

Metatarsals and foot phalanges from the Sima de los Huesos Middle Pleistocene site (Atapuerca, Burgos, Spain)

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Abstract

This study provides a complete, updated and illustrated inventory, as well as a comprehensive study, of the metatarsals and foot phalanges (forefoot) recovered from the Middle Pleistocene site of Sima de los Huesos (SH, Atapuerca, Spain) in comparison to other *Homo* comparative samples, both extant and fossils. This current updated review has established a minimum number of individuals (MNI) of 17, which represent 58.6% of the 29 dental individuals identified within the SH sample. An exclusive or autoapomorphic combination of traits can be recognized within the SH hominin foot sample. A few traits appear primitive or plesiomorphic when compared with earlier *Homo* individuals and other recent modern humans. There are other metrical and morphological traits that SH hominins and Neandertals have in common that sometimes represent shared derived traits in this evolutionary line, most of which are probably related to robusticity. Furthermore, some exclusive autoapomorphic traits are observed in the SH sample: a very broad first metatarsal, long and broad hallucal proximal foot phalanges and possibly extremely robust lateral distal foot phalanges compared to those of Neandertals and modern humans. In these last traits, the SH metatarsals and pedal phalanges are even more robust than in Neandertals. They are herein named as “hyper-Neandertal” traits, which could suggest a slight gracilization process in this evolutionary line, at least in the hallux toe. Finally, some paleobiological inferences are made in relation to body size (stature and body mass) and some associations are proposed within the SH sample.

KEYWORDS

body size, feet, inventory, neandertal ancestors, stature estimation

1 | INTRODUCTION

The role of the foot is significant to locomotion and body size estimations (McHenry, 1992; Pablos, Gómez-Olivencia, et al., 2013a; Trinkaus, 1975; Trinkaus, Robson Brown,

et al., 2017b), which makes their studies highly relevant in human evolution. Despite their scarcity in the *Homo* fossil record prior to Neandertals and *Homo sapiens*, foot fossils also clear up some taxonomic issues and establish evolutionary relationships among

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different species/groups (Harcourt-Smith et al., 2015; Lu et al., 2011; Pablos et al., 2012; Trinkaus, 1983; Will et al., 2017). Moreover, when isolated foot fossils are discovered it is not always easy to taxonomically assign them to a specific species (Haile-Selassie et al., 2012; Mallegni & Busoni, 1986).

Before Neandertals, very few foot fossils exist in the *Homo* fossil record, and they are typically geographically and chronologically distant, thus hindering their comparisons (Hammond et al., 2021; Harcourt-Smith et al., 2015; Lordkipanidze et al., 2007; Pablos et al., 2012; Pearson et al., 2008; Rightmire et al., 2006; Sun-joo et al., 2019). In order to gain a better understanding of the origin of the morphology of the Neandertal foot, it is necessary to study the Early and Middle Pleistocene specimens of genus *Homo* in depth. In general, Neandertal feet are morphologically and biomechanically similar to those of recent and fossil modern humans in overall size and proportions (Endo & Kimura, 1970; McCown & Keith, 1939; Pearson et al., 2020; Pomeroy et al., 2017; Trinkaus, 1983, 2016; Vandermeersch, 1981). One of the main characteristics that differentiates modern humans from Neandertals is the robusticity of the latter in comparison to the former. However, some metric and morphological traits distinguish each group/population. Neandertal tarsal bones tend to be larger with large articular surfaces, and their metatarsals and foot phalanges are wider than recent and fossil modern humans (Pablos et al., 2014; Pablos, Gómez-Olivencia, & Arsuaga, 2019a; Pablos, Martínez, et al., 2013b; Pearson et al., 2020; Pomeroy et al., 2017; Trinkaus, 1983; Trinkaus, Robson Brown, et al., 2017b; Vandermeersch, 1981). These traits differentiating Neandertals from *Homo sapiens* have traditionally been attributed to more biomechanical stress and greater general robustness of the postcranial skeleton in Neandertals (Arsuaga et al., 2015; Trinkaus, 1975; Vandermeersch, 1981). Recent modern humans, though gracile, probably descend from robust groups from Africa (Bonmatí et al., 2010; Di Vincenzo et al., 2015; Simpson et al., 2008; Trinkaus, 2012), indicating that a strong gracilization process relative to archaic humans, including the narrowing of the whole foot without a decrease in length, has gradually taken place from the Early Pleistocene to present-day populations (Chirchir et al., 2015; Ryan & Shaw, 2015).

In this study, we present a metric and morphological study, together with a complete graphic and descriptive inventory, of the metatarsals and foot phalanges (fore-foot) from the Middle Pleistocene site of Sima de los Huesos—SH (Atapuerca, Burgos, Spain). More than 7000 human fossils have been recovered from this site throughout more than 40 years of excavation and research (Arsuaga et al., 2014, 2015), of which more than 500 belong to the foot (Pablos, 2015). They belonged to a

minimum of 29 individuals from both sexes, mostly corresponding to late adolescents or young adults (Bermúdez de Castro et al., 2021). They are closely related to Neandertals, both genetically (Meyer et al., 2014, 2016), and morphologically, in spite of some exclusive or autoapomorphic traits present in this Middle Pleistocene population (Arsuaga et al., 2014, 2015; Bermúdez de Castro et al., 2023; Carretero et al., 1997; Gómez-Olivencia et al., 2007; Martínez & Arsuaga, 1997; Pablos et al., 2014; Pablos, Martínez, et al., 2013b). All the human remains from SH were found in the lithostratigraphic unit—LU-6 (Aranburu et al., 2017), which has been dated to 430–450 ka (Arsuaga et al., 2014; Demuro et al., 2019). The most likely hypothesis suggests that these skeletons were complete when deposited as an act of intentional funerary behavior of anthropic origin (Arsuaga et al., 1991; Arsuaga, Martínez, Gracia, Carretero, et al., 1997b; Sala et al., 2016; Sala, Arsuaga, Pantoja-Pérez, et al., 2015b; Sala, Pantoja-Pérez, et al., 2023a). Finally, body size will be estimated based on the dimensions of the metatarsals.

Our main objective is to morphologically and metrically characterize the metatarsal and foot phalangeal sample from SH in the context of the evolution of the genus *Homo*. The observed morphology is discussed from a biomechanical and phylogenetic perspective. We provide a proxy for body size based on the maximum metatarsal length. Additionally, we offer a comparative study of other known foot fossils from the Early, Middle and Late Pleistocene.

2 | MATERIALS AND METHODS

More than 500 fossils constitute the SH foot sample, of which 135 belong to metatarsals and 289 to foot phalanges (Arsuaga et al., 2015; Pablos, 2015; Pablos et al., 2017). They represent nearly the same number of specimens in the entire Neandertal world record, and there are many more than what are found in the worldwide *Homo* fossil record prior to *Homo sapiens* and Neandertals.

2.1 | Comparative samples and variables studied

Several *Homo* fossil samples have been used for metric and morphological comparisons of the SH metatarsal and phalanges (see Arsuaga et al., 2014; Pablos et al., 2012, 2014, 2017; Pablos, Gómez-Olivencia, & Arsuaga, 2019a; Pablos, Gómez-Olivencia, Maureille, et al., 2019b; Pablos, Martínez, et al., 2013b; Pomeroy et al., 2017; Trinkaus et al., 2014 for details), mainly focusing on Neandertal

and early modern human samples. The data sources are mainly bibliographic, but some original specimens/samples have been measured and studied by the authors (e.g., La Ferrassie, La Chapelle-Aux-Saints, Tabun, Jarama VI, Regourdou, Cro-Magnon, Gough's Cave, Abri Pataud, Skhul 9, TD6-*H. antecessor*, etc.). Our early modern human sample is divided into Middle Paleolithic modern humans (MPMH) and Upper Paleolithic modern humans (UP). The MPMH sample is essentially composed of the MIS 5 fossils from Skhul and Qafzeh (McCown & Keith, 1939; Vandermeersch, 1981). The MIS 6–7 Omo-Kibish 1 specimen is considered a MPMH despite its age of around 233 ka (Pearson et al., 2008; Vidal et al., 2022) and the fact that it exhibits some morphological differences relative to the Late Pleistocene modern humans (Pablos et al., 2012, 2018; Pearson et al., 2008). Our UP sample is composed of western Eurasian Upper Paleolithic modern humans (see Pablos, Gómez-Olivencia, Maureille, et al., 2019b) for details). Despite morphological changes throughout this period, especially in stature and body proportions, leg and foot robusticity and morphology do not appear to have changed during this time (Trinkaus, 2015; Trinkaus, Wotjal, et al., 2017a).

When available and appropriate, we have included some Eurasian Middle and Early Pleistocene *Homo* fossils in order to assess possible ancestral patterns of pedal morphology, such as the *Homo* specimens from the Dmanisi, TD6-*H. antecessor*, Klasies river, Omo river, Swartkrans, Olduvai, Jinniushan and Koobi Fora samples; and isolated specimens such as Gunang, Tianyuan, Baringo, Arago, etc. In addition, data from three recent/late Holocene comparative samples are included: the Hamann-Todd Osteological collection from the North American 20th century of known sex (Cleveland Museum of Natural History; $n = 244$), the San Pablo Medieval collection of estimated sex (Universidad de Burgos; $n = 45$), and the unshod Woodland Amerindian collection of unknown sex from the site of Libben, Ohio (Kent State University; $n = 40$; Trinkaus, 1975). This last comparative modern human sample is used to take into consideration the fact that the footwear use in recent populations might influence foot morphology. All three recent modern human samples are pooled sex samples. It is very difficult to correctly identify the phalanges of the foot by toe and side (see below). In the modern comparative samples, this identification was made by the authors on the basis of the general decrease in size of the phalanges within the same foot to the lateral side, the degree of relative medial deviation of the distal tuberosity in the fourth and fifth medial and distal phalanges relative each other, the articulation with the metatarsals and other phalanges, and some anatomical points established in several anatomical atlases.

In some of the comparative specimens, the antimeres of a given bone are preserved (e.g., La Ferrassie 1 and 2, Amud 1, Sunghir 1, Tabun 1, and the Shanidar, Skhul, Qafzeh, Dolní Věstonice and Předmostí samples). In these cases we averaged the available bilateral measurements to provide a mean value for each individual.

In other cases/sites the association of individuals is not clear (e.g., Cro-Magnon, Krapina and Moula Guercy samples); for those sites we considered the bones separately (but see Trinkaus et al. (2021) for a discussion about Cro-Magnon feet associations). This was made to better represent the general morphology of individuals rather than elements. Previous studies have shown that there were no significant differences between the left and right foot bones (Bidmos & Dayal, 2003; Pablos, Gómez-Olivencia, et al., 2013a; Saldías et al., 2016). The anatomical variables studied in the present study are linear measurements used in other studies of foot remains, largely following the Martin system (Bräuer, 1988; but see Trinkaus, 1975, 1983, 2016; Pablos et al., 2012; Pablos, Gómez-Olivencia, and Arsuaga, 2019a; Pablos, Gómez-Olivencia, Maureille, et al., 2019b; Pomeroy et al., 2017; Pearson et al., 2020 for details). The metrical variables were selected in order to describe the general morphology and articular size of each bone. Some of these variables permit differentiation of Neandertal pedal remains from other samples. Additionally, some of these variables are related to body size (McHenry & Berger, 1998; Pablos, Gómez-Olivencia, et al., 2013a).

The calculation of the minimum number of individuals (MNI) is usually estimated by identifying the most frequently occurring element in the sample considering adult and immature individuals separately. However, the MNI of the lateral phalanges, specifically those of the second to fifth toe, requires further explanation. There is a great difficulty in correctly determining these phalanges of the foot by toe and side (see below). To calculate the MNI of these elements, a conservative method is applied. The total number of phalanges is divided by the total number of toes in a skeleton. For example, the SH sample includes 93 non-hallucal proximal phalanges. The minimum number of elements (MNE) is 70 as determined by the most represented portion (i.e., the diaphysis and/or the distal end). Out of these, 35 have been identified as immature specimens and 35 as adult. Dividing this number by eight, which is the maximum number of non-hallucal proximal phalanges in a human skeleton, we obtain a MNI of 4.375 individuals. Therefore, at least five adult individuals are represented in the SH sample. We are well aware that this method is highly conservative. However, it enables us to quantify the sample, bearing in mind that this calculation is likely underestimate.

In this study, we refer to exclusive traits as autoapomorphic or derived traits that are exclusive to a population/group. On the other hand, the term primitive is used here to refer to plesiomorphic or ancestral traits.

2.2 | Sex estimation

We are well aware of the limitations of sex assignment in fossil populations. In spite of it, here we try to make initial and approximate assignments to sex based on general size of the metatarsals and foot phalanges, despite the dependence on a reference population. For it, we used similar methods to those used to establish sex from the tali and calcanei from SH (Pablos et al., 2014; Pablos, Martínez, et al., 2013b). The method consists in performing a principal component analysis (PCA) on the raw variables of each element. We compared the coordinates of the first factor from PCA, usually related to general size, in males and females from the modern samples and we found significant differences ($p < 0.05$) between the sexes. In order to try to extrapolate that sexual dimorphism to metatarsals and foot phalanges from SH, we first compared the Neandertal and *Homo sapiens* fossils that usually are considered of known sex. The male fossils fall within the range of variation of modern males for this first factor, and are significantly different from the modern females. The same happens with the fossils that are generally considered to be females: they are in the range of variation of modern females and significantly different from the modern males. Furthermore, when applicable, we confirm our results to those obtained from discriminant function analysis (e.g., Bidmos et al., 2021; Castejón-Molina & Pablos, 2021; Mountrakis et al., 2010).

2.3 | Statistical and osteometric analysis

A comparative univariate analysis of all variables was carried out. We performed a Kruskal-Wallis test to compare differences between the SH and Neandertal, UP, MPMH and recent modern human samples. When a significant difference ($p < 0.05$) was found for a variable, we performed a Mann-Whitney test on all possible pairs of samples to determine which ones were significantly different (Mann & Whitney, 1947). We adjusted the p-values for these comparisons using the Dunn-Sidak method ($1 - (1 - \alpha)^{1/n}$) (Rafter et al., 2002). This method established a new threshold for the significance level at $p < 0.025$. To compare individual values from with the averages from the different samples, Z-scores were calculated when the comparative sample size was ≥ 4 , and a value of 1.96 was considered significant ($p < 0.05$; Sokal & Rohlf, 2003).

3 | RESULTS

In general, the SH feet collection displays both complete bones and fragments in different stages of preservation corresponding to both juvenile and adult individuals. In some cases the fusion scar is still visible, thus indicating an adolescent age for these individuals or specimens. Over the course of than 40 years of excavation and laboratory work, some of the fragments are glued together to make complete bones (e.g., the cranium and other postcranial bones; Gómez-Olivencia et al., 2007; Bonmatí et al., 2010; Arsuaga et al., 2014, 2015; Rodríguez et al., 2016; Carretero, Rodríguez, et al., 2023b; Carretero, García-González, et al., 2023a; García-González et al., 2023). The metatarsals also underwent this gluing process, and so did the phalanges, albeit in fewer instances, as indicated below.

The SH metatarsals and foot phalanges correspond to a minimum number of 17 individuals based on the hallucal proximal phalanx (Table 1), which correspond to 58.7% of the total 29 individuals established using the dental remains (Bermúdez de Castro et al., 2021). Table 2 provides a summary of the statistics for the SH and comparative samples of the main variables considered in this study.

3.1 | Hallucal metatarsal

There are 18 first metatarsals that have been recovered from the Sima de los Huesos site (Pablos et al., 2017), corresponding to a minimum of 15 elements and 11 individuals (Arsuaga et al., 2015), represented by six adults and five juveniles (Table 1 and Figure 1). The complete inventory of hallucal metatarsals from SH is displayed in Table 3.

Neandertal hallucal metatarsals tend to be relatively shorter and broader than those of recent humans, though not significantly (Pablos et al., 2017; Pearson et al., 2020). Both the Gunang fossil from Korea and the hallucal metatarsal from Tianyuan do not display significant differences with the comparative samples (Shang & Trinkaus, 2010; Sun-Joo et al., 2019). However, Baringo (BK-158), D3442 from Dmanisi (Lordkipanidze et al., 2007) and the Klasies River (Rightmire et al., 2006) hallucal metatarsals are as narrow as OH8, suggesting they are small-bodied hominins unlike the rest of the comparative samples displayed here (Figure 2).

The adult first metatarsals from SH are broader than those of the Neandertals and the rest of the comparative samples in the proximal breadth (Table 2 and Figure 2). Among the five immature metatarsals recovered from SH, two of them (AT-863 and AT-977) display the presence of pseudoepiphysis at the distal end as an epigenetic non-pathological trait (Figure 3), representing the oldest evidence of the presence of this trait in the hominin fossil record.

TABLE 1 Minimum number of individuals established by the metatarsals and the foot phalanges in SH.

Element	NR	MNE	MNI	Adult			Imm
				Total	Male	Female	
First metatarsal	18	15	11	6	3	–	5
Second metatarsal	13	8	5	4	2	–	1
Third metatarsal	17	13	9	6	2	–	3
Fourth metatarsal	13	11	8	5	3	–	3
Fifth metatarsal	14	11	7	4	2	–	3
Metatarsal indet	60	–	–	–	–	–	–
Hallucal proximal phalanx	33	24	17	9	2	–	8
Hallucal distal phalanx	23	19	10	6	3	–	4
Proximal phalanx toe II–V	93	70	10	5	–	–	5
Intermediate phalanx toe II–V	76	73	11	8	–	–	3
Distal phalanx toe II–V	64	64	8	6	–	–	2

Note: Sex has been assigned preliminarily based on what was previously proposed by Pablos et al. (2017) using the methodology proposed by Pablos, Martínez, et al. (2013b); Pablos et al. (2014).

Abbreviations: Imm, immature individuals; MNE, minimum number of elements; MNI, minimum number of individuals established with each anatomical part; NR, number of remains.

3.2 | Second metatarsal

A total of 13 second metatarsal fragments (Table 4) comprise the SH sample for this element (Pablos et al., 2017). They belonged to a minimum of eight elements and five individuals (Arsuaga et al., 2015). Four individuals represented by second metatarsal are adults, two of which are probably males, and one fossil (AT-1659) probably corresponds to an immature one (Table 1 and Figure 4). All four complete second metatarsals and one additional incomplete metatarsal are composed of two glued elements.

