

## The Foot in the *Homo* Fossil Record

Adrián Pablos

Centro Mixto UCM-ISCIH de Investigación  
sobre Evolución y Comportamiento Humanos  
c/Monforte de Lemos, 5  
28029 Madrid, Spain

Área de Antropología Física  
Departamento de Ciencias de la Vida  
Universidad de Alcalá  
28871 Alcalá de Henares, Madrid, Spain

Senckenberg Center for Human Evolution and Paleoenvironment  
Paleoanthropology  
Eberhard Karls Universität Tübingen  
Rümelinstrasse 23  
D-72070 Tübingen, Germany  
adrizaino@yahoo.es

**Abstract:** *In this article, the foot in the Homo fossil record throughout the world is reviewed. The main problem with the study of foot remains is the paucity of fossils from this anatomical area, in particular from the earlier members of the genus Homo. In spite of this, a comprehensive review of the morphology of the entire fossil record for the foot has been achieved. All the fossils belonging to the genus Homo are proposed to be biped due to the presence of longitudinal and transversal arches, the robusticity pattern of the metatarsals and an adducted hallux. Even in the early members of the genus Homo, the morphology of the foot is modern-like, with size being practically the only variation observed. Of the foot remains attributed to the genus Homo, two morphotypes become apparent: small-sized and large-sized individuals. It is important though to take into account that the earliest Homo feet belonging to smaller individuals could not belong to the genus Homo. Later, a new robust bauplan appears in the Homo fossil record for the foot represented by Homo erectus/ergaster, Homo antecessor, the hominins from Sima de los Huesos and Neandertals. Finally, modern humans display long feet that are gracile compared with their ancestors. An examination of the morphology of the Neandertal foot and of the foot from Sima de los Huesos confirms the evolutionary relationship between these two populations. However, enough differences exist between the two samples to indicate that they are in fact morphologically distinct. A parallel gracilization process is proposed in both modern humans and Neandertals.*

**Keywords:** *Atapuerca, Pleistocene, feet, tarsal, metatarsal, genus Homo*

### Der Fuß in der Fossilüberlieferung der Gattung *Homo*

**Zusammenfassung:** Im vorliegenden Beitrag werden sämtliche archäologisch nachgewiesenen fossilen Fußknochen von Vertretern der Gattung *Homo*, ausgenommen der anatomisch moderne Mensch, betrachtet. Das Hauptproblem, das beim Studium der Fußknochen besteht, ist deren Seltenheit im archäologischen Befund. Dies gilt umso mehr dann, wenn es um ältere Vertreter der Gattung *Homo* geht. Dennoch ist es gelungen, einen umfassenden Überblick über die Morphologie des Fußes für das gesamte fossil überlieferte Material zu gewinnen. Für alle fossil nachgewiesenen Vertreter der Gattung *Homo* wird angenommen, dass sie aufrecht gingen. Diese Annahme beruht vor allem auf dem Vorhandensein von Längsbögen und Querbögen bei den Füßen, auf dem Robustizitätsmuster der Mittelfußknochen (Metatarsien) und schließlich auf der abgespreizten Großzehe. Selbst bei den frühen Vertretern der Gattung *Homo* ähnelt die Morphologie des Fußes derjenigen moderner Menschen, und praktisch die einzigen Unterschiede bestehen in der Größe. Von daher scheinen bei den Fußüberresten zwei Morphotypen

mit der Gattung *Homo* verbunden zu sein: es gibt kleine und große Individuen. Darüber hinaus muss jedoch berücksichtigt werden, dass die ältesten der Gattung *Homo* zugewiesenen kleineren Individuen vielleicht doch nicht zu *Homo* gehören. Später erscheint dann ein neuer robuster Bauplan für den Fuß, wie er durch die Fossilien von *Homo erectus/ergaster*, *Homo antecessor*, die Menschen aus der Sima de los Huesos in Atapuerca bei Burgos (Spanien) und die Neandertaler repräsentiert wird. Moderne Menschen schließlich zeigen lange Füße, die im Vergleich mit denjenigen ihrer Vorfahren grazil sind. Die Fußmorphologie der Neandertaler und der Menschen aus der Sima de los Huesos ermöglicht es, den entwicklungsgeschichtlichen Zusammenhang zwischen beiden Populationen zu bestätigen. Andererseits unterscheiden sie sich aber in ausreichendem Maße voneinander, um sie als morphologisch unterschiedlich zu klassifizieren. Ein parallel verlaufender Prozess der Grazilisierung des Fußes wird sowohl für die Neandertaler als auch für die modernen Menschen angenommen.

