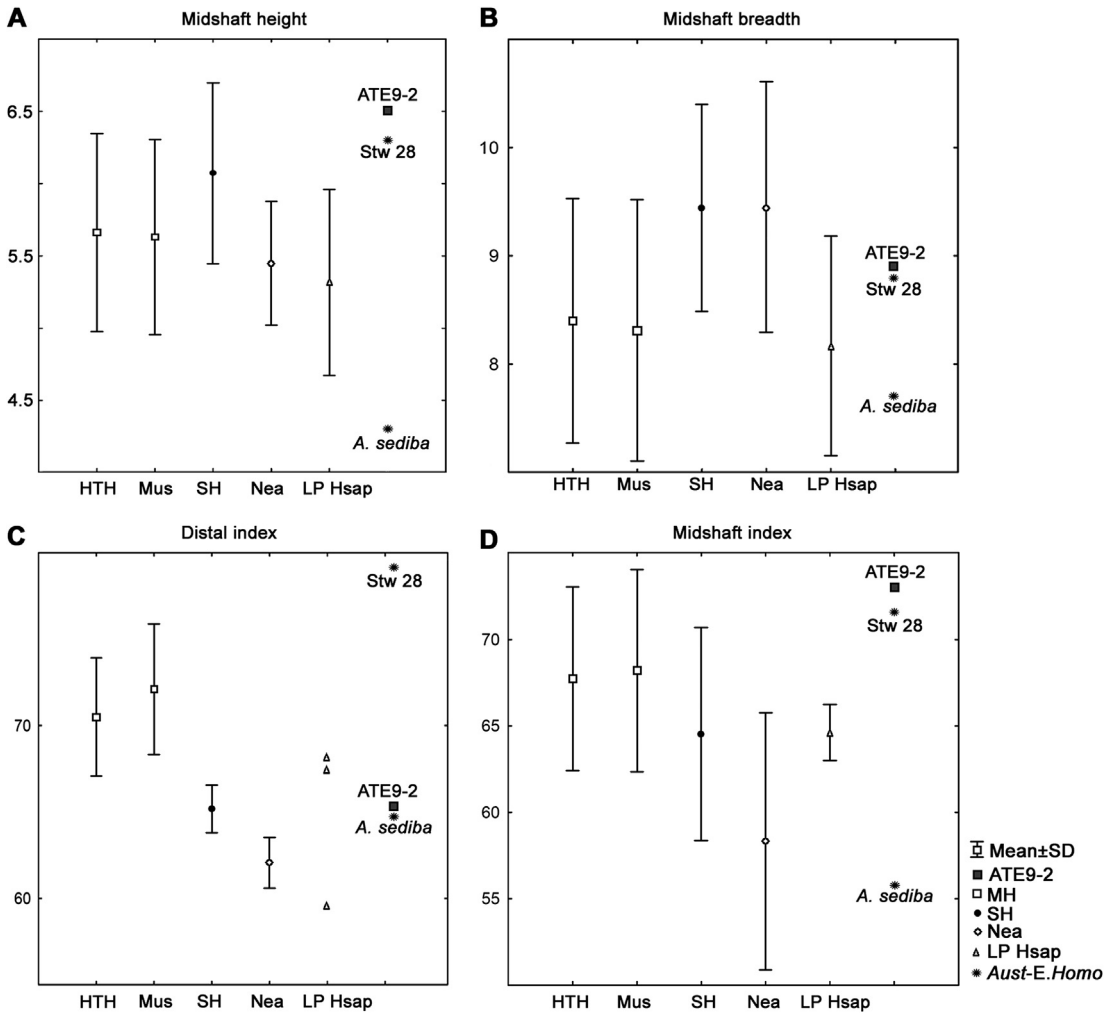

Figure 3. Univariate analysis of ATE9-2 and the comparative samples. HTH = Modern Humans (MH) – Hamann-Todd Osteological collection, Mus = Modern humans from Musgrave (1970), SH = Sima de los Huesos, Nea = Neandertals, LP Hsap = Late Pleistocene *H. sapiens*, *Aust*-E.*Homo* = *Australopithecus* or early *Homo*, *A. sediba* = UW.88.121 of *A. sediba*. SD = standard deviation. A) Midshaft height (in mm), B) Midshaft breadth (in mm), C) Distal index, D) Midshaft index.

among early hominins. Other early hominin phalanges show higher values, which are closer to or above the chimpanzee mean (Susman et al., 1984, 2001; Susman, 1989).