The second metatarsals of the comparative samples do not exhibit any significant differences (Pablos et al., 2012) for the proximal breadth considered in this study, except the UP specimens which are significantly narrower than those of recent modern humans (Table 2 and Figure 2). The Arago-43 second metatarsal is proximally narrower than the averages of all the comparative samples, that is, it is below the average values of all the samples, but this is significant only with the SH sample. However, this data should be taken with caution due to the small sample size of SH second metatarsals ($n = 4$) and the fragmentary nature of the Arago metatarsal. The ATD6-25 metatarsal of *Homo antecessor* from the Early Pleistocene levels at Gran Dolina in Atapuerca does not differ significantly from any of the samples in regard to the proximal breadth (Lorenzo et al., 1999; Pablos et al., 2012), this is also true with Jinniushan (Lu et al., 2011), Klasies river (Rightmire et al., 2006), and the Omo-323-76-2117 (Daver et al., 2018) second metatarsals. The second metatarsals from SH are not significantly broader than those of the

comparative samples, which is likewise the case with other elements of the foot and the postcranial skeleton (Arsuaga et al., 2015; Pablos et al., 2017).

3.3 | Third metatarsal

The number of third metatarsal fragments in the existing SH sample increases to 17, belonging to 13 elements and 9 individuals (Table 5), of which six are adults from the right side and two are probably males (Pablos et al., 2017). The other three individuals are represented by the two immature left third metatarsals and the right AT-252, which does not fit in the morphology and dimensions of the former (Table 1 and Figure 5).

The analysis with the comparative samples using the proximal breadth (M6a) indicates that both the SH and Neandertal third metatarsals are significantly broader than those from UP and three modern human populations (Pablos et al., 2017; Pablos, Gómez-Olivencia, Maureille, et al., 2019b). The early modern human Chinese third metatarsal from Tianyuan (Shang & Trinkaus, 2010) is broader than all the specimens and samples considered here, except those from the Neandertals Kiik-Koba 1 and Shanidar 1. Among the other third metatarsals within the comparative *Homo* fossils record, there are clearly two groups in terms of this variable (Table 2 and Figure 2). Both are narrower than the SH and Neandertal third metatarsals. The first group, composed by Omo F511, KNM-ER 803, KNM-ER 1823, SKX 38529, OH8, and D2021 from Dmanisi (Gabunia



FIGURE 1 Representation of some of the hallucal metatarsals from Sima de los Huesos including complete adult bones (upper row), complete juvenile bones (second row) and fragments (lower row) in medial and proximal views. Note that AT-993, AT-2712, and AT-4811 are displayed in lateral view. Scale bar = 2 cm. See Table 3 for details about the identification.

et al., 1999; Susman et al., 2001), fall within the range of variation for recent and Upper Paleolithic modern humans, but they are below the average of SH and

Neandertals. A second group that includes SKX 247, OH 43.1, KNM-ER 997 (own data on casts), and KNM-ER 77071 (Hammond et al., 2021) is composed of narrower

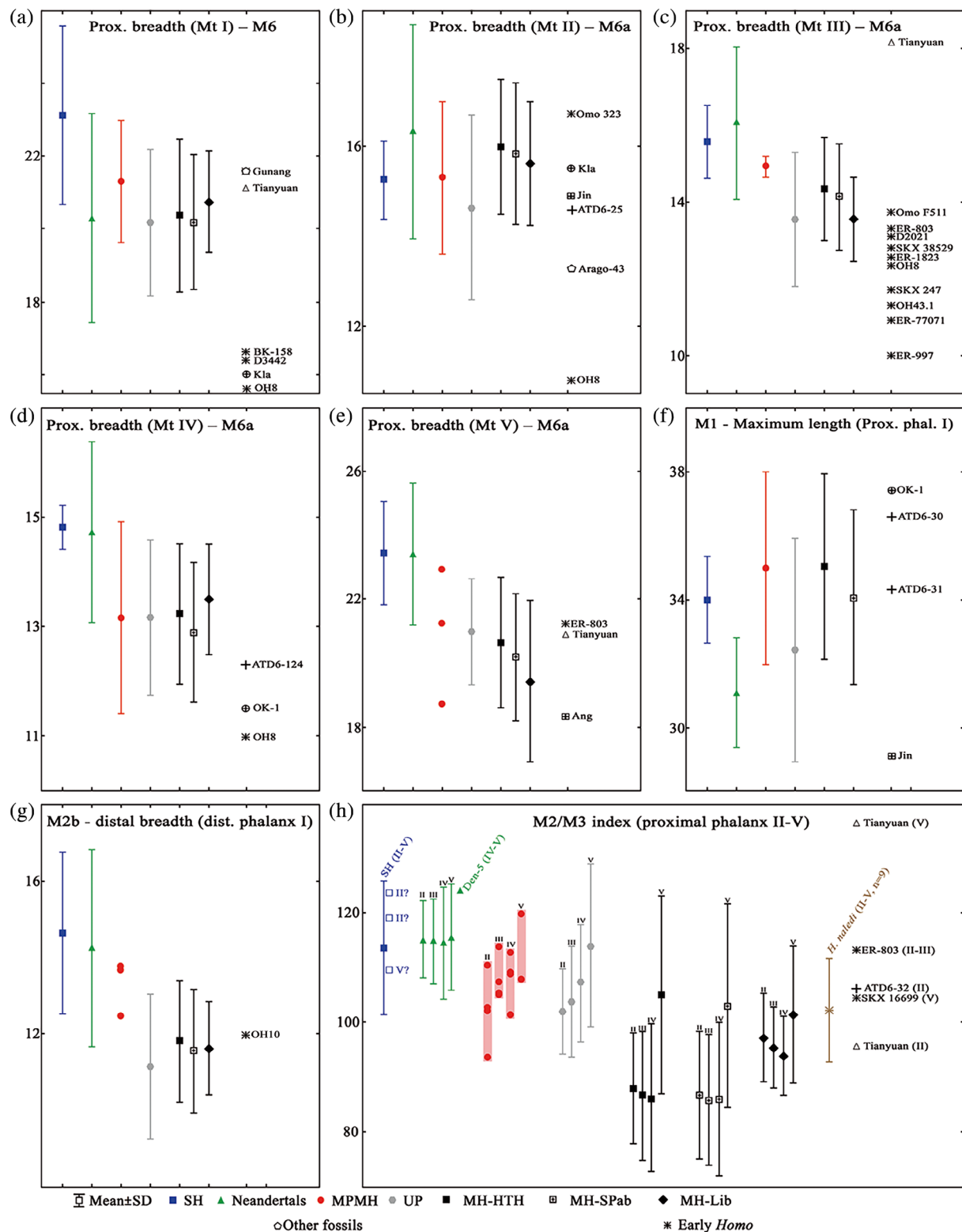


FIGURE 2 Univariate analysis of the Sima de los Huesos (SH) sample foot remains. (a) Proximal breadth (M6) of first metatarsal (in mm). (b) Proximal breadth (M6a) of second metatarsal (in mm). (c) Proximal breadth (M6a) of third metatarsal (in mm). (d) Proximal breadth (M6a) of fourth metatarsal (in mm). (e) Proximal breadth (M6a) of fifth metatarsal (in mm). (f) Maximum length (M1) of the proximal hallux phalanx (in mm). (g) Distal breadth (M2b) of the distal hallux phalanx (in mm). (h) Midshaft index (M2-midshaft breadth/M3-Midshaft height) of the proximal foot phalanges from toes II–V (in mm). In this last subfigure, the number of toes (II–V) is provided for each series/fossil. Data from Pablos et al. (2012, 2014); Pablos, Martínez, et al. (2013b) and present study. Ang, Anghilak Cave; Jin, Jinniushan; Kla, Klasies River Mouth; MH-HTH, Modern humans-Hamann-Todd Osteological collection; MH-Lib, Modern Humans-Libben-Amerindians collection (unshod); MH-SPab, San Pablo Medieval collection; MPMH, Middle Paleolithic modern humans; UP, Upper Paleolithic.

TABLE 2 Mean and SD of the variables of the Sima de los Huesos (SH) metatarsals (in mm) and other comparative samples.

		SH	Nea	UP	MPMH	MH-HTH	MH-Lib	MH-SPab
Hallucal (first) Metatarsal	Prox. breadth (Mt I)—M6	23.1 ± 2.4 [20.0–25.3] (n = 4)	20.3 ± 2.9 [16.7–27.1] (n = 12)	20.2 ± 2.0 [15.3–24.0] (n = 25)	21.3 ± 1.7 [18.9–23.5] (n = 7)	20.4 ± 2.1 [15.5–26.8] (n = 151)	20.7 ± 1.4 [17.0–23.6] (n = 39)	20.2 ± 1.8 [16.5–24.1] (n = 44)
Second Metatarsal	Prox. breadth (Mt II)—M6a	15.2 ± 0.9 [14.3–16.3] (n = 4)	16.3 ± 2.4 [12.8–19.9] (n = 14)	14.6 ± 2.0 [12.0–20.2] (n = 13)	15.3 ± 1.7 [13.2–17.9] (n = 5)	16.0 ± 1.5 [13.0–19.5] (n = 150)	15.6 ± 1.4 [12.7–18.3] (n = 40)	15.8 ± 1.6 [12.7–19.8] (n = 45)
Third Metatarsal	Prox. breadth (Mt III)— M6a ^{2,4,5,6}	15.6 ± 1.0 [14.1–16.7] (n = 6)	16.1 ± 2.0 [12.0–19.8] (n = 16)	13.5 ± 1.7 [10.1–17.5] (n = 12)	14.9 ± 0.3 [14.5–15.1] (n = 4)	14.3 ± 1.3 [11.4–18.3] (n = 148)	13.5 ± 1.1 [11.1–16.0] (n = 40)	14.1 ± 1.4 [11.3–17.8] (n = 45)
Fourth Metatarsal	Prox. Breadth (Mt IV)— M6a ^{2,4,5,6}	14.8 ± 0.4 [14.4–15.3] (n = 4)	14.7 ± 1.7 [11.2–17.4] (n = 13)	13.2 ± 1.4 [10.5–15.0] (n = 16)	13.2 ± 1.8 [11.5–15.0] (n = 3)	13.2 ± 1.3 [10.2–17.5] (n = 148)	13.5 ± 1.0 [11.6–15.5] (n = 40)	12.8 ± 1.3 [10.3–16.2] (n = 44)
Fifth Metatarsal	Prox. Breadth (Mt V)— M6a ^{2,4,5,6}	23.4 ± 1.6 [21.3–25.5] (n = 5)	23.4 ± 2.3 [18.9–26.7] (n = 13)	21.0 ± 1.7 [17.8–23.8] (n = 15)	21.1 [18.8–23.0] (n = 3)	20.6 ± 2.1 [16.7–27.8] (n = 148)	19.4 ± 2.6 [12.3–24.9] (n = 40)	20.2 ± 2.0 [16.6–24.3] (n = 45)

Note: Mean ± SD, range [] and sample size (n) are shown. Bold letters and superscript indicate significant differences between SH with some of the samples (Z-score >1.96 in absolute terms; $p < 0.05$); 1 = Neandertals, 2 = UP, 3 = MPMH, 4 = Recent modern humans (HTOC-HTH), 5 = Recent modern humans (Libben Amerindians), 6 = Recent modern humans (San Pablo Medieval collection). SH, Sima de los Huesos; Nea, Neanderthals; MPMH, Middle Paleolithic Modern Humans; UP, Upper Paleolithic Modern Humans; MH-HTH, Modern humans Hamann-Todd Osteological collection; MH-Lib, Modern humans Libben, Amerindians unshod (Trinkaus, 1975). MH-SPab, Modern humans; San Pablo Medieval collection. The SH sample includes: First metatarsal: AT-987, AT-1711, AT-2496, and AT-2808. Second metatarsal: AT-988 + AT-991, AT-992 + AT-1138, AT-2158 + AT-2159, and AT-3142 + AT-3171. Third metatarsal: AT-989, AT-994 + AT-997, AT-2711, AT-2825 + AT-3172, AT-4424, and AT-5428. Fourth metatarsal: AT-534, AT-978, AT-990 + AT-1149, and AT-2181 + AT-2715. Fifth metatarsal: AT-1015, AT-1016 + AT-2827, AT-2710, AT-3143, and AT-5582. Data from Trinkaus (1975, 1983, 2016); Vandermeersch (1981); Pablos et al. (2012, 2017); Pablos, Gómez-Olivencia, Maureille, et al. (2019b); Arsuaga et al. (2015); Pearson et al. (2020), and own data.

specimens, which are even smaller than all the modern human samples, thus indicating that they correspond to small-sized individuals. This second group includes the *Homo naledi* third metatarsals (Harcourt-Smith et al., 2015). This South African species is typically located near the small-sized individuals and far from the large-sized fossils for all the elements and nearly all the variables of the metatarsals and phalanges.

3.4 | Fourth metatarsal

The most recent review and update of the SH fourth metatarsals inventory has allowed us to identify a total of 13 fragments in the entire existing collection. They belonged to a minimum of 11 elements based on the proximal epiphysis and the laterality of all of the elements (Table 6). The MNI is eight. Five right fourth metatarsals belonged to five adult individuals, three of which are considered males (Pablos et al., 2017). Another three right immature fourth metatarsals represent the non-adult individuals in the sample (Table 1 and Figure 6).

The metrical analysis of the proximal breadth (M6a) of the fourth metatarsals from Sima de los Huesos indicates that both Neandertals and SH fourth metatarsals are proximally significantly broader than those from UP and

the three modern human populations (Pablos et al., 2017; Pablos, Gómez-Olivencia, Maureille, et al., 2019b). The fourth metatarsals of Omo-Kibish 1 (Pearson et al., 2008) and ATD6-124 from the TD6 early Pleistocene level of Gran Dolina (Pablos et al., 2012) are just as narrow, if not narrower, than the recent and fossil modern human comparative samples (Figure 2). This suggests that a wide and robust fourth metatarsal could be a shared derived trait between Neandertals and SH hominins, unlike *Homo antecessor* and recent and fossil modern humans (Arsuaga et al., 2015; Pablos et al., 2012, 2017).

3.5 | Fifth metatarsal

To date, 14 fifth metatarsal remains have been found and identified in the SH human collection (Table 7 and Figure 7). They represent a minimum number of elements of 11 metatarsals. The MNI calculated based on the proximal end and the state of development is seven, represented by four right adult elements and three right immature fifth metatarsal fossils (Table 1).

The proximal end of the SH fifth metatarsals is significantly broader (Table 2 and Figure 2) than in the UP and modern human individuals (Arsuaga et al., 2015; Pablos et al., 2017). This is also the case in Neandertals relative to

TABLE 3 Inventory of hallucal metatarsals from SH.

Label	Side	Age	Anatomical description
AT-863	L	Im	Diaphysis and distal articulation. Slightly eroded at the proximal end.
AT-977	R	Im	Diaphysis and distal articulation
AT-987	R	Ad	Complete
AT-993	L	Ad	Distal articulation and fragment of diaphysis. Eroded at the medial area
AT-996	R	Ad	Head fragment
AT-1711	L	Ad	Complete. Slightly eroded at the base
AT-1970	R	Ad	Fragment of distal articulation
AT-2494	R	Im	Diaphysis and distal articulation. Eroded at the base
AT-2496	R	Ad	Complete
AT-2712	R	Ad	Head fragment
AT-2714	R	Im	Fragment of diaphysis and head. Eroded through the diaphysis
AT-2808	L	Ad	Complete
AT-3145	L	Im	Diaphysis and distal articulation. Eroded at the distal plantar area
AT-4441	R	Ad	Complete. Slightly eroded at the base and the head
AT-4442	L	Ad	Fragment of lateral side of the head
AT-4533	L?	Ad	Dorsal fragment of proximal epiphysis
AT-4811	L	Ad	Proximal epiphysis
AT-6504	L	?	Fragment of distal articulation (?)

Abbreviations: Ad, adult; Im, immature; L, left; R, right.



FIGURE 3 Dorsal views and detail of AT-863 and AT-977 immature hallucal metatarsals showing the pseudoepiphysis fusion in both bones.

fossil and modern *Homo sapiens* (Pablos, Gómez-Olivencia, Maureille, et al., 2019b). Therefore, the broad base of Neandertal and SH fifth metatarsals likely represents a derived

character shared between these two taxonomical groups probably related to general body robusticity (Arsuaga et al., 2015). The fifth metatarsals of Tianyuan (Shang & Trinkaus, 2010) and KNM-ER 803f, although narrow, do not differ significantly from the comparative samples in terms of the proximal breadth. The diminutive Middle Paleolithic Anghilak metatarsal V (AH-1) from Uzbekistan was identified as a non-diagnostic element (Glantz et al., 2008). The proximal breadth of this fossil is significantly narrower than the fifth metatarsals from SH and Neandertals. Hence, despite the Middle Paleolithic association with AH-1, we can probably rule out this fossil as Neandertal or similar to the SH population, confirming the complication of the paradigm linking Middle Paleolithic cultures with Neandertals in Central Asia (Glantz et al., 2008).

3.6 | Unidentified metatarsal fragments

There are 135 metatarsal fragments that have been recovered from the SH site. 75 of which have been identified at least to the level of number of toes (see above). Most of the 60 additional metatarsal fossils are composed of diaphysis fragments and distal ends/immature

TABLE 4 Inventory of second metatarsals from SH.

Label	Side	Age	Anatomical description
AT-988 + AT-991	R	Ad	Complete. Eroded at the diaphysis and base
AT-992 + AT-1138	L	Ad	Complete. Slightly eroded at the plantar area of the base
AT-1659	L	Im	Fragment of base and diaphysis slightly eroded at the base
AT-2158 + AT-2159	L	Ad	Complete
AT-2713 + AT-2842	R?	Ad	Diaphysis and head
AT-3142 + AT-3171	R	Ad	Complete
AT-3173	R	Ad	Base and diaphysis
AT-3174	L	Ad	Base and diaphysis

Abbreviations: Ad, adult; Im, immature; L, left; R, right.

epiphyses (Figure 8). All 60 of these unidentifiable metatarsal fragments belonged to toes II through V (Table 8), and 39 fragments are from immature individuals as they preserve an unfused metaphyseal surface. Eight fragments are from adult individuals, and it has not been possible to establish the individual's age at death for 13 of them.