**Schlagwörter:** Atapuerca, Pleistozän, Füße, Tarsus, Metatarsus, Gattung *Homo*

## Introduction

There are complications involved in trying to establish who were the first representatives of the genus *Homo*. Most of the Early *Homo* record is composed of cranio-dental remains (Leakey et al. 1964; Walter et al. 1991). A recently discovered mandible from Ledi-Geraru (Ethiopia) places the oldest evidence in the time frame of 2.75-2.8 myr (Villmoare et al. 2015). Together with other anatomical areas of the postcranial skeleton, foot remains represent important evidence in understanding human evolution. This is due to the foot's role in locomotion and weight transmission, and because feet act as a proxy for body size (Harcourt-Smith and Aiello 2004).

A few foot remains have been recovered prior to Neandertals (Day and Napier 1964; Trinkaus 1975; Lorenzo et al. 1999; Lordkipanidze et al. 2007; Lu et al. 2011; Pablos et al. 2012; Boyle and DeSilva 2015). It is also debatable whether most of the feet in the Early Pleistocene African record do in fact belong to the genus *Homo* or to *Paranthropus* (Day and Napier 1964; DeSilva 2009). The fact that foot bones are tiny, can easily roll and are easily lost could explain the scarcity of these elements in the *Homo* fossil record. Studies of this anatomical area in the genus *Homo* previous to Neandertals are limited due to the scarcity of foot bones found in the *Homo* fossil record. There is a bias in Eurasia as hardly any foot fossils have been recovered from a time period extending one million years, from the Early Pleistocene site of Dmanisi dated to c. 1.8 myr (Lordkipanidze et al. 2007) to the TD6 level of Atapuerca dated to c. 900 kyr (Table 1) (Lorenzo et al. 1999; Pablos et al. 2012). In the European Middle Pleistocene some foot bones have been recovered and studied, mainly from the Sima de los Huesos site in Atapuerca, Spain (Pablos et al. 2013b, 2014, in press; Arsuaga et al. 2015), and some fossils from Arago in Tautavel, France (Lamy 1982; Lumley 2015). During the Late Pleistocene more foot bones have been found and studied, which belong mainly to Neandertals, *Homo sapiens* and *Homo floresiensis* (Trinkaus 1975, 1983a; Vandermeersch 1981; Jungers et al. 2009a; Lu et al. 2011; Harvati et al. 2013).

The reconstruction of body size and stature is usually estimated using the long bones (McHenry 1992; Carretero et al. 2012; Elliott et al. 2015). However, the dearth of complete long bones does not always allow us to make such estimations. Thus, when there are no complete long bones at a site, the preferred method is to use the foot bones in order to estimate corporal size and stature (McHenry 1992; Pablos et al. 2013a; Boyle and DeSilva 2015).