Discussion and conclusions

Our comparative analysis of ATE9-2 supports previous assertions that the morphology of the hand, at least as far as we can ascertain from study of the fifth proximal phalanges, appears to have remained quite stable during the Early, Middle and Late Pleistocene (Vandermeersch, 1981; Trinkaus, 1983; Lorenzo et al., 1999; Ward et al., 2014). Relatively broad phalangeal trochleas seem to be the primitive morphology for *Homo*, ATE9-2, the TD6 sample, SH and Neandertals, although modern humans show derived relatively narrow phalangeal trochleas (Lorenzo et al., 1999; Carretero et al., 2001). In common with Neandertals, SH and TD6 populations, ATE9-2 displays a robust proximal phalanx, probably related to a greater overall bodily robusticity. The only differences seen in the available fossil record for the fifth proximal hand phalanx are the broad diaphyses and distal articulations shared by Neandertals (Musgrave, 1973; Trinkaus, 1983) and SH samples.

The expansion of the distal articulation in the fifth proximal hand phalanges in SH and in Neandertals could be an adaptation for an increased stress level at the fingertip (Trinkaus, 1983). It could also reflect the evolutionary relationship between these two populations (Arsuaga et al., 1997b, 2014; Carretero et al., 1997; Martínez and Arsuaga, 1997; Gómez-Olivencia et al., 2007; Bonmatí et al., 2010; Martinón-Torres et al., 2013; Pablos et al., 2013, 2014) or that both the SH population and Neandertals exhibit a broad and robust body size. The body robusticity of these hominins is indicated by the robust and very broad pelves with very long superior pubic rami, long femoral necks, absolutely and relatively long clavicles, mediolaterally broad axes, long transversal processes in the lumbar vertebrae, large thoraxes, large tali with broad lateral malleolar facets and robust calcanei with broad sustentaculum tali (Carretero et al., 1997, 2004; Arsuaga et al., 1999; Gómez-Olivencia et al., 2007, 2009; Bonmatí et al., 2010; Pablos et al., 2012, 2013, 2014). As was previously proposed, this robust morphotype is probably the primitive condition within the genus *Homo* from which modern humans departed (Arsuaga et al., 1999; Bonmatí et al., 2010).

Compared with raw measurements of later specimens, Stw 28 only differs significantly in midshaft height, but because of this the proximal and distal indices of Stw 28 are significantly different from all of the comparative samples including ATE9-2. The phalanx of *A. sediba* is smaller and with different proportions than all of the later fifth proximal phalanges. *Australopithecus* fossils usually

display curved proximal hand phalanges (Susman et al., 1984, 2001). In contrast, it is accepted that phalanges from the genus *Homo* are straighter, except those of OH 7 (Susman and Creel, 1979; Susman et al., 1984) and other early *Homo* or *Paranthropus* specimens from Swartkrans. Our study indicates that the diaphysis of ATE9-2 is as straight as other phalanges of later members of the genus *Homo*, some South African fossils and modern humans, but is different from the curved phalanges of *Australopithecus afarensis* and OH 7.

Hand morphology has been linked to tool manufacture in a number of studies (Susman, 1994; Marzke, 1997; Marzke and Marzke, 2000; Susman et al., 2001), and on the basis of the straightness of the diaphyses in the proximal phalanges from Swartkrans it has been proposed that tools were likely used by all early hominins from two million years ago (Susman, 1994, 1998). Our analyses indicate some differences in fifth proximal phalanx morphology between African *Australopithecus*/early *Homo* and Eurasian Pleistocene samples, but given the apparent stability in hand morphology over the past 1.4 Ma, future studies should examine in more detail the discrepancy between this stability and the radical changes in tool technology and manufacturing processes over the same time period. It is possible that either the morphology of the hand is not related to the advances in lithic technology or that the morphological features needed for manufacturing complex technologies arose early in the evolution of the genus *Homo*. Ideally, more fossil hand bones, particularly from the Early and Middle Pleistocene are needed to test this hypothesis, but further detailed morphological and biomechanical research is possible on the proximal phalanges, such as ATE9-2, already existing in the fossil record, which to date have received very little attention.

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Appendix A. Supplementary online material

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jhevol.2014.08.007

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