All of these currently unidentifiable elements might be associated with other elements discovered in future field excavations, possibly resulting in more complete and identifiable metatarsals. This will provide the basis for further metrical and morphological research in the future.

3.7 | Proximal hallucal phalanges

A total of 33 fragments comprise the SH hallucal proximal phalanx sample (Table 9 and Figures 9 and 10). They correspond to a minimum number of elements of 24. The MNI calculated with the proximal phalanx of the first toe is 17 based on the laterality, anatomical incompatibility, and age at death of the proximal end (Table 1). We identified nine adult individuals, two of which were probably males (Pablos et al., 2017). Another seven individuals are represented by immature non-fused proximal hallucal phalanges. Additionally, an adolescent individual has been identified based on fossil AT-4437, which displays a partially fused proximal epiphysis. In modern populations this fusion takes place at around 14–18 years old (Cardoso & Severino, 2010).

Table 10 displays some selected metrical variables from the SH proximal hallucal phalanges in comparison with the comparative samples (Arsuaga et al., 2015; Pablos et al., 2017; Pablos, Gómez-Olivencia, Maureille, et al., 2019b). The SH proximal hallucal phalanges are

significantly longer than those of Neandertals (Figure 2), that which are shorter than both MPMH and recent MH samples (Pablos, Gómez-Olivencia, Maureille, et al., 2019b; Trinkaus & Hilton, 1996). In SH, the hallucal proximal pedal phalanges exhibit shaft hypertrophy, similar to that of Neandertals, relative to MH populations (Arsuaga et al., 2015). The distal end of the proximal hallucal phalanges for both SH and Neandertals, are broader than those of recent modern humans (Pablos et al., 2017; Pablos, Gómez-Olivencia, Maureille, et al., 2019b).

The proximal hallucal phalanges of *Homo antecessor* from the TD6 Early Pleistocene level of Gran Dolina, also in Atapuerca, are long and narrow, especially ATD6-30 (Lorenzo et al., 1999). Interestingly, the proximal phalanx of the first toe of Omo-Kibish 1 is broad and long (Pearson et al., 2008). The proximal hallucal phalanx of the *Homo erectus* from Jinniushan (Lu et al., 2011) is shorter than all of the comparative samples. Thus, more fossils would be needed to establish the polarities of these traits in genus *Homo*.

3.8 | Distal hallucal phalanges

In the Sima de los Huesos site, 23 fossils corresponding to hallucal distal phalanges have been recovered to date (Table 11 and Figure 11). They represent at least 19 elements based on the proximal diaphysis. The minimum number of individuals estimated with the distal phalanx of the foot of toe I is 10 (Table 1). Six right specimens represent adult individuals, three of which are believed to belong to males (Pablos et al., 2017). Four additional juveniles have been identified by the proximal metaphysis of left phalanges.

As previously mentioned (Pablos et al., 2017; Pablos, Gómez-Olivencia, Maureille, et al., 2019b; Trinkaus,



FIGURE 4 Representation of some of the second metatarsals from Sima de los Huesos including adult complete bones and one probably immature (AT-1659) in medial and proximal views. Scale bar = 2 cm. See Table 4 for details about the identification.

1975), most of the Neandertals and SH foot phalanges are broad and robust in comparison to recent modern humans. In terms of the hallucal distal phalanx, the distal end of those found in SH, as well as those of Neandertals, are significantly broader than those of UP and recent modern humans, hence exhibiting an expanded distal tuberosity (Table 10 and Figure 2). The distal hallucal phalanx OH 10 found in Olduvai (Day & Napier, 1966), supposedly belonging to *Homo habilis*, is similar to those of our recent modern human comparative samples and narrower than those of SH and Neandertals. The possibility that OH 10 is a representative of *H. habilis*, and assuming that its morphology is typical for this species, suggests that broad distal

hallucal phalanges could be a derived shared trait in the Neandertal-SH lineage. This supposed apomorphy in this evolutionary line should be taken with caution until new fossil remains are found.

In SH, some of the distal phalanges of the first toe display slight hallux valgus deviation (Figure 11), which could represent the oldest occurrence of this trait in the human fossil record. New fossils, especially from *H. antecessor* and/or *H. ergaster*, and in-depth studies of phalanx and metatarsal associations in the SH foot collection will shed light on this trait.

3.9 | Proximal lateral foot phalanges

The sample of proximal non-hallucal foot phalanges from SH rises to 93, corresponding to 70 elements based on the diaphysis and/or the distal end (Table 12 and Figures 12 and 13). Out from those 70 elements, 35 are adults and 35 are juveniles. The minimum number of individuals is 10: five adults and five immatures (Table 1).

Assigning the lateral proximal foot phalanges to a specific toe is not easy if there is no complete or nearly complete set from the same individual (at least from one side; e.g., Carretero et al., 2015) which is the case of the intermediate and distal foot phalanges, as well as the proximal phalanges of the hand (Lorenzo et al., 2015; Pablos, Gómez-Olivencia, & Arsuaga, 2019a). Identification is typically based on the medial-to-lateral decreasing size, mainly length, from toe II to toe V for the same individual, and the articulation with metatarsals or intermediate phalanges. Unfortunately, those articulation joints are subject to a great deal of movement and are quite lax, so they usually lead to more doubts than clarity in regard to the associations. Even when just one individual is present, a certain degree of uncertainty exists if there are only a few phalanges (e.g., Pablos, Gómez-Olivencia, Maureille, et al., 2019b). Therefore, comparisons are not always possible due to an imprecise identification in large accumulations of comingled remains (Harcourt-Smith et al., 2015; Trinkaus, 2016), and sometimes the phalanges are compared by considering the four lateral toes all together due to the difficulty in their identification (Lorenzo et al., 1999). The siding of the proximal foot phalanges is carried out based on several traits. One of them is the medial deviation of the distal trochlea. In the phalanges from toe V, this deviation is usually more pronounced and it helps to suggest identifying some phalanges as belonging to the fifth toe.

The midshaft index values (Mid-shaft breadth-M2 $\times$ 100/Mid-shaft height-M3) for SH and for the comparative samples are displayed in Table 10 and Figure 2. Although three proximal foot phalanges from SH are

TABLE 5 Inventory of third metatarsals from SH.

Label	Side	Age	Anatomical description
AT-252	R?	Im	Fragment of diaphysis. Eroded at the base
AT-503	L?	Ad	Fragment of proximal shaft
AT-703 + AT-704	L	Im	Complete. Eroded at the base and the head
AT-989	R	Ad	Complete. Slightly eroded at the plantar area of the base
AT-994 + AT-997	L	Ad	Complete. Eroded at the base
AT-1660	R	Ad?	Proximal diaphysis
AT-1823 + AT-1834	R	Im	Complete
AT-1872	L	Im?	Base and diaphysis. Eroded at the base
AT-2711	R	Ad	Complete
AT-2825 + AT-3172	R	Ad	Complete
AT-4424	R	Ad	Complete. Slightly eroded at the base
AT-5428	L	Ad	Complete. Eroded at the head and diaphysis
AT-5580	R	Ad	Diaphysis and head

Abbreviations: Ad, adult; Im, immature; L, left; R, right.

suggested to belong to toe II and V (see Table 12), we provide the mean and SD of all the SH proximal foot phalanges altogether due to the uncertainty in their identifications. In general, the midshaft index in recent modern humans is similar in toes II–IV and is <100 on average in all cases. The fifth toe of these current populations tends to be more robust (a broader than high shaft) relative to toes II–IV. This pattern of a broader fifth toe relative to the height of the proximal foot phalanges is also seen in the UP sample. In this last comparative sample, the average of the midshaft index is slightly over 100. A similar pattern seems to appear in MPMH, but the small sample size precludes any comparison. In Neandertals, the pattern is different: in all the toes, the midshaft index average of the proximal phalanges is close to 115 and there is no clear increase in robusticity in the fifth toe (Pablos, Gómez-Olivencia, Maureille, et al., 2019b), thus reinforcing the higher robusticity in all Neandertal toes. The proximal phalanx Denisova 5 of toe IV–V (Mednikova, 2011), fits in better with the Neandertal variability. Assuming that all lateral toes (II–V) are represented in the SH proximal foot phalanges sample, the pattern of shaft hypertrophy in this Middle Pleistocene population is more similar to that seen in Neandertals than that of recent modern humans and UP. The average midshaft index in *Homo naledi* is around 100 for all non-hallucal phalanges (Harcourt-Smith et al., 2015). This pattern observed in the proximal lateral phalanges from *H. naledi* differs from the SH-Neandertal patterns and is intermediate in recent modern humans and UP. The Tianyuan Late Pleistocene skeleton preserves two proximal foot phalanges, presumably belonging to

toes II and V (Shang & Trinkaus, 2010). The pattern of proximal foot phalanges in this individual, although unusual, is more like that of UP than Neandertals and recent modern humans. The *Homo ergaster* proximal phalanx KNM-ER 803r from toe II–III (Day & Leakey, 1974), is more similar to the second-third proximal phalanges in SH-Neandertals. The Early Pleistocene proximal phalanx ATD6-32, probably from toe II (Lorenzo et al., 1999), does not fit in with the recent modern human pattern, and is more similar to Late Pleistocene populations. The likely fifth proximal foot phalanx SKX 16699 (Susman et al., 2001) falls within the range of variation for each fifth proximal foot phalanx from all the comparative samples. If we assume that ER-803r and ATD6-32 are representatives of the *H. ergaster* and *H. antecessor* species, respectively, we can conclude that robust proximal foot phalanges are present in these two species. This indicates that gracile proximal foot phalanges in recent modern humans could represent a derived trait, thus suggesting a gracilization process in recent modern humans relative to Early Pleistocene *Homo* species (Arsuaga, 2010; Arsuaga et al., 2015; Carretero et al., 2004). More well-identified fossils are needed in order to more clearly establish the polarity of this trait in the *Homo* fossil record.

In UP, the proximal non-hallucal phalanges decrease in robusticity in the midshaft in relation to Neandertals (Pablos, Gómez-Olivencia, Maureille, et al., 2019b) and the SH population, which is a reflection of the reduction of habitual loads on the foot phalanges. This supports the habitual use of footwear in UP individuals (Trinkaus, 2005). Hence, the shaft hypertrophy in SH and Neandertal proximal foot phalanges in toes II–V

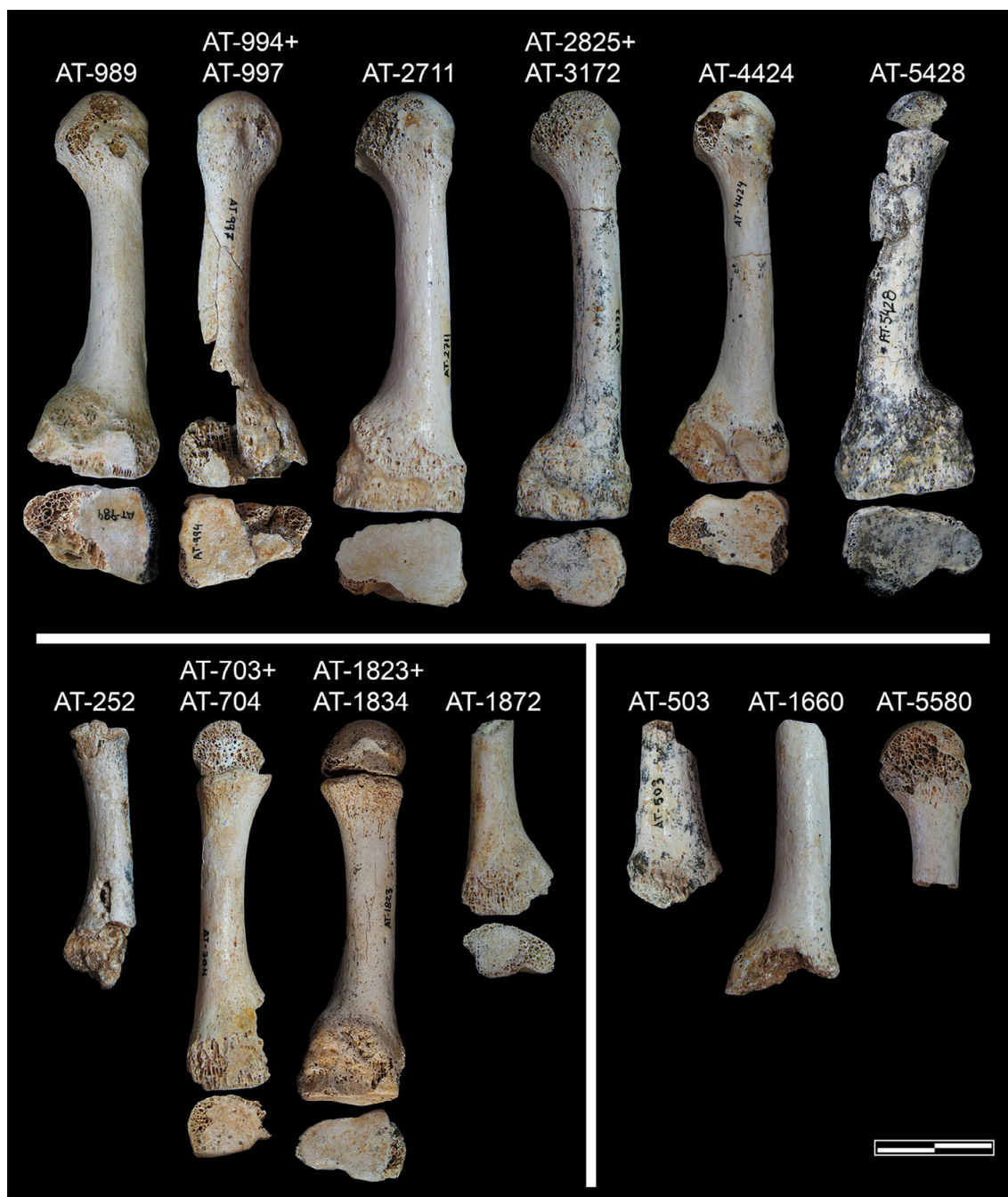


FIGURE 5 Representation of some of the third metatarsals from Sima de los Huesos including adult complete or nearly complete bones (upper row), immature ones (bottom left) and fragments (bottom right) in medial and proximal views. Scale bar = 2 cm. See Table 5 for details about the identification.

suggests increased habitual loads on the foot phalanges, thus implying the non-habitual use of rigid footwear in this Middle Pleistocene population and in Neandertals.

There are 93 proximal non-hallucal phalanges represented in the SH site, while worldwide, just 88 lateral proximal phalanges from Neandertals and 183 from fossil *Homo sapiens* populations have been identified in the fossil record for this anatomical element in all known contexts (e.g., Endo & Kimura, 1970; McCown & Keith, 1939;

Pablos, Gómez-Olivencia, Maureille, et al., 2019b; Trinkaus, 1975, 1983, 2016; Trinkaus et al., 2014; Vandermeersch, 1981 for details of some of the samples).

3.10 | Intermediate foot phalanges

In the SH site, 76 intermediate foot phalanges have been recovered and identified to date (Table 13 and Figures 14 and 15). They represent a minimum of

Label	Side	Age	Anatomical description
AT-534	R	Ad	Base and diaphysis
AT-978	L	Ad	Complete, eroded at the base
AT-990 + 1149	R	Ad	Complete. Eroded at midshaft and base
AT-1308	R	Im	Base and diaphysis
AT-1445	L?	Ad?	Fragment of base
AT-2181 + AT-2715	R	Ad	Complete. Eroded at the plantar area of the head
AT-2845	R?	Ad	Fragment of diaphysis
AT-3144	R	Im	Eroded base and diaphysis
AT-3467	R	Im?	Proximal fragment of diaphysis
AT-4489	L	Im	Base and diaphysis. Eroded
AT-7001	R	Ad	Fragment of proximal diaphysis

Abbreviations: Ad, adult; Im, immature; L, left; R, right.

TABLE 6 Inventory of fourth metatarsals from SH.

73 elements and 11 individuals, eight of them adults and three juveniles (Table 1).

The difficulty of correctly identifying intermediate foot phalanges is similar to the aforementioned difficulty with the proximal pedal phalanges (e.g., Pablos, Gómez-Olivencia, Maureille, et al., 2019b). Again, identification is typically done based on the medial-to-lateral decreasing size from finger II to finger V for the same individual. The siding of the intermediate phalanges of the foot is based on the lateral deviation of the distal end.

When comparing the midshaft index (Mid-shaft breadth-M2 $\times$ 100/Mid-shaft height-M3) for intermediate foot phalanges, the SH intermediate pedal phalanges ($n = 55$), supposedly comprising the second to fifth toes, appear to be more robust (shafts broader than height) than most of those of the comparative samples, on average (Table 14). However, these differences are only statistically significant when compared with the second to fourth toes of MPMH and to the second to third toes of recent modern humans. In general, Neandertal intermediate foot phalanges are more robust than those of recent modern humans (Pablos, Gómez-Olivencia, Maureille, et al., 2019b). They display a broad diaphysis relative to the shaft height, albeit not always significantly, due to the small sample sizes of the different comparative populations/samples (Figure 16).

The intermediate pedal phalanges from the TD6 Early Pleistocene level of Gran Dolina ATD6-33 and ATD6-34 (toes II and II–III, respectively; Lorenzo et al., 1999) are more gracile than in SH and Neandertals with respect to the midshaft index. However, the ATD6-35 intermediate foot phalanx from toe IV–V (Lorenzo et al., 1999) do not significantly differs from the comparative samples in this index, it is clearly below the average for SH and Neandertal phalanges (Figure 16). These three *Homo antecessor* phalanges are generally more gracile than the comparative samples, though not significantly. The probable

Homo ergaster intermediate foot phalanx SKX-344 from Swartkrans from toe II–V (Susman, 1989) is significantly more robust than MPMH and the Libben Amerindians modern humans for toes II and III. The second to fifth toe intermediate phalanx SKX-1261, which also supposedly belonged to *H. ergaster*, belongs to the same individual from the same site of SKX-344 (Susman, 1989). In this case, however, there are no significant differences between any of the comparative samples for any of the toes. Finally, the *H. ergaster* KNM-ER 803 L (II) and KNM-ER 803 k (III) intermediate foot phalanges (Day & Leakey, 1974) are more gracile than in SH and Neandertals regarding the midshaft index. Hence, the *H. ergaster* and *H. antecessor* intermediate phalanges were likely more gracile than those of the SH-Neandertal lineage. In the Dinaledi Chamber, at Rising Star Cave system, 12 *H. naledi* intermediate pedal phalanges have been recovered (Harcourt-Smith et al., 2015). They are significantly more robust than modern humans for the second toe, but more gracile than the fourth toe in Libben Amerindians. In this context, the SH and Neandertal intermediate foot phalanges were likely more robust than the comparative samples. Nevertheless the small comparative sample sizes and the scarce fossil record preclude any well-founded conclusion regarding the robustness pattern of this element.

In this regard, it is remarkable that in only one site from the Middle Pleistocene—the Sima de los Huesos—76 intermediate foot phalanges have been recovered and identified over the course of more than 40 years of excavation and research. Out of those, 59 are adults and 55 are complete enough to be measured and studied. In contrast, the worldwide world fossil record includes just about 50 Neandertal intermediate foot phalanges, recovered from different chronologies, in burials and other contexts, which are adult and juveniles. For Paleolithic *H. sapiens* (UP and MPMH) this number rises to around 70 (adult and immature ones), considering burials and other contexts and

FIGURE 6 Representation of some of the fourth metatarsals from Sima de los Huesos including adult complete or nearly complete bones (upper row), immature ones (bottom left) and fragments (bottom right) in medial and proximal views. Note that AT-1445 is displayed in lateral and proximal views. Scale bar = 2 cm. See Table 6 for details about the identification.



situations (e.g., McCown & Keith, 1939; Endo & Kimura, 1970; Trinkaus, 1975, 1983, 2016; Vandermeersch, 1981; Trinkaus et al., 2014; Trinkaus, Robson Brown, et al., 2017b; Pablos, Gómez-Olivencia, Maureille, et al., 2019b for details of some of the samples).

3.11 | Distal lateral non-hallucal foot phalanges

There are 64 fossils and equally 64 elements in the SH distal lateral non-hallucal phalanges of the foot (Table 15

and Figures 15 and 17). They belonged to a minimum of eight individuals, six of them adults and two juveniles (Table 1).

Once more, similar to the proximal and intermediate lateral foot phalanges, there are some uncertainties and issues in the identification of lateral distal non-hallucal foot phalanges to the correct number of toes (e.g., Pablos, Gómez-Olivencia, Maureille, et al., 2019b). In this case, the assignment to a right toe is based on medial-to-lateral decreasing size from toe II to toe V for the same individual. The siding of the distal lateral phalanges of the foot is based on the lateral deviation of the distal tuberosity

Label	Side	Age	Anatomical description
AT-308	R	Im	Base and diaphysis. Eroded at distal end
AT-586	R	Im	Fragment of base and diaphysis
AT-1015	L	Ad	Base and fragment of diaphysis
AT-1016 + 2827	R	Ad	Complete. Eroded at proximal end
AT-1125	L	Ad	Distal end
AT-2710	R	Ad	Complete
AT-3143	R	Ad	Base and diaphysis
AT-4430	L	Im	Fragment of base
AT-5582	R	Ad	Base and diaphysis. Eroded at distal end
AT-5681	R	Ad	Distal end
AT-6193	L	Im	Fragment of diaphysis
AT-7010	L	Ad?	Fragment of base

Abbreviations: Ad, adult; Im, immature; L, left; R, right.

TABLE 7 Inventory of fifth metatarsals from SH.

(Pablos, Gómez-Olivencia, & Arsuaga, 2019a). Sometimes, an elevated medial deviation of the distal end and/or a minimum size suggests a likely identification of the fifth toe (Pablos, Gómez-Olivencia, & Arsuaga, 2019a).

The comparison of the SH midshaft index for the distal non-hallucal pedal phalanges with the comparative samples brings to light significant differences between the entire SH sample (toes II–V) and the distal phalanges of nearly all recent modern humans for toes II–V (Table 14 and Figure 16). This suggests that SH has more robust distal phalanges (shafts broader than height) than the recent modern human samples. There are no significant differences between SH and the Neandertal, UP and MPMH samples, nor between these populations. The latter is probably due to the small sample size of correctly identified distal foot phalanges in the *Homo* fossil record. The *H. naledi* distal foot phalanges (toes II–V; Harcourt-Smith et al., 2015) do not exhibit any significant differences with any of the comparative samples, thus indicating that the robusticity of the distal phalanges from this African Middle Pleistocene population is not higher than other *Homo* fossils. The Early Pleistocene distal foot phalanx ATD6-68 of *Homo antecessor* (Lorenzo et al., 1999) does not have any significant differences for toes II–V with respect to the comparative samples. The distal phalanx KNM-ER 803 m, supposedly belonging to a fourth to fifth toe of a *Homo ergaster* individual (Day & Leakey, 1974), is significantly more gracile in the midshaft index than the Neandertal fourth toes. Once again, however, the small Neandertal sample size should be kept in mind in order to reach reliable conclusions.

In the SH site, there are 64 distal lateral non-hallucal foot phalanges, 54 of them belonging to adult individuals. Out of these, 53 are complete enough to be studied here. As is the case with the proximal and intermediate foot

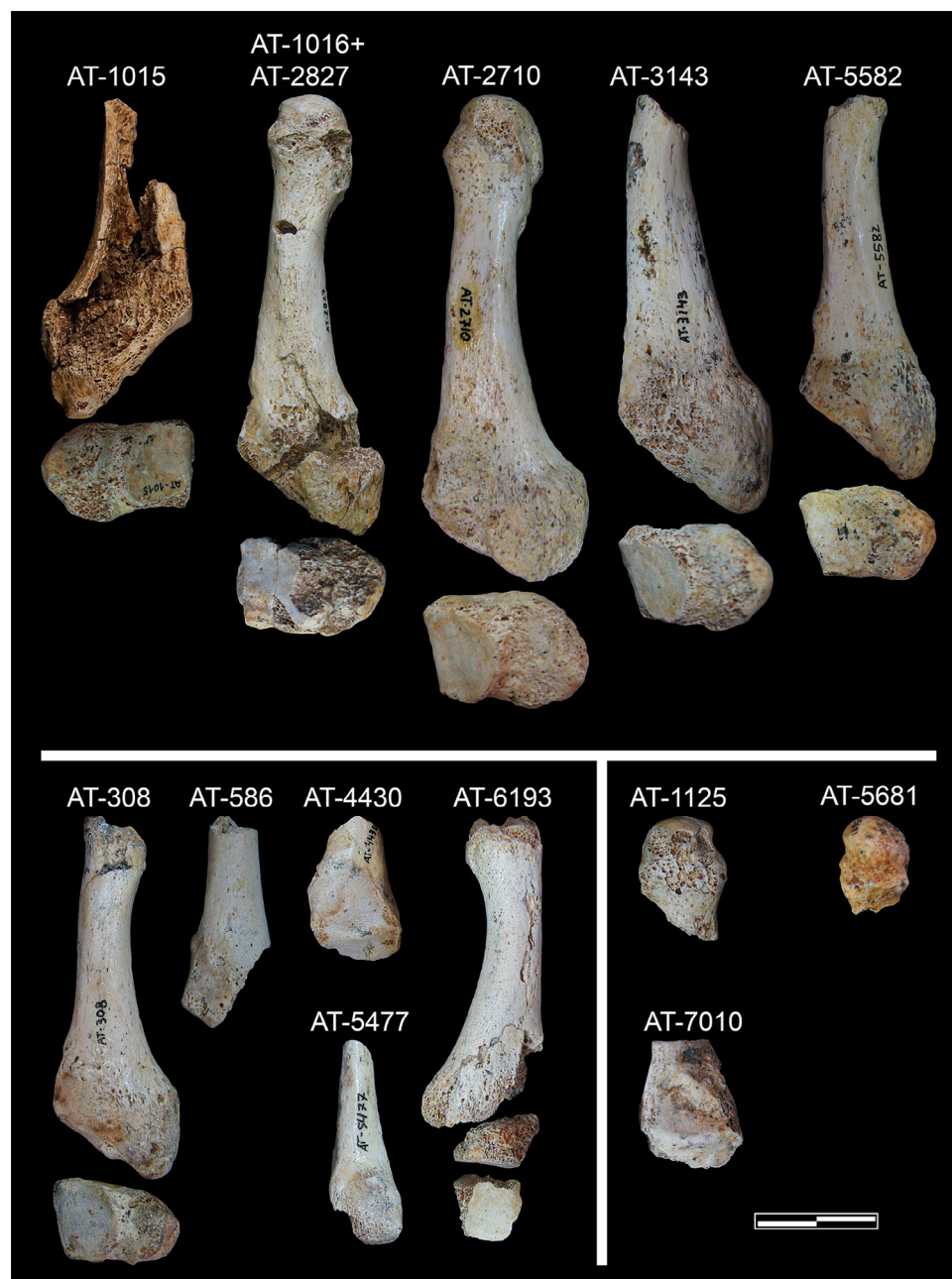
phalanges, these values are considerably higher than those of Neandertals in the worldwide fossil record ($n = 33$, including adults and juveniles). In the Paleolithic *Homo sapiens* sample (including UP and MPMH) throughout the entire the world, only around 50 distal non-hallucal phalanges have been discovered and identified (Pablos, 2015).

4 | PALEOBIOLOGICAL INFERENCES (STATURE, BODY MASS, AND PALEOPATHOLOGY)

In this study, we are well aware of the difficulty and limitations brought about by using forensic samples to estimate body size (i.e., stature and body mass) of fossil specimens. Moreover, regression formulae based on femoral head diameter or bi-iliac breadth for body mass and femoral and tibial length for stature are usually preferred (Auerbach & Ruff, 2004; Carretero et al., 2012). With this in mind and in spite of it, we attempted to estimate these parameters in order to glean insight into the body size of the hominins from SH.

The most accurate method for estimating stature in past populations involves as many elements affecting stature as possible from the same individual, such as the Fully method (Fully, 1956; Raxter et al., 2006). However, the hominin fossil skeletons, when they exist, are often too incomplete to apply this method. Therefore, it is usually better to rely on the femur and the tibia, which are both directly involved in stature. In the Sima de los Huecos, there are some tibiae and femora that are complete enough to calculate body height (Arsuaga et al., 2015; Carretero et al., 2012). However, we provide stature estimations based on the first to fourth metatarsals from SH

FIGURE 7 Representation of some of the fifth metatarsals from Sima de los Huesos including adult complete or nearly complete bones (upper row), immature ones (bottom left) and fragments (bottom right) in dorsal and proximal views. Note that AT-4430, AT-5477, and AT-7010 are displayed in medial view. Scale bar = 2 cm. See Table 7 for details about the identification.



in order to facilitate comparisons with other Pleistocene sites where no complete long bones are present, but that do have metatarsals.

The stature estimates using the SH metatarsals are based on the maximum length of first to fourth metatarsals when applying the formulae provided by Pablos, Gómez-Olivencia, et al. (2013a). As recommended by Pablos, Gómez-Olivencia, et al. (2013a), when the sex of the metatarsals is known or can be estimated, sex-specific equations are preferable since these will provide statures with a lower Standard Error of Estimate (SEE) and thus the estimates are more accurate. In the SH sample, all the metatarsals for which it is possible to estimate the sex have been established as males or allophyssus (Pablos

et al., 2017; but see Pablos, Martínez, et al., 2013b; Pablos et al., 2014 for the methodology of sex estimations in SH). Likewise, most of the SH long bones are identified as males (Carretero et al., 2012). We applied the male formula for the male-identified metatarsals from SH, and both male and female formulae for those elements classified as allophyssus. In this last case, we calculated the average male and female values for each bone. The overrepresentation of male individuals in the SH metatarsal sample may be due mainly to two factors: (a) The Sima de los Huesos site has still not been completely excavated, and moreover some of the metatarsals are fragmentary. This could mask the presence of female individuals in the SH metatarsals sample. (b) The sex

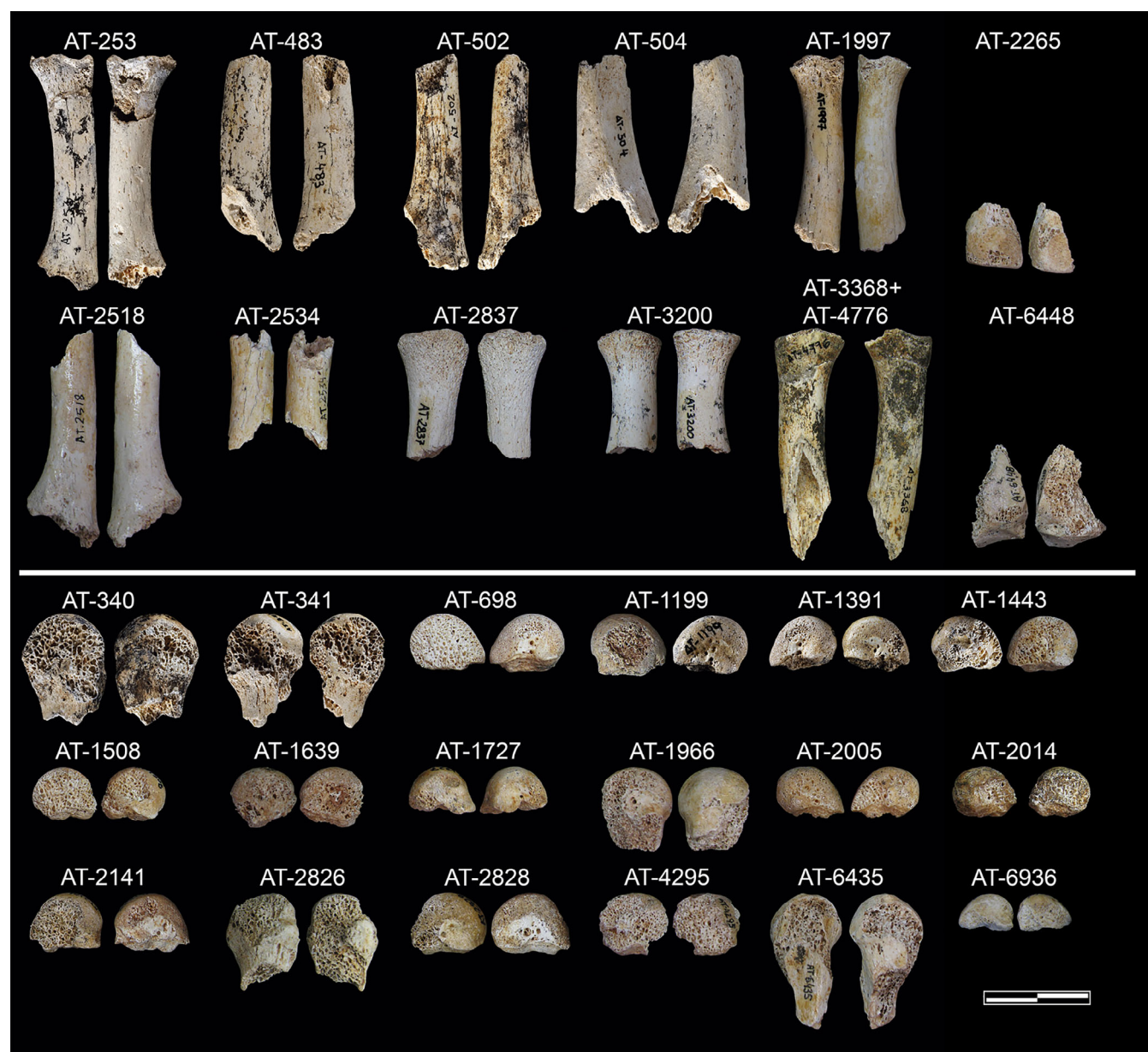


FIGURE 8 Representation of some of the unidentified metatarsal fragments from Sima de los Huesos, including diaphyses (upper two rows) and distal ends and immature epiphyses (lower two rows) in medial and lateral views. Note that AT-2265 and AT-6448 are displayed in lateral and dorsal views. Scale bar = 2 cm. See Table 8 for details about the identification.

estimates from foot remains in the large SH foot collection and in *Homo* fossils are based mainly on the general size of the bone (Alonso-Llamazares & Pablos, 2019; Castejón-Molina & Pablos, 2021; Pablos et al., 2014; Pablos, Martínez, et al., 2013b). The high robusticity and general size of the metatarsals from SH (see above) could be assigning individuals who could be females as allophyssus or even males. However, when estimating the sex based on the tarsals from SH, there is equal representation from both sexes: males and females (Pablos et al., 2014, 2017; Pablos, Martínez, et al., 2013b). Therefore, Table 16 provides the results of the stature of male

individuals, as well as from the entire metatarsal sample in SH, taking into account each individual metatarsal and altogether as group.

The average stature calculated from the SH male metatarsals is 175.1 ± 2.0 cm ($n = 12$). For the entire metatarsals sample from SH, the stature estimation is 173.7 ± 2.9 cm ($n = 17$; Table 16). Similar statures have been estimated for the SH male tali (173.9 ± 1.4 cm; $n = 6$; Pablos et al., 2017) and for the male calcanei (175.7 ± 1.9 cm; $n = 7$; Pablos et al., 2014). These results are similar, albeit slightly higher, than those obtained using the femora and the tibiae from SH: 168.1 ± 3.2 cm

TABLE 8 Inventory of unidentifiable metatarsals from SH.

Label	Toe	Side	Age	Description	Label	Toe	Side	Age	Description
AT-253	II–IV	?	Im	Diaphysis	AT-3208	II–IV	?	Im	Distal epiphysis
AT-340	II–IV	?	Ad	Distal epiphysis	AT-3209	II–IV	?	Im	Distal epiphysis
AT-341	II–IV	?	Ad	Distal epiphysis	AT-3210	II–IV	?	Im	Distal epiphysis
AT-483	II–IV	?	?	Diaphysis	AT-3368	II–IV	?	Im	Diaphysis
AT-502	II–IV	?	?	Diaphysis	AT-4295	II–IV	?	Im	Distal epiphysis
AT-504	II–IV	?	Ad	Diaphysis	AT-4488	II–IV	?	Im	Distal epiphysis
AT-698	II–IV	?	Im	Distal epiphysis	AT-4565	II–IV	?	Im	Distal epiphysis
AT-1199	II–IV	L?	Im	Distal epiphysis	AT-4706	II–III?	L	Ad	Base and diaphysis
AT-1391	II–IV	R?	Im	Distal epiphysis	AT-4707	II–IV	?	Im	Distal epiphysis
AT-1443	II–IV	?	Im	Distal epiphysis	AT-4773	II–IV	?	?	Diaphysis
AT-1508	II–IV	?	Im	Distal epiphysis	AT-4775	II–IV	?	?	Diaphysis
AT-1639	II–IV	?	Im	Distal epiphysis	AT-4776	II–IV	?	Im	Diaphysis
AT-1727	II–IV	?	Im	Distal epiphysis	AT-4933	II–V?	?	?	Diaphysis
AT-1966	II–IV	L?	Ad	Distal epiphysis	AT-5417	II–IV	?	Im	Distal epiphysis
AT-1997	II–IV	R?	Im	Diaphysis	AT-5421	II–IV	?	Im	Distal epiphysis
AT-2005	II–IV	L?	Im	Distal epiphysis	AT-5435	II–IV	?	Im	Distal epiphysis
AT-2014	II–IV	?	Im	Distal epiphysis	AT-5732	II–V	?	?	Diaphysis
AT-2141	II–IV	R?	Im	Distal epiphysis	AT-6352	II–IV	?	?	Diaphysis
AT-2262	II–IV	?	Im	Distal epiphysis	AT-6433	II–IV	?	Im	Diaphysis
AT-2265	II–IV	?	Im	Base fragment	AT-6434	II–IV	?	Im	Distal epiphysis
AT-2306	II–IV	?	Im	Distal epiphysis	AT-6435	II–IV	?	Ad	Diaphysis
AT-2373	II–IV	?	Im	Distal epiphysis	AT-6448	II–IV	?	?	Base fragment
AT-2518	II–IV	?	Ad?	Diaphysis	AT-6449	II–V?	?	?	Diaphysis
AT-2534	II–IV	?	Im?	Diaphysis	AT-6475	II–IV	?	?	Diaphysis
AT-2785	II–IV	R?	Im	Distal epiphysis	AT-6484	II–IV	?	?	Diaphysis
AT-2826	II–IV	?	Ad	Distal epiphysis	AT-6505	II–IV	?	Im	Diaphysis
AT-2828	II–IV	R?	Im	Distal epiphysis	AT-6506	II–IV	?	?	Diaphysis
AT-2837	II–IV	?	Im	Diaphysis	AT-6509	II–IV	?	?	Diaphysis
AT-2865	II–IV	?	Im	Distal epiphysis	AT-6741	II–V?	?		Diaphysis
AT-3200	II–IV	?	Im	Diaphysis	AT-6936	II–IV	?	Im?	Diaphysis

Abbreviations: Ad, adult; Im, immature; L, left; R, right.

($n = 8$) for males, 156.1 ± 2.5 cm ($n = 2$) for females, and 165.7 ± 5.8 cm ($n = 10$) for the entire SH sample of femora and tibiae (Carretero et al., 2012).

In order to estimate body mass from the SH metatarsals, in this study we used the formula of least squares for human-based regression provided by McHenry and Berger (1998). The body mass assessment was based on data from the mediolateral breadth and dorsoplantar height of the base and head of the first metatarsals and the mediolateral breadth of the second metatarsals from SH. As mentioned above, all the metatarsals from the SH sample are classified as males or allophyssus. Therefore, Table 16 provides the average body mass estimates for each element for males

and for the total sample, as well as for the entire SH metatarsal sample altogether. It has been established above that the first metatarsals from SH are very wide. This provides higher body mass estimates than those obtained for the second metatarsals, which could reflect the breadth of this element rather than actual body mass. The body mass average estimate obtained from the SH male metatarsals is 79.5 ± 8.9 kg. Taking into account the sex-assigned metatarsals and those with non-assigned to sex, we calculated a mean body mass of 76.8 ± 8.6 kg (Table 16). These values are higher than those obtained from the tali (69.7 ± 10.0 kg; $n = 20$) and the femoral head (69.2 ± 11.3 ; $n = 5$) in the SH sample (Arsuaga et al., 2014, 2015; Pablos et al., 2017).

TABLE 9 Inventory of proximal hallucal phalanges from SH.

Label	Side	Age	Anatomical description
AT-96	L	Ad	Complete
AT-685 + AT-2035	R	Im	Complete
AT-687	R	Ad	Complete
AT-722	L?	Ad	Fragment of base and diaphysis
AT-898	L	Ad	Complete
AT-899	R	Ad	Complete
AT-1041	L?	Im	Complete. Eroded at proximal end
AT-1324	R?	Im	Complete. Eroded at proximal end
AT-1482	L	Ad	Proximal fragment
AT-1652	L?	?	Fragment of distal trochlea
AT-1657	R?	Im	Fragment of proximal epiphysis
AT-1684 + AT-2419	L	Im	Complete
AT-1878	R?	Ad	Complete. Eroded at the base
AT-1888	L?	Im	Complete
AT-1933	R	Ad	Complete
AT-2180	L?	Im	Complete. Slightly eroded
AT-2311	L	Im	Complete
AT-2420	R?	Im	Fragment of proximal epiphysis
AT-2726	R	Im	Complete
AT-2869	R	?	Fragment of distal trochlea
AT-3119	L?	Ad	Fragment of base
AT-3275	L?	IM	Proximal epiphysis
AT-4228	L?	Im	Complete. Longitudinally eroded
AT-4437	L	Adol	Fragment of base and diaphysis
AT-4467	R	Ad	Complete
AT-5388	?	Im	Proximal epiphysis
AT-5645	L	Ad	Fragment of base
AT-6462	?	Ad	Fragment of base
AT-6487	?	Im	Fragment of proximal epiphysis
AT-6898	R	Ad	Proximal fragment

Abbreviations: Ad, adult; Adol, Adolescent (fusing); Im, immature; L, left; R, right.

Interestingly, the body mass estimates obtained with pelvis 1 from SH combining the length of the associated femora for stature estimates and the bi-iliac breadth (90.3–92.5 kg) (Bonmati et al., 2010) are not so different from those estimates of one of the biggest associated individuals represented by two feet (foot 1 and foot 2, see below) from the SH metatarsal sample (84.1 ± 7.1 kg; see below). If we consider all the body mass estimates of these foot associations (foot 1 and 2), keeping in mind that the tarsals (89.2–92.2 kg) and metatarsals are similar to the results from pelvis 1 (Pablos & Arsuaga, 2024; Pablos et al., 2017), this suggests that these feet could belong to one large SH individual, similar in body size to the one represented by

pelvis 1 from the SH collection, or at least to one similar in body size.

The only specimen from the SH foot collection with a traumatic/pathological condition is the fourth metatarsal AT-534. In this fossil, new periostitic bone formation can be distinguished on the dorso-lateral surface of the diaphysis. The remodeling reaction is not invasive of the underlying cortical bone, and there is no evidence of fracture lines. A stress fracture caused by mechanical stress with no acute trauma was proposed for this individual (Gracia-Téllez et al., 2012). These lesions occur as a result of repeated, prolonged, and rhythmic loads, exercises that were probably frequent in these hunter-gatherer Middle



FIGURE 9 Representation of some of the adult proximal hallucal phalanges from Sima de los Huesos in dorsal and proximal views. Scale bar = 2 cm. See Table 9 for details about the identification.

Pleistocene populations. A similar lesion at a more advanced stage was also observed in the Early Pleistocene *Homo antecessor* fourth metatarsal (ATD6-124; Martín-Francés et al., 2015) and in the Middle Pleistocene second metatarsal SdD2 from Sedia del Diavolo (Riga et al., 2022), confirming these kinds of fatigue traumas in Early and Middle Pleistocene populations and high levels of prolonged load. These kinds of fractures happen frequently in experienced runners that change to barefoot running, and usually heal without long-term effects (Giuliani et al., 2011). They indicate that structures in the foot also need time to adapt to the different loading, without which metatarsal stress fractures may occur. The Pleistocene populations likely were habitually barefoot and this could be one of the causes of the metatarsal stress fractures.

5 | METATARSAL AND FOOT PHALANGES ASSOCIATIONS

In the Sima de los Huesos site, the human fossils typically appear fragmented with post-depositional fractures, likely caused by the overlying sediment (Sala, Arsuaga, Martínez, & Gracia-Téllez, 2015a). This supports the aforementioned refittings within the same bone because there are no post-depositional deformation processes documented for any fossil. Although a complete individual is yet to be found in SH, it has been proposed that complete skeletons were deposited at this site (Arsuaga et al., 1990, 2015). They are fragmented, mixed, and comingled, but not all are associated. In the last 40 years the collection has grown considerably and some



FIGURE 10 Representation of some of the immature proximal hallucal phalanges from Sima de los Huesos in dorsal and proximal views. Note that AT-1652 is displayed in dorsal view and AT-2869 in distal view. Scale bar = 2 cm. See Table 9 for details about the identification.

associations between different elements are cautiously proposed in an attempt to reconstruct the body shape of these Middle Pleistocene hominins (Bonmatí et al., 2010; Gómez-Olivencia et al., 2007; Rodríguez et al., 2016). In this regard, the continuously growing collection of

human fossils from SH represents quite similar individuals in terms of age at death, shape, and size (Arsuaga et al., 2014, 2015), and it is possible that we are currently associating different elements that are likely from separate individuals, taking into account the current

TABLE 10 Mean and SD of the variables of the Sima de los Huesos (SH) phalanges (in mm) and other comparative samples.

	SH	Nea	UP	MPMH	MH-HTH	MH-lib	MH-SPab
Proximal hallucal phalanx	Maximum length—M1 ¹	34.0 ± 1.3 [32.8–36.8] (n = 7)	31.1 ± 1.7 [28.4–33.7] (n = 14)	32.4 ± 3.5 [26.2–39.0] (n = 14)	35.0 ± 3.0 [31.8–39.7] (n = 6)	35.0 ± 2.9 [28.5–44.0] (n = 244)	34.1 ± 2.8 [27.5–39.4] (n = 43)
	Breadth of diaphysis—M2 ^{4,5,6}	13.8 ± 1.6 [11.8–15.8] (n = 9)	13.1 ± 1.6 [10.3–15.6] (n = 16)	13.2 ± 1.2 [11.3–15.6] (n = 16)	13.4 ± 0.6 [12.9–14.3] (n = 4)	12.6 ± 1.1 [10.9–15.2] (n = 40)	12.1 ± 1.6 [8.7–15.1] (n = 43)
	Dist. Breadth—M2b ^{5,6}	17.6 ± 1.2 [15.8–19.0] (n = 7)	17.4 ± 1.7 [14.4–19.7] (n = 13)	16.7 ± 1.2 [15.2–18.6] (n = 8)	17.6 ± 1.4 [16.7–20.0] (n = 5)	16.4 ± 1.5 [13.0–21.7] (n = 244)	16.0 ± 1.4 [14.0–20.6] (n = 44)
Distal hallucal phalanx	Dist. Breadth—M2b ^{2,4,5,6}	14.6 ± 2.1 [11.6–17.1] (n = 8)	14.2 ± 2.6 [10.3–18.5] (n = 8)	11.2 ± 1.9 [7.5–13.0] (n = 7)	13.3 [12.5–13.9] (n = 3)	11.8 ± 1.6 [7.4–16.0] (n = 169)	11.6 ± 1.2 [9.2–15.3] (n = 37)
Proximal phalanx (II–V)	Midshaft index (M2 × 100/M3)–II ^{2,4,5,6}	113.7 ± 12.2 [81.8–135.5] (n = 21)	115.1 ± 7.1 [105.9–127.2] (n = 16)	102.0 ± 7.8 [82.1–111.5] (n = 17)	102.5 ± 6.9 [93.8–110.6] (n = 4)	87.8 ± 10.2 [63.0–119.4] (n = 169)	86.6 ± 11.7 [56.9–116.1] (n = 34)
	Midshaft index (M2 × 100/M3)–III ^{2,4,5,6}		114.7 ± 7.8 [101.7–129.2] (n = 13)	103.8 ± 10.1 [80.8–120.0] (n = 17)	108.2 ± 4.2 [105.2–114.3] (n = 4)	86.6 ± 11.8 [57.8–122.5] (n = 169)	85.7 ± 12.0 [64.3–111.6] (n = 35)
	Midshaft index (M2 × 100/M3)–IV ^{4,5,6}		114.5 ± 10.2 [97.8–129.2] (n = 9)	107.2 ± 10.7 [92.8–130.0] (n = 16)	109.1 ± 5.2 [101.8–112.9] (n = 4)	86.2 ± 13.6 [53.9–120.7] (n = 169)	85.9 ± 14.0 [58.2–116.8] (n = 35)
	Midshaft index (M2 × 100/M3)–V ^{4,5,6}		115.6 ± 9.7 [98.4–133.3] (n = 11)	114.1 ± 15.0 [91.3–140.0] (n = 12)	114.1 [108.1–120.1] (n = 2)	105.1 ± 18.0 [55.6–166.7] (n = 169)	103.1 ± 18.6 [66.4–169.3] (n = 37)

Note: Mean ± SD, range [] and sample size (n) are shown. Bold letters and superscript indicate significant differences between SH with some of the samples (Z-score > 1.96 in absolute terms; $p < 0.05$);

1 = Neanderthals, 2 = UP, 3 = MPMH, 4 = Recent modern humans (HTOC-HTH), 5 = Recent modern humans (Libben Amerindians), 6 = Recent modern humans (San Pablo Medieval collection). The SH sample includes: Proximal hallucal phalanx: AT-96, AT-687, AT-898, AT-899, AT-1482, AT-1878, AT-1933, AT-4467 and AT-6898. Distal hallucal phalanx: AT-192, AT-918, AT-2310, AT-2576, AT-3149, AT-4447, AT-4472 and AT-5612. Proximal non-hallucal phalanges: AT-80 (II), AT-527 (II), AT-87 (V), AT-99 (II–V), AT-135 (II–V), AT-160 (II–V), AT-1028 (II–IV), AT-1476 (II–IV), AT-1481 (II–IV), AT-2018 (II–V), AT-2238 (II–III), AT-2499 (II–III), AT-2527 (II–III), AT-2817 (II–III), 4486 (II–V), AT-5402 (II–V), AT-5642 (II–V), AT-5657 (II–V), AT-6823 (II–V) and AT-6922 (II–IV). Data from Trinkaus (1975, 1983, 2016); Vandermeersch (1981); Pablos et al. (2012, 2017); Pablos, Gómez-Olivencia, Maureille, et al. (2019b); Arsuaga et al. (2015); Pearson et al. (2020) and own data.

Abbreviations: MH-HTH, Modern humans–Hamann-Todd Osteological collection. MH-Lib, Modern humans–Libben, Amerindians unshod (Trinkaus, 1975); MH-SPab, Modern humans–San Pablo Medieval collection; MPMH, Middle Paleolithic Modern Humans; Nea, Neanderthals; SH, Sima de los Huesos; UP, Upper Paleolithic Modern Humans.

TABLE 11 Inventory of distal hallucal phalanges from SH.

Label	Side	Age	Anatomical description
AT-192	R	Ad	Complete
AT-674	R	Im	Complete (base and diaphysis)
AT-680	?	Im	Diaphysis and head. Eroded
AT-911	L	Im	Complete (Diaphysis and head)
AT-918	L	Ad	Complete
AT-1430	R	Im	Diaphysis and head. Eroded
AT-1442	R?	Im?	Fragment of diaphysis
AT-2017	L?	Im	Diaphysis and head. Eroded
AT-2310	R	Ad	Complete. Slightly eroded at the base
AT-2576	R	Ad	Complete. Eroded at the base
AT-3122	R?	Im	Proximal epiphysis
AT-3149	R	Ad	Complete. Eroded at the base
AT-3483	L?	Im	Diaphysis and head. Eroded
AT-4439	L	Im	Proximal epiphysis.
AT-4447	L	Ad	Complete
AT-4458 + AT-4464	R	Im	Complete
AT-4472	L	Ad	Complete
AT-4764	L	Ad	Proximal fragment
AT-5612	L	Ad	Complete. Slightly eroded at the base
AT-5688	R	Ad	Complete. Eroded
AT-6855	L?	Im	Diaphysis and head
AT-6862	R?	Ad	Proximal fragment

Abbreviations: Ad, adult; Im, immature; L, left; R, right.

collection. However, the ongoing excavation may provide new elements that are a better fit than previous ones, and thus the associations suggested now could slightly change upon future reviews of the collection. Therefore, in this study we tentatively propose the most likely associations between different metatarsals and foot phalanges at this point taking into account all the foot remains recovered from SH to date. This is based on the present-day state of the sample, the general size, metrical dimensions, shape, general morphology and that of the articular facets, bilateral asymmetry, state of development, anatomical congruence, etc. Previous research has allowed us to assign the sex to some foot fossils depending on the general size and metrical differences of the bones based on current populations (Pablos et al., 2014, 2017; Pablos, Martínez, et al., 2013b), providing another possibility that needs to be taken into account in order to establish associations.

5.1 | Foot 1 and foot 2 association

In the Sima de los Huesos site, 30 different fossils of two nearly complete feet have been recovered, likely

belonging to the same male adult individual (Pablos & Arsuaga, 2024). This foot association corresponds to the named foot 1 (right) and foot 2 (left) from the SH foot collection. These fossils have been associated based on their state of development, general size, anatomical congruence, bilateral asymmetry, and sexual assignment. Previously it was suggested that both tali (AT-966; right and AT-980; left) were associated with one single individual (Lorenzo et al., 1998; Pablos, Martínez, et al., 2013b). Likewise, it was proposed that two calcanei (AT-981; right and AT-971; left) corresponded to a single individual (Lorenzo et al., 1998; Pablos et al., 2014). All of them probably belong to the individual represented by the tarsometatarsal skeletons foot 1 and foot 2. This individual preserves nearly all of the tarsals from both sides, except the left lateral cuneiform (Pablos & Arsuaga, 2024). Of all the bones associated with this individual, most of them have been identified as males within the SH foot variation (Pablos et al., 2014, 2017; Pablos, Martínez, et al., 2013b). Thus, this individual is considered male and is one of the biggest of the SH foot collection. In all cases, all the epiphyses are completely fused, and the general developmental stage indicates that they belonged to an adult individual.



FIGURE 11 Representation of some of the distal hallux phalanges from Sima de los Huesos in dorsal and proximal views. Scale bar = 2 cm. See Table 11 for details about the identification. At the upper two rows are represented the adult ones. At the lower two rows are represented the immature ones.

The first metatarsals AT-987 (right) and AT-2808 (left) likely belong to this adult individual because they display similar morphology and dimensions. These two specimens

have significant development of the tuberosity for the insertion of the anterior tibial muscle. The second metatarsals AT-988 + AT-991 (right) and AT-992 + AT-1138 (left)

TABLE 12 Inventory of proximal non-hallucal phalanges from SH.

Label	Toe	Side	Age	Description	Label	Toe	Side	Age	Description
AT-80	II?	R?	Ad?	Diaph & tr	AT-2183	II-V	L	Im	Diaph & tr (er)
AT-87	V?	R	Ad	Complete	AT-2238	II-III	L	Ad	Diaph & tr (er)
AT-99	II-V	L	Ad?	Diaph & tr (er)	AT-2287	II-IV	R?	Im	Diaph & tr (er)
AT-120	IV-V	R	Im	Diaph & tr	AT-2360	II-V	L?	Im	Diaph & tr (er)
AT-134	II-IV	L?	Ad?	Diaph & tr (er)	AT-2371	II-V	?	Im	Diaph (er)
AT-135	II-V	R?	Ad?	Diaph & tr (er)	AT-2372	II-V	?	Im	Diaph & tr (er)
AT-159	II-V	R	?	Diaph & tr (er)	AT-2499	II-III	R	Ad	Complete
AT-160	II-V	R	Ad	Complete (er)	AT-2527	II-III	R	Ad	Complete (er)
AT-190	II?	L?	Im	Diaph & tr (er)	AT-2529	II-IV	L	Ad?	Diaph & tr (er)
AT-525	II-IV	L	Ad	Prox epiph (er)	AT-2538	II-III	R?	Ad?	Tr (er)
AT-527	II?	L	Ad?	Diaph & tr (er)	AT-2579	II-III	L	Im	Diaph & tr
AT-543	II-V	L?	Im	Prox epiph	AT-2817	II-III	R	Ad	Complete
AT-546	II-III	L?	Im	Prox epiph	AT-2820	II-III	L	Ad	Complete
AT-577	IV-V	?	Im	Diaph & tr	AT-2847	II-V	?	Im	Diaph (er)
AT-579	II?	R?	Im	Prox epiph (er)	AT-2866	II-V	L	Im	Diaph & tr (er)
AT-701	IV-V?	R	Im	Diaph & tr (er)	AT-3478	II-V	?	?	Diaph & tr (er)
AT-761	IV-V?	R	Im	Diaph & tr	AT-4438	II-V	?	Ad?	Diaph
AT-762	IV-V?	R	Im	Diaph & tr	AT-4449	II-V	?	Im	Prox epiph
AT-902	II-IV	R?	Im?	Tr (er)	AT-4469	II-V	?	Im	Epif dist
AT-908	II-IV	?	Im	Diaph & tr (er)	AT-4481	II-V	?	?	Tr
AT-914	II?	L?	Im?	Prox epiph	AT-4482	II-V	L	Im	Complete
AT-915	II-V	L	Im?	Diaph & tr (er)	AT-4485	II-V	?	?	Tr
AT-921	II-V	?	Im	Prox epiph	AT-4486	II-V	R	Ad	Complete
AT-1025	II-IV	L	Im	Diaph & tr	AT-4487	II-V	L?	Im	Prox epiph
AT-1028	II-IV	R	Ad?	Diaph & tr (er)	AT-4631	II-V	L	?	Tr (er)
AT-1181	II-V	R?	?	Diaph & tr (er)	AT-4704	II-V	R	Im	Complete (er)
AT-1303	II-V	?	Im	Diaph & tr (er)	AT-4711	II-V	?	Im	Complete (er)
AT-1361	II-V	L	Ad?	Diaph & tr (er)	AT-4715	II-V	?	Im	Prox epiph
AT-1421	II?	R?	Im	Prox epiph frag	AT-5402	II-V	L?	Ad	Prox epiph & diaph
AT-1431	IV-V?	?	Im?	Diaph & tr (er)	AT-5642	II-III	R	Ad	Complete
AT-1454	II-V	R?	Im	Diaph & tr (er)	AT-5657	II-V	L	Ad	Complete
AT-1455+ AT-1703	II-V	L?	Im	Complete (er)	AT-6480	II-V	?	Im	Prox epiph (er)
AT-1456	II-V	L?	Im	Diaph & tr (er)	AT-6481	II-V	?	Im	Prox epiph (er)
AT-1457	II-V	?	?	Diaph (er)	AT-6482	II-V	?	Im	Prox epiph (er)
AT-1476	II-IV	R	Ad?	Diaph & tr (er)	AT-6483	II-V	?	Im	Prox epiph (er)
AT-1481	II-IV	L	Ad?	Diaph & tr (er)	AT-6485	II-V	?	Im	Prox epiph (er)
AT-1517	II-V	R	?	Diaph & tr (er)	AT-6486	II-V	?	Im	Prox epiph (er)
AT-1518	II-V	R	Im?	Tr	AT-6488	II-V	?	Im	Prox epiph (er)
AT-1525	V?	L	Im	Diaph & tr (er)	AT-6489	II-V	?	?	Frag. tr
AT-1653	II-V	?	Im	Diaph (er)	AT-6490	II-V	?	Im	Prox epiph (er)
AT-1820	II-V	L?	Im	Diaph y tr (er)	AT-6492	II-V	?	?	Distal frag
AT-2004	II-V	L	Im	Complete	AT-6493	II-V	?	Im	Prox epiph (er)
AT-2006	II-V	L	Im	Diaph & tr	AT-6571	II-V	?	Im	Prox epiph

TABLE 12 (Continued)

Label	Toe	Side	Age	Description	Label	Toe	Side	Age	Description
AT-2009	IV-V	L	Im	Complete	AT-6823	II-V	L?	Ad	Complete (er)
AT-2011	IV-V	L	Im	Diaph & tr	AT-6833	II-V	?	Ad?	Distal half
AT-2018	II-V	L	Ad?	Diaph & tr (er)	AT-6922	II-IV	?	Ad	Complete (er)

Abbreviations: Ad, adult; Diaph, Diaphysis; Epiph, Epiphysis; Er, Eroded; Frag, Fragment; Im, immature; L, left; R, right; Prox, Proxima; Tr, Trochlea.

probably belong to the same individual due to their similarities in morphology and dimensions. The third metatarsals AT-989 (right) and AT-994 + AT-997 (left) belong to the same single adult individual because they are metrically and morphologically similar. We also associated the fourth metatarsals AT-990 + AT-1149 (right) and AT-978 (left) from the SH sample to foot 1 and 2. Both of them are assigned to the male sex. With respect to the fifth metatarsals collection, AT-1016 + AT-2827 (right) and AT-1015 (left) are proposed as belonging to this individual. All of these elements fit correctly in pairs: e.g., the first right metatarsal perfectly articulates with the right second metatarsal, which equally fits with the third one, and so on. This also occurs with all articulation between metatarsals and tarsals.

The stature estimates for this individual represented by foot 1 and foot 2 based on the first to fourth metatarsal maximum lengths from both sides has been calculated using the formulae proposed by Pablos, Gómez-Olivencia, et al. (2013a). We applied the male-specific equations of pooled ancestry populations for each metatarsal from this association as recommended by Pablos, Gómez-Olivencia, et al. (2013a). The average stature calculated with the first to fourth metatarsals from both sides is 174.1 ± 0.8 cm for this foot association. Using the formula of least squares for human-based regression provided by McHenry and Berger (1998) for the first and second metatarsals from foot 1 and foot 2, we obtained an average body mass for this individual of 83.9 ± 7.0 kg. When we average these estimates from the metatarsals with those calculated with the tarsals and with the combination of tarsals and metatarsals from this same individual (Pablos & Arsuaga, 2024), we obtained a mean stature of 173.9 ± 0.9 cm and a mean body mass of 79.5 ± 7.9 kg for this foot association. These estimates are similar to those of pelvis 1 from SH, one of the biggest in the Sima de los Huesos collection (Bonmati et al., 2010). The body mass index for the tarso-metatarsal skeleton of foot 1 and foot 2 calculated here as the body mass (in kg) divided by height squared (in m) is 27.74 which could suggest some overweight according to the International Obesity Task Force (Cole & Lobstein, 2012). This fact suggests that the musculature of this individual, and that from all the individuals from SH, is higher to that observed in recent modern humans because the corporal

cylinder is broader than in recent populations (Arsuaga et al., 1999; Carretero et al., 2018; Carretero, Rodríguez, et al., 2023b; García-González et al., 2023; Gómez-Olivencia et al., 2010; Rodríguez et al., 2016, 2018, 2023b). This likely denotes the high robusticity of this Middle Pleistocene population, that is, for the same stature, the bodies are broader than current and fossil modern humans. This “wide *Homo*” bauplan consisting of a large thorax with broad shoulders and pelvises, and great musculature and body mass probably derives from earlier populations such as *Homo ergaster/antecessor* from which *Homo sapiens* departed (Arsuaga, 2010; Arsuaga et al., 2015; Carretero et al., 1999, 2004; Carretero, Rodríguez, et al., 2023b; García-González et al., 2009; Lorenzo et al., 2015; Pablos et al., 2012; Rodríguez et al., 2023a).

5.2 | Other metatarsal associations

There are other two first metatarsals (AT-2496, right and AT-993, left) that are proposed here as belonging to another single adult individual due to their similar morphology and dimensions. Finally, we cannot rule out the possibility that the hallual metatarsals AT-2712 (right) and AT-1711 (left) belong to a third adult individual among the first metatarsals from SH including foot 1 and 2 described above.

In terms of the SH second metatarsals collection, the right AT-3142 + AT-3171 displays a slight bone overgrowth probably due to an arthrosic process. The right third metatarsal AT-4424 displays an arthropathy or arthrosis at the level of the articular facet for the second metatarsal. These pathological characteristics indicate that these two metatarsals could very well belong to the same adult individual.

5.3 | Foot phalanges associations

With respect to the SH foot phalanges, the hallual proximal phalanges AT-1933 (right) and AT-898 (left) have similar dimensions, proportions, and morphology. The phalanx AT-898 could belong to a male individual; therefore, this association probably represents the same male

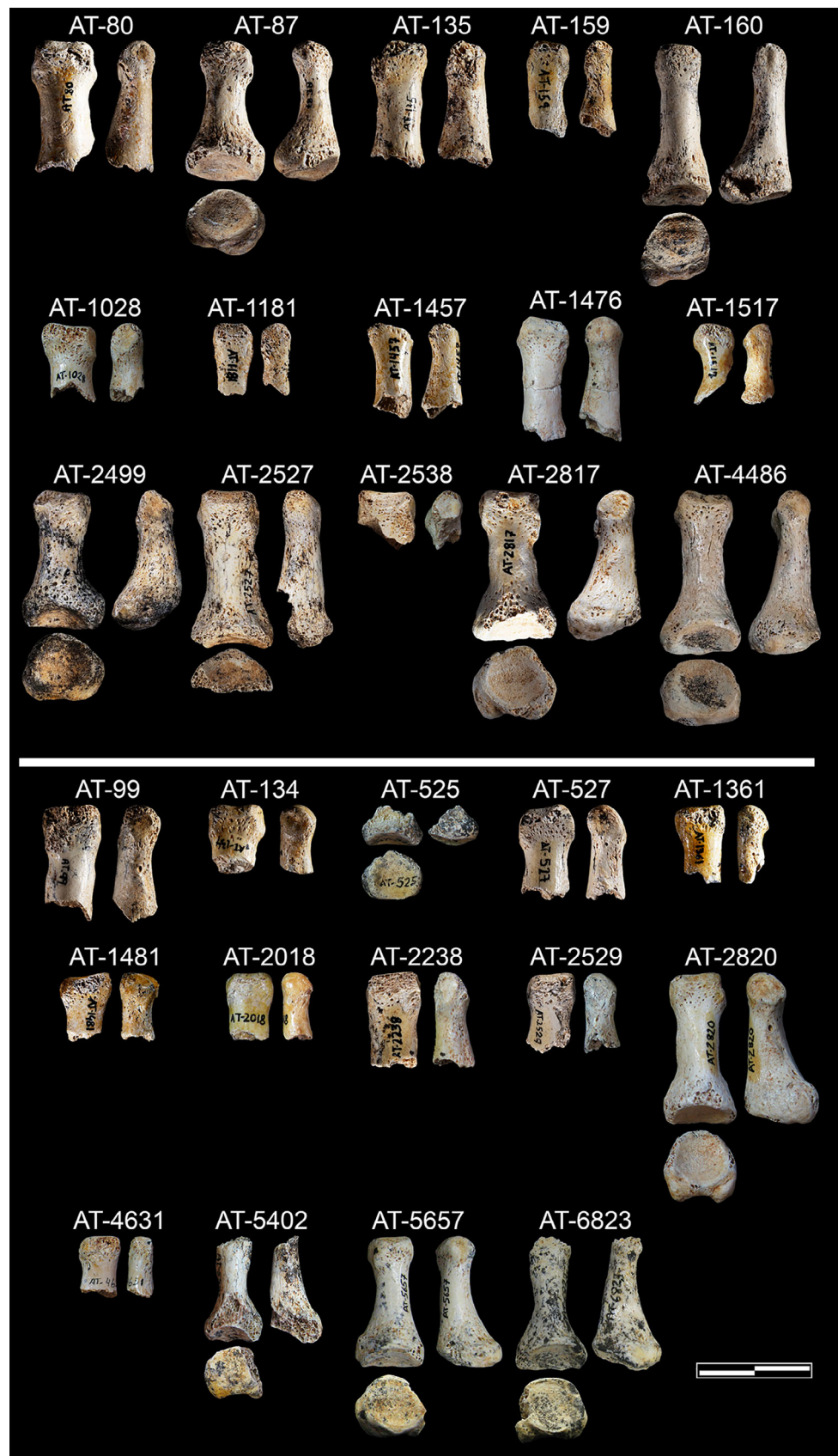


FIGURE 12 Representation of some of the adult proximal foot phalanges of toes II-V from Sima de los Huesos in dorsal, medial and proximal views. At the upper two rows are represented the right and undetermined ones. At the lower two rows are shown the left ones. Scale bar = 2 cm. See Table 12 for details about the identification.



FIGURE 13 Representation of some of the immature proximal foot phalanges of toes II–V from Sima de los Huesos in dorsal, medial and proximal views. Note that in the lowest rows are shown some not fused proximal epiphyses. Scale bar = 2 cm. See Table 12 for details about the identification.

TABLE 13 Inventory of intermediate foot phalanges from SH.

Label	Toe	Side	Age	Description	Label	Toe	Side	Age	Description
AT-88	II-III?	R?	Ad	Complete	AT-2016	IV-V	?	Ad	Complete
AT-109	II-IV	L?	Ad	Complete	AT-2305	II-IV?	R?	Ad	Complete (er)
AT-111	IV-V	R	Ad	Complete	AT-2352	II-IV	R?	Ad	Diaph & tr (er)
AT-114	II-V	?	Im	Diaph & tr	AT-2415	II-III	?	Ad	Complete (er)
AT-115	V?	R?	Ad	Complete	AT-2416	V?	R?	Ad	Complete
AT-214	II-III	?	Ad	Complete	AT-2519	II-III?	R?	Ad	Complete
AT-265	II-III	L?	Ad	Complete	AT-2727	II-III?	R?	Ad	Complete
AT-513	II-IV	?	Ad	Prox epiph (er)	AT-2744	II-III	L?	Ad	Complete
AT-514	II-IV	L?	Ad	Complete	AT-2801	II-III	R?	Ad	Complete
AT-516	V?	?	Ad	Complete	AT-2802	II-IV	L?	Ad	Complete
AT-521	II-V	L	Ad	Complete	AT-2807	IV-V	?	Ad	Complete
AT-522	II-V	?	Ad	Complete (er)	AT-2812	II-V	?	Im	Tr (er)
AT-523	IV-V	?	Ad	Complete	AT-2814	II-III	L?	Ad	Complete
AT-524	V?	L	Ad	Complete	AT-2818	II-III	L	Ad	Complete
AT-541	II-V	R	Ad	Diaph & tr (er)	AT-2832	II-V	L?	Im	Diaph & tr (er)
AT-545	IV-V	R	Im	Diaph & tr	AT-2934	II-V	?	Im	Diaph & tr
AT-903	II-V	?	Im-Ad	Complete	AT-3146	V?	?	Ad	Complete
AT-905	II-V	?	Im	Diaph & tr (er)	AT-3214	II-V	?	Im	Diaph & tr
AT-906	V	L	Ad	Complete	AT-3215	V	R?	Ad	Complete
AT-913	II-V	L	Ad	Complete	AT-3369	?	?	?	Frag Base?
AT-1032	II-V	?	Im	Diaph & tr	AT-3470	II-V	?	Ad	Complete (er)
AT-1033	II-V	?	Im	Diaph & tr	AT-3476	II-V	R?	Ad	Complete
AT-1285	IV-V	?	Ad	Complete	AT-3773	II-V	?	Ad	Complete
AT-1349	II-IV	?	Ad	Complete	AT-3774	II-III	?	Ad	Complete
AT-1394	II-V	L	Ad	Complete	AT-3775	II-V	?	Ad	Tr (er)
AT-1432	IV-V	L	Ad	Complete (er)	AT-4423	II-V	?	Im	D + T
AT-1433	IV-V?	R	Ad	Complete	AT-4450	IV-V	R	Ad	Complete
AT-1434	II-V	R	Ad	Complete	AT-4452	II-V	?	Im	Prox epiph
AT-1488	II-III?	R?	Ad	Diaph & tr (er)	AT-4459	II-V	?	Im	D + T
AT-1503	IV-V	L	Ad	Complete	AT-4462	IV-V	L?	Ad	Complete
AT-1510	II-III	R?	Ad	Complete	AT-4479	II-V	?	Im	D + T
AT-1511	II-V	R?	Ad	Complete	AT-4713	IV-V	?	Im	D + T
AT-1644	V	R	Ad?	Diaph & tr (er)	AT-5403	II-III?	?	Ad	Complete (er)
AT-1656	II?	?	Ad	Diaph & tr (er)	AT-5640	II-V	?	Ad	Complete (er)
AT-1767	II-V	L	Ad	Complete	AT-6615	II-V	L	Ad	Complete
AT-2002	II-V	?	Im-Ad	Complete	AT-6815	II-II	?	Ad	Complete
AT-2003	II-V	?	Im	Diaph & tr	AT-6867	IV-V?	L	Ad	Complete (er)
AT-2007	V	?	Ad	Complete	AT-6927	III-IV	L	Ad	Complete

Abbreviations: Ad, adult; Diaph, Diaphysis; Epiph, Epiphysis; Er, Eroded; Frag, Fragment; Im, immature; L, left; R, right; Prox, Proxima; Tr, Trochlea.

adult individual. Likewise, the distal hallucal phalanges AT-3149 (right) and AT-5612 (left) display dimensions and morphology compatible with the same adult

individual. Both of them have been estimated to belong to male individuals within the SH foot variation.



FIGURE 14 Representation of some of the adult intermediate foot phalanges from Sima de los Huesos in dorsal, medial and proximal views. At the upper four rows are represented the right and undetermined ones. At the lower three rows are shown the left ones. Scale bar = 2 cm. See Table 13 for details about the identification.



FIGURE 15 Representation of some of the immature intermediate (upper three rows) and distal (lower two rows) foot phalanges of toes II-V from Sima de los Huesos in dorsal, medial and proximal views. Scale bar = 2 cm. See Tables 13 and 15 for details about the identification.

In regard to the SH lateral foot phalanges, the great similarities in general and articular sizes prevent us from establishing any other associations with certainty. Nevertheless, here we provide several probable associations of foot phalanges (Figure 18). The intermediate foot phalanx AT-1285 and the distal foot phalanx AT-1438 fit quite well into the current SH foot collection. The proximal phalanx AT-2820, the intermediate AT-2818, and the distal phalanx AT-2822 have similar articular dimensions and display one of the best fittings with articular congruence within the SH foot phalanges. A third possible association includes AT-2527 (proximal), AT-2519 (intermediate), and AT-920 (distal). These associations could represent Frankenstein-like associations within the SH human collection belonging to different individuals. They likely represent the most feasible associations at this time, but future review and new fossils from the site might alter these associations or contradict them.

6 | DISCUSSION

The Sima de los Huesos population and Neandertals exhibit some similar traits in the whole skeleton (Arsuaga et al., 2014, 2015; Carretero et al., 1997; Pablos et al., 2017). In this sense, the comparative study of metatarsals and foot phalanges from Sima de los Huesos presented here has allowed us to establish some traits shared with Neandertals, which confirms the evolutionary relationship between these two paleodemes as evolutionary sister groups as previously established by other anatomical parts (Arsuaga et al., 2014, 2015; Carretero, García-González, et al., 2023a; Pablos et al., 2014; Pablos, Martínez, et al., 2013b). However, in some traits the forefoot from the SH collection exhibit subtle differences with Neandertals, such as a very broad and robust first metatarsal, a long and broad proximal hallux phalanx, and more robust lateral distal foot phalanges (Table 17). There are some metrical and morphological differences with the other comparative samples, both chronologically earlier and later, that distinguish the SH population from other species of genus *Homo*. In spite of these results, the near absence of foot phalanges and metatarsals corresponding to *H. ergaster/erectus*, *H. antecessor* or other earlier *Homo* paleodemes tentatively precludes us from ascertaining more in-depth evolutionary relationships with other *Homo* species based on metatarsals and foot phalanges.

Most of the traits that distinguish SH and Neandertal forefoot from recent modern humans and Late Pleistocene *H. sapiens* are related to the overall bodily robustness of these two populations (Table 17). This robusticity pattern observed in the SH and Neandertals foot in some points could constitute the primitive or plesiomorphic condition inherited from *H. antecessor* or other earlier species of genus *Homo* (Arsuaga, 2010; Lorenzo et al., 2015; Pablos et al., 2012), or it could represent shared traits by the SH-Neandertals evolutionary line (Arsuaga et al., 2014, 2015; Pablos et al., 2014; Pablos, Martínez, et al., 2013b). Among the likely derived traits shared by SH and Neandertal feet are the broad bases of third to fifth metatarsals, a broad and robust distal hallux phalanx, and robust intermediate foot phalanges. In general, Neandertals display robust foot elements in comparison to recent and fossil *H. sapiens* populations (Pablos, Gómez-Olivencia, Maureille, et al., 2019b; Pearson et al., 2020; Pomeroy et al., 2017; Trinkaus, Robson Brown, et al., 2017b), such as those of the SH foot collection. These similarities or differences likely reflect taxonomical relationships between SH and Neandertals, but they might also reflect similar movements on similar substrates (e.g., Dunn et al., 2014).

TABLE 14 Mean and SD of the variables of the SH intermediate and distal phalanges (in mm) and other comparative samples.

	SH	Nea	UP	MPMH	MH-HTH	MH-lib	MH-SPab
Intermediate phalanx (II-V)	Midshaft index (M2 × 100/M3)-II ^{3,4,5,6}	162.6 ± 18.1 [122.8–208.6] (n = 55)	158.2 ± 14.1 [137.1–173.4] (n = 6)	146.9 [135.4–155.3] (n = 3)	139.9 ± 13.3 [126.4–156.1] (n = 4)	140.0 ± 19.1 [102.4–202.3] (n = 166)	134.8 ± 16.0 [116.3–202.2] (n = 29)
							144.7 ± 22.4 [102.0–184.9] (n = 28)
	Midshaft index (M2 × 100/M3)-III ^{3,4,5}	159.4 ± 14.1 [146.3–173.0] (n = 4)	153.6 [132.2–175.0] (n = 2)	140.7 ± 12.3 [130.2–157.7] (n = 4)	152.9 ± 26.8 [82.3–220.6] (n = 162)	148.0 ± 21.2 [108.5–185.4] (n = 22)	151.7 ± 28.7 [110.4–207.5] (n = 24)
	Midshaft index (M2 × 100/M3)-IV ³	165.1 ± 20.5 [137.5–186.9] (n = 4)	147.9 [119.3–185.7] (n = 3)	136.0 ± 22.7 [113.4–166.7] (n = 5)	169.0 ± 26.2 [106.7–244.0] (n = 144)	172.0 ± 20.3 [129.8–223.7] (n = 20)	161.9 ± 25.8 [119.1–211.7] (n = 20)
Distal phalanx (II-V)	Midshaft index (M2 × 100/M3)-V	202.4 [178.3–224.3] (n = 3)	172.2 [169.4–175.0] (n = 2)	164.9 [139.4–190.5] (n = 2)	164.4 ± 25.0 [107.9–230.7] (n = 110)	-	159.0 ± 20.1 [127.6–202.6] (n = 18)
	Midshaft index (M2 × 100/M3)-II ^{4,6}	116.8 ± 16.9 [93.7–160.5] (n = 53)	108.8 ± 14.0 [97.2–131.7] (n = 5)	105.1 (n = 1)	112.9 [103.8–121.9] (n = 2)	108.8 ± 17.3 [69.6–180.3] (n = 166)	122.1 ± 18.2 [104.8–164.4] (n = 14)
							101.4 ± 17.6 [77.6–144.1] (n = 15)
	Midshaft index (M2 × 100/M3)-III ⁴	99.7 [95.9–103.4] (n = 2)	116.7 [116.7–116.7] (n = 2)	107.1 [91.7–118.3] (n = 3)	102.5 ± 13.9 [72.7–142.6] (n = 165)	122.9 ± 18.6 [92.3–142.3] (n = 16)	108.0 ± 14.5 [90.5–145.9] (n = 16)
Midshaft index (M2 × 100/M3)-IV ^{4,5,6}	Midshaft index (M2 × 100/M3)-IV ^{4,5,6}	112.0 ± 6.7 [105.5–120.8] (n = 4)	110.9 [101.0–120.0] (n = 3)	115.2 [109.3–121.2] (n = 2)	106.5 ± 15.7 [70.6–160.0] (n = 156)	102.0 ± 12.8 [84.3–125.5] (n = 11)	100.7 ± 11.0 [87.0–122.5] (n = 12)
	Midshaft index (M2 × 100/M3)-V ^{4,5}	98.2 ± 16.7 [69.9–113.4] (n = 5)	123.6 [106.8–140.4] (n = 2)	98.6 [98.0–99.1] (n = 2)	111.5 ± 23.6 [72.9–207.7] (n = 154)	104.2 ± 13.3 [69.8–131.6] (n = 20)	105.9 ± 17.7 [84.9–136.6] (n = 8)

Note: Mean ± SD, range [] and sample size (n) are shown. Bold letters and superscript indicate significant differences between SH with some of the samples (Z-score > 1.96 in absolute terms; $p < 0.05$);

1 = Neandertals, 2 = UP, 3 = MPMH, 4 = Recent modern humans (HTOC-HTH), 5 = Recent modern humans (Libben Amerindians), 6 = Recent modern humans (San Pablo Medieval collection). Data from Trinkaus (1975, 1983, 2016); Vandermeersch (1981); Pablos et al. (2012, 2017); Pablos, Gómez-Olivencia, Maureille, et al. (2019b); Arsuaga et al. (2015); Pearson et al. (2020) and own data.

Abbreviations: MH-HTH, Modern humans–Hamann-Todd Osteological collection. MH-Lib, Modern humans–Libben, Amerindians unshod (Trinkaus, 1975); MH-SPab, Modern humans–San Pablo Medieval collection; MPMH, Middle Paleolithic Modern Humans; Nea, Neanderthals; SH, Sima de los Huesos; UP, Upper Paleolithic Modern Humans.

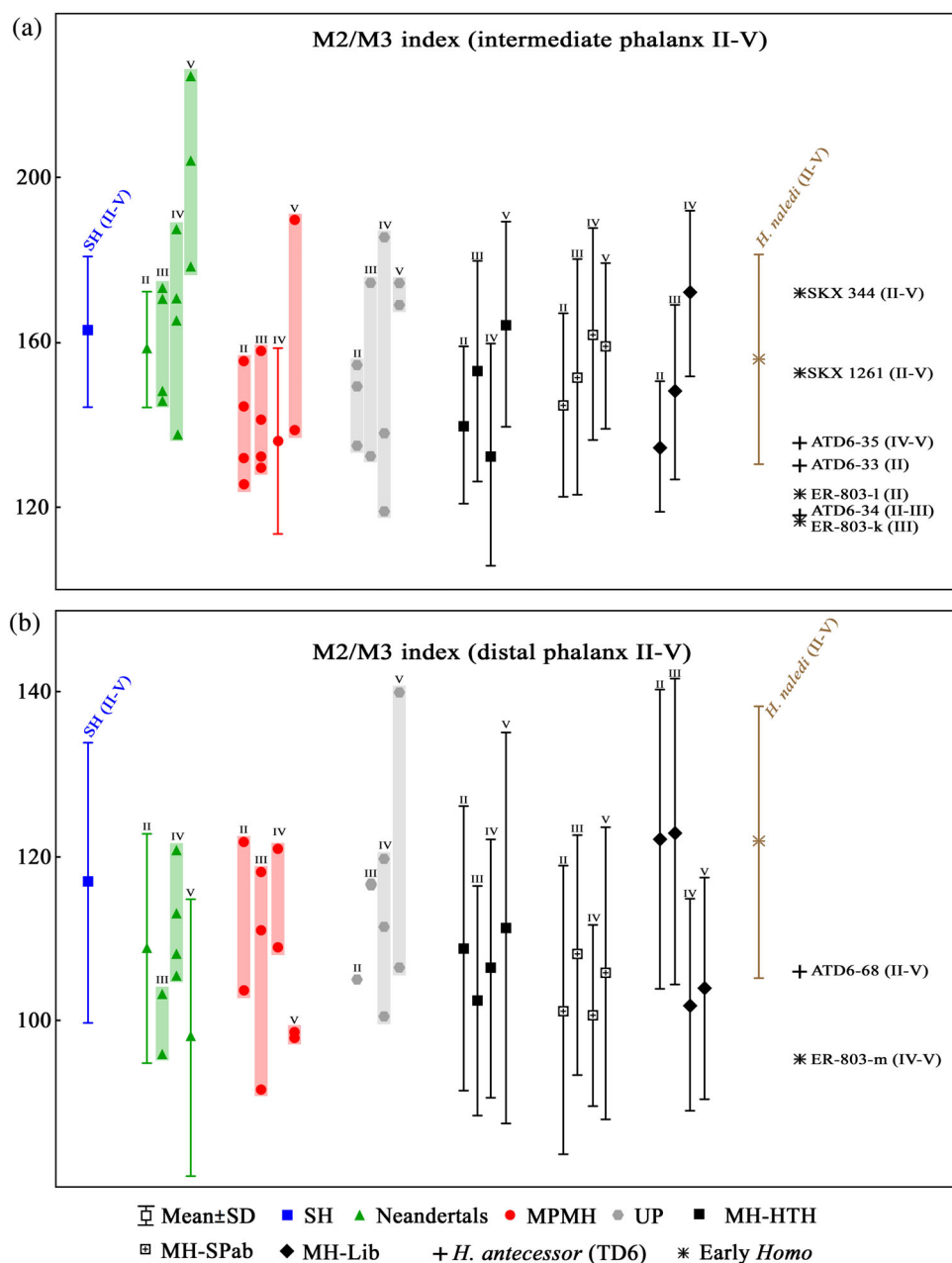


FIGURE 16 Univariate analysis of the foot phalanges from the Sima de los Huesos (SH) sample. (a) Midshaft index of the lateral intermediate phalanges (M2-midshaft breadth/M3-Midshaft height). (b) Midshaft index of the lateral distal phalanges (M2-midshaft breadth/M3-Midshaft height). Data from Pablos et al. (2017); Pablos, Gómez-Olivencia, and Arsuaga (2019a); Pablos, Gómez-Olivencia, Maureille, et al. (2019b) and present study. The number of toe (II to V) is provided for each series/fossil. MH-HTH, Modern humans-Hamann-Todd Osteological collection; MH-Lib, Modern Humans-Libben-Amerindians collection (unshod); MH-SPab, San Pablo Medieval collection; MPMH, Middle Paleolithic modern humans; UP, Upper Paleolithic.

and thus we cannot rule out functional similarities between SH and Neandertals.

The barefoot (or unshod) runners often land on the forefoot or the midfoot generating smaller collision forces than shod rear-foot strikers because barefoot facilitates a more plantarflexed foot strike causing an increased prevalence of an forefoot strike or midfoot strike and subsequent reduction in impact loading (Hall et al., 2013; Lieberman et al., 2010). Additionally, the presence of a strong longitudinal arch in genus *Homo* functionally improves the mass-spring mechanics of running by storing and releasing elastic energy (Lieberman et al., 2010). The presence of robust proximal pedal phalanges in Neandertals indicates that a supportive footwear was rare

in Neandertals (Trinkaus, 2005). The shaft hypertrophy in SH proximal foot phalanges suggests the non-habitual use of rigid footwear. So, probably the SH hominins walked and ran with a forefoot strike more than a rear foot strike.

However, at some points, SH metatarsals and foot phalanges are even more robust than Neandertals (Table 17). The few aforementioned traits in which Neandertals are broader than recent modern humans but slightly more gracile than the SH population for metatarsals and foot phalanges suggest a slight gracilization process in Neandertals, at least in the first toe, if we consider the population from Sima de los Huesos as one of the possible roots of Neandertals (Arsuaga et al., 2014;

TABLE 15 Inventory of distal foot phalanges from SH.

Label	Toe	Side	Age	Description	Label	Toe	Side	Age	Description
AT-110	II-V	?	Ad	Complete	AT-1938	II-V	?	Ad	Complete (er)
AT-112	II-V	?	Ad	Complete	AT-1964	II-IV	L	Ad	Complete
AT-526	II-IV	?	Ad	Complete (er)	AT-2010	II-V	?	Im	Complete
AT-538	II-III	R?	Ad	Complete	AT-2012	IV-V	?	Im	Diaph & tr
AT-678	II-V	R?	Ad	Complete	AT-2107	II-III	?	Ad	Complete
AT-679	II-V	L?	Ad	Complete	AT-2417	II-IV	?	Ad	Complete
AT-681	II-IV	L?	Ad	Complete	AT-2418	V	?	Ad	Complete
AT-900	II-IV?	R	Ad	Complete	AT-2735	II-III	R?	Ad	Complete
AT-904	II-III	?	Ad	Complete	AT-2745	II-IV	?	Ad	Complete
AT-907	II-III	?	Ad	Complete	AT-2804	IV-V	?	Ad	Complete
AT-920	II-III	?	Ad	Complete (er)	AT-2805	IV-V	L?	Im	Diaph & tr
AT-935	II-IV	?	Ad	Complete	AT-2821	IV-V	R?	Im	Diaph & tr
AT-1031	II-III	?	Ad	Complete	AT-2822	II-III	L	Ad	Complete
AT-1034	II-V	L?	Ad	Complete	AT-2829	II-V	?	Im?	Fragment
AT-1188	II-V	R	Ad	Complete	AT-3147	II-V	R?	Ad	Complete
AT-1202	II-V	?	Ad	Complete	AT-3266	II-III	L?	Ad	Complete
AT-1347	II-V	?	Ad	Complete (er)	AT-3267	II-III	R?	Ad	Complete
AT-1355	IV-V	L?	Ad	Complete	AT-3469	II-III	R?	Ad	Complete
AT-1356	II-V	?	Ad	Complete (er)	AT-3482	II-III	L	Ad	Complete
AT-1357	IV-V?	?	Ad	Complete (er)	AT-3776	IV-V	L?	Ad	Complete
AT-1395	II-IV	?	Ad	Complete	AT-3777	IV-V	?	Im	Diaph & tr
AT-1435	IV-V	R?	Im-Ad	Complete	AT-4414	II-V	R?	Ad	Complete
AT-1436	II-III?	R?	Ad	Complete	AT-4419	V	L?	Ad	Complete
AT-1437	II-III?	?	Ad	Complete	AT-4454	II-V	L?	Ad	Complete
AT-1438	II-III	R?	Ad	Complete	AT-4455	II-V	L?	Ad	Complete (er)
AT-1439	IV-V	R?	Ad	Complete	AT-4463	II-V	R?	Ad	Complete
AT-1440	II-V	L?	Im	Diaph & Tr	AT-4633	II-IV	?	Ad	Complete
AT-1441	IV-V	D?	Im-Ad	Complete	AT-5643	II-IV	?	Ad	Complete (er)
AT-1490	II-V	?	Ad	Complete	AT-6494	II-V	?	II-V	Fragment
AT-1507	II-III	L?	Ad	Complete	AT-6554	II-III	L	Ad	Complete
AT-1736	II-V	?	Ad	Complete (er)	AT-6671	IV-V	?	Im	Diaph & tr
AT-1841	II-V	?	Ad	Complete (er)	A-6858	II-V	R?	Ad	Complete

Abbreviations: Ad, adult; Diaph, Diaphysis; Er, Eroded; Im, immature; L, left; R, right; Tr, Trochlea.

Hublin, 2014). Some metatarsal and pedal phalanx traits in the Neandertal and SH population have been suggested to be related to a large corporal size, robusticity, and to increased biomechanical stress (Arsuaga et al., 2015; Pablos et al., 2017; Trinkaus, Robson Brown, et al., 2017b). Something similar happens in other areas of the postcranial skeleton: that is, Neandertals have some bones that are broader and/or with more robust traits than those of modern humans, which are associated with a broader corporal cylinder. However, in the

SH population, these characteristics are even more robust/broad than Neandertals, such as the breadth of the first toe. Here, we call them hyper-Neandertal traits because Neandertals are broader than modern humans. But the SH hallux is even broader than that of Neandertals. The projected lateral malleolar facet of the talus in Neandertals is significantly even more projected in SH (Pablos, Martínez, et al., 2013b). In Neandertals, the calcaneus has a more projected sustentaculum tali in comparison with recent modern humans (Pablos, Gómez-

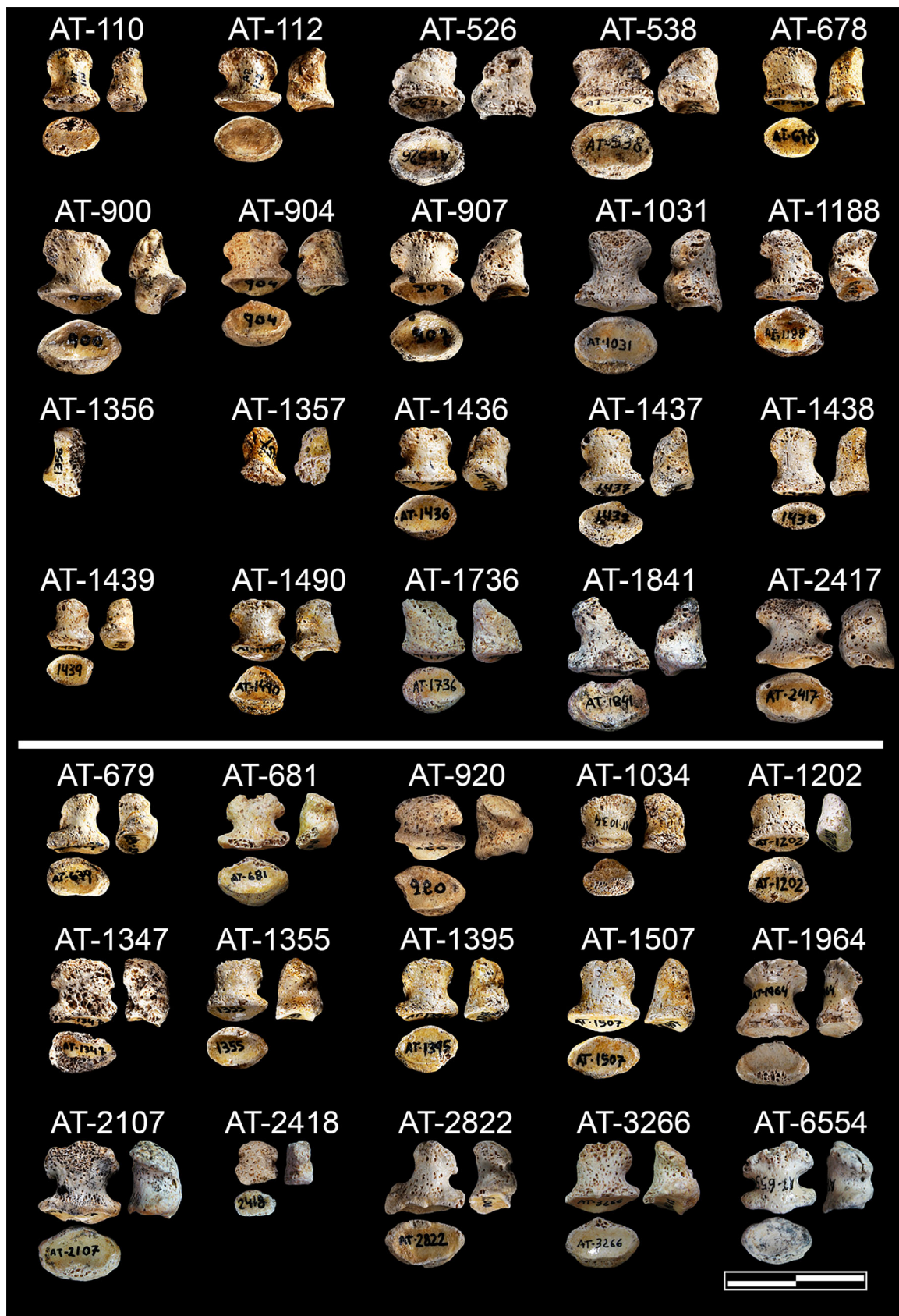


FIGURE 17 Representation of some of the adult distal foot phalanges of toes II-V from Sima de los Huesos in dorsal, medial and proximal views. At the upper three rows are represented the right and undetermined ones. At the lower two rows are shown the left ones. Scale bar = 2 cm. See Table 15 for details about the identification.

TABLE 16 Stature (in cm) and body mass (in kg) estimations from the SH metatarsals.

	I	II	III	IV	SH total
<i>Stature from metatarsals</i>					
Male	173.1 ± 0.3 (n = 3)	176.1 ± 2.4 (n = 3)	175.5 ± 2.0 (n = 3)	175.6 ± 2 (n = 3)	175.1 ± 2.0 (n = 12)
Female	–	–	–	–	–
All	172.4 ± 1.4 (n = 4)	174.2 ± 4.3 (n = 4)	173.4 ± 2.9 (n = 6)	175.6 ± 2 (n = 3)	173.7 ± 2.9 (n = 17)
<i>Body mass from metatarsals</i>					
Male	84.7 ± 6.0 (n = 3)	71.7 ± 6.6 (n = 2)	–	–	79.5 ± 8.9 (n = 5)
All	81.1 ± 8.8 (n = 4)	71.2 ± 4.8 (n = 3)	–	–	76.8 ± 8.6 (n = 7)

Note: Mean ± SD and sample size (n) are shown.

TABLE 17 Summary of selected traits in metatarsals and foot phalanges in fossil and extant humans.

Element	<i>H. ergaster</i>	<i>H. antecessor</i>	SH	Neandertals	<i>H. sapiens</i>
Mt I	Narrow?	–	+Broad	Broad	Narrow
Mt II	–	Narrow	Narrow	Narrow	Narrow
Mt III	Narrow	–	Broad	Broad	Narrow
Mt IV	–	Narrow	Broad	Broad	Narrow
Mt V	Narrow	–	Broad	Broad	Narrow
PP I	–	Long and narrow	Long and broad	Short and broad	Long/short and narrow
DP I	–	–	Broad	Broad	Narrow
PP II–V	Robust?	Robust?	Robust	Robust	Gracile
IP II–V	Gracile?	Gracile?	Robust	Robust	Gracile?
DP II–V	Gracile	Gracile?	+Robust	Robust?	Gracile

Note: Plesiomorphic (red) and derived (blue) trait for SH, *H. neanderthalensis* and *H. sapiens* clades. Autoapomorphic traits exclusive to SH relative to Neandertals are shown in green. Colorless cells indicate uncertain polarity. *H. sapiens* clade includes both recent and fossil samples. Modified and updated from Arsuaga et al. (2015).

Abbreviations: DP, Distal phalanx; IP, Intermediate phalanx; Mt, Metatarsal; PP, Proximal phalanx.

Olivencia, Maureille, et al., 2019b; Trinkaus, 1975). In SH, the sustentaculum tali of the calcaneus is significantly more projected than in Neandertals (Pablos et al., 2014). The SH pelvis displays a bi-iliac breadth that is broader than that of Neandertals, the iliac height and the maximum sacral breadth have lower values in Neandertals, and the pubic ramus is craniocaudally thinner in Neandertals relative to the SH sample in a significant way (Arsuaga et al., 2015; Bonmatí et al., 2010). The humeral cortical area of the SH sample is higher than that of Neandertals (Arsuaga et al., 2015). The posterior arch of the atlas in SH hominins is more significantly robust than the slender ones observed in Neandertals (Arsuaga et al., 2015; Gómez-Olivencia et al., 2007; Gómez-Olivencia & Arsuaga, 2023). The lumbar vertebrae and the transverse process in the third lumbar in SH are larger and longer, respectively, in SH relative to Neandertals (Bonmatí et al., 2010). The SH first ribs have a tuberculo-ventral chord that is larger than in Neandertals

(Gómez-Olivencia et al., 2010). The SH radii are longer than in Neandertals, and the neck and diaphysis are medio-laterally larger (Rodríguez et al., 2016). Taking into account the stature estimates, Neandertals probably reduced their stature slightly, albeit not significantly, compared with their ancestors: the people from SH (Arsuaga et al., 2015; Carretero et al., 2012; Will et al., 2017).

Recent modern humans were more gracile than their ancestors in Africa (Ryan & Shaw, 2015). Neandertals are robust relative to recent modern humans. But in some areas, especially in the hallux, they were also a little more gracile than their own ancestors, the hominins from Sima de los Huesos. Hence, we suggest here that a slight gracilization process at least in the first toe likely occurred in Neandertals relative to their ancestors, parallel to what occurred in the recent modern human lineage. We are well aware that this hypothesis may sound a little bit risky and controversial on some points, mainly because



FIGURE 18 Representation of some of the most probably foot phalanges associations proposed inside the SH foot collection (see main text for details).

of some biases in the *Homo* fossil record in terms of sex assignment, individual variation, as well as many problems related to the robusticity and its skeletal expression. Only more fossils and specific studies will clarify or refute this gracilization hypothesis in the future. The average body mass estimations based on the base of first and second metatarsals from SH (76–80 kg) are slightly higher than those obtained from the talus and femur for the SH sample (Arsuaga et al., 2014, 2015; Pablos et al., 2017). This may be due to the fact that the first metatarsals from SH are very wide compared to Neandertals and the other comparative samples, which could provide higher estimates of body mass estimates than those obtained for the second metatarsal. But the estimates obtained from the SH Pelvis 1 (90.3–92.5 kg) (Bonmatí et al., 2010) are similar to those obtained for the associations foot 1 and foot 2. This could suggest that these SH foot associations could belong to one individual similar in proportions and body size to that of the Pelvis 1 individual. Associating elements for the more than 7000 human fossils belonging to nearly 30 individuals from SH is no easy feat due to the morphological and metrical similarities among the different individuals. The presence in the SH sample of all anatomical elements making up the skeleton, including the tiny distal pedal phalanges, together with the fact that some elements have been associated suggests that

complete skeletons were deposited at the SH chamber. The exceptional conservation of the fragile foot phalanges indicates that complete bodies rather than isolated bones arrived at the SH site (Sala, Martínez, et al., 2023b). Furthermore, the large quantity of foot phalanges compared to Neandertals and Upper Paleolithic *H. sapiens* throughout the world fossil record suggests that complete skeletons were deposited in the site. It is remarkable that even most of the classically considered burials of Neandertals and Paleolithic *H. sapiens* and large accumulations of skeletons and/or human fossils do not always preserve all the foot phalanges (Pablos, Gómez-Olivencia, & Arsuaga, 2019a; Pablos, Gómez-Olivencia, Maureille, et al., 2019b). The preservation of such a large quantity of foot phalanges in the SH collection in relation to the total of estimated individuals confirms that complete skeletons were deposited in the SH chamber. Carnivores and geological agents were previously ruled out as accumulator agents of the SH hominin sample (Aranburu et al., 2017; Arsuaga et al., 1990; Arsuaga, Martínez, Gracia, Carretero, et al., 1997b; Sala et al., 2014; Sala, Arsuaga, Martínez, & Gracia-Téllez, 2015a; Sala, Martínez, et al., 2023b). All of this, on top of the fact that more foot phalanges have been recovered from this one site than from burial contexts and large accumulations of Neandertals and Upper Paleolithic *H. sapiens* throughout the entire worldwide *Homo* fossil record, is compatible with an act of intentional funerary behavior in this Middle Pleistocene site as previously suggested (Arsuaga et al., 1990; Arsuaga, Martínez, Gracia, Carretero, et al., 1997b; Sala et al., 2016; Sala, Arsuaga, Pantoja-Pérez, et al., 2015b; Sala, Pantoja-Pérez, et al., 2023a).

7 | CONCLUSIONS

The study of the metatarsals and foot phalanges (forefoot) from the Sima de los Huesos Middle Pleistocene site has allowed us to establish some likely primitive traits in this population, probably related to general robusticity of the body. Furthermore, there are some traits that associate the SH hominins with Neandertals. Some of them could be considered derived in relation to the scarce early record of genus *Homo* prior to the Middle Pleistocene, and others might represent shared derived traits by both SH and Neandertals. This confirms that SH and Neandertals represent sister evolutionary groups (Arsuaga et al., 2014; Arsuaga, Martínez, Gracia, & Lorenzo, 1997a). Additionally, we observed some autoapomorphic traits exclusive to the SH paleodeme that differentiate Neandertals from modern humans, both recent and fossil. Among the characters differentiating SH and Neandertals feet, some from the first toe have been established as robust in Neandertals and more robust in SH. This cautiously suggests to the

possibility of a slight gracilization process at least in the hallux of Neandertals compared to their ancestors: the hominins from Sima de los Huesos. However, we are well aware that more Early and Middle Pleistocene foot fossils, along with further studies, are necessary in order to definitively confirm or refute this hypothesis.

The abundant metatarsal and phalanx record from SH has allowed us to complete a detailed characterization of the foot skeleton for this paleodeme and makes it possible to compare this sample with other *Homo* populations (Table 17). The metatarsals and foot phalanges from the Sima de los Huesos site are generally more robust than the recent and fossil *Homo sapiens* comparative samples (Table 17). For some elements, this robusticity in SH is similar to Neandertals, as is the case with the third, fourth, and fifth metatarsals, the proximal and distal hallucal phalanges, and the proximal and intermediate lateral foot phalanges. Some other postcranial traits shared by SH and Neandertals have been established for other anatomical parts of the skeleton (Arsuaga et al., 2015; Bonmatí et al., 2010; Carretero et al., 1997; Gómez-Olivencia & Arsuaga, 2023; Pablos et al., 2017; Pablos, Martínez, et al., 2013b), thereby confirming the evolutionary relationship between these Pleistocene populations. For other bones, such as the first metatarsal, the proximal hallucal phalanx, and the lateral distal phalanges, the SH fossils are even more robust and broader than Neandertals (Table 17). In this regard, it is worth mentioning the first toe with the hallucal metatarsals from SH, which are broader than the already broad Neandertal hallucal metatarsals compared to recent modern humans. This is probably an autoapomorphic trait in the SH population and suggests a likely slight gracilization process at least in the width of the first toe from SH compared to Neandertals. The proximal hallucal phalanges from SH are longer than those of Neandertals, whose large breadth make them more robust. These robusticity traits in the SH first toe are suggested here as autoapomorphic traits to this Middle Pleistocene population with respect to Neandertals and the entire currently known genus *Homo*. The distal non-hallucal pedal phalanges from SH are broader than those of Neandertals. Nonetheless, in this case, the small sample size of well-identified phalanges prevents us from establishing any firm evolutionary polarity.

Without a doubt, the SH population exhibits high robusticity in the postcranial skeleton in general (Arsuaga et al., 1999, 2015; Gómez-Olivencia et al., 2007; Bonmatí et al., 2010; Pablos et al., 2017; Carretero et al., 2011, 2023a; García-González et al., 2023; Rodríguez et al., 2023a), and in the metatarsal and pedal phalanges in particular. This concurs with the previously proposed large corporal size for the SH population and its primitive biotype (Arsuaga, 2010; Carretero et al., 2004).

Finally, the large representation of tiny distal pedal phalanges in the SH hominin collection, even more than in the entire worldwide fossil record for Neandertals and fossil *Homo sapiens*, supports the previously established proposal of an accumulation of complete skeletons in this chamber (Arsuaga et al., 1990; Arsuaga, Martínez, Gracia, Carretero, et al., 1997b; Sala, Martínez, et al., 2023b). This fact is in line with the previous proposal that the hominin sample from SH represents a deliberate accumulation by other humans as an act of intentional funerary behavior.

AUTHOR CONTRIBUTIONS

Adrián Pablos: Conceptualization; formal analysis; funding acquisition; methodology; writing – original draft; supervision; writing – review and editing; investigation. **Juan Luis Arsuaga:** Funding acquisition; writing – review and editing; supervision; project administration; conceptualization.

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