Site/group	Chronology	Species/population	Geography	Foot remains	Main references
Shungura Formation	2.2-2.36 myr	Early <i>Homo</i> (#)	Ethiopia	Unassociated talus, calcaneus, phalanx and metatarsals	1, 2, 3 among others
Olduvai	1.8-1.9 myr	<i>Homo habilis</i> (#)	Tanzania	Nearly complete feet, phalanx and metatarsals	2, 4 among others
Koobi Fora	1.5-2 myr	Early <i>Homo</i> (#)/ <i>Homo ergaster</i>	Kenya	Several isolated elements	5, 6, 7, 8 among others
Swartkrans	1-1.8 myr	Early <i>Homo</i> (#)/ <i>Homo ergaster</i>	South Africa	Several isolated elements	2, 9, 10 among others
Dmanisi	c. 1.8 myr	<i>Homo erectus/georgicus</i>	Georgia	11 elements from several individuals	11, 12
TD6 level - Gran Dolina (Atapuerca)	900-950 kyr	<i>Homo antecessor</i>	Spain	14 foot remains from several adult and immature individuals	13, 14, 15
Arago	400-600 kyr	<i>Homo erectus taulevensis</i>	France	One fragmentary metatarsal	16, 17, 18
Sima de los Huesos (Atapuerca)	c. 430 kyr	*	Spain	More than 500 foot remains (tarsals, metatarsals and phalanges)	19, 20, 21, 22
Jinniushan	c. 200 kyr	Archaic <i>Homo sapiens</i> / <i>Homo erectus</i>	China	Two feet from a female individual	23, 24, 25
Omo-Kibish	c. 195 kyr	Early <i>Homo sapiens</i> (§)	Ethiopia	11 elements from a female individual	26, 27, 28
Neandertals	Late Pleistocene	<i>Homo neanderthalensis</i>	Eurasia	Multiple foot bones from different individuals (isolated and associated)	29, 30, 31, 32 among others
Late Pleistocene <i>Homo sapiens</i>	Late Pleistocene	<i>Homo sapiens</i>	Africa and Eurasia	Multiple foot bones from different individuals (isolated and associated)	29, 31 among others
Liang Bua cave	17-95 kyr	<i>Homo floresiensis</i>	Indonesia	more than 30 foot bones from LB1 individual, and several unassociated elements	33, 34, 35, 36

**Table 1:** Main sites with foot remains attributed to the genus *Homo*.

\*The hominins from Sima de los Huesos usually have been classified as *Homo heidelbergensis* (Arsuaga et al. 1997b). However, recent morphological (Arsuaga et al. 2014) and genetic (Meyer et al. 2014) studies consider these hominins as ancestors of Neandertals. # The taxonomic assignment of these fossils is not clear. They could belong to *Homo*, *Australopithecus* or *Paranthropus*. § This specimen has been assigned to Early *Homo sapiens* (Day 1969), but several studies question the taxonomic affinity of these remains, and they are considered a morphological gap between archaic and modern humans (Arsuaga et al. 1997b; Pearson et al. 2008; Pablos et al. 2012).

Recent publications have appeared on the large collection (NR = 107) of foot fossils belonging to different individuals of the species *Homo naledi* (Berger et al. 2015) from the Dinaledi Chamber in South Africa (Harcourt-Smith et al. 2015). This site does not currently provide a precise chronology (Dirk et al. 2015) and is therefore not included in Table 1.

Key to references: 1 = Deloison(1986). 2 = McHenry (1994). 3 = Gebo and Schwartz (2006). 4 = Day and Napier (1964). 5 = Day (1976). 6 = Lamy(1983). 7 = Wood (1976). 8 = Boyle and DeSilva(2015). 9 = Susman and de Ruiter(2004). 10 = Balter et al. (2008). 11 = Gabounia et al. (2002). 12 = Lordkipanidze et al. (2007). 13 = Lorenzo et al. (1999). 14 = Berger et al. (2008). 15 = Pablos et al. (2012). 16 = Lamy (1982). 17 = Falguères et al. (2004). 18 = Lumley (2015). 19 = Arsuaga et al. (2014). 20 = Pablos et al. (2013b). 21 = Pablos et al. (2014). 22 = Pablos et al. (in press). 23 = Chen et al. (1994). 24 = Rosenberg et al. (2006). 25 = Lu et al. (2011). 26 = Day (1969). 27 = Pearson et al. (2008). 28 = McDougall et al. (2008). 29 = Trinkaus (1975). 30 = Trinkaus (1983b). 31 = Vandermeersch (1981). 32 = Harvati et al. (2013). 33 = Brown et al. (2004). 34 = Roberts et al. (2009). 35 = Jungers et al. (2009b). 36 = Jungers et al. (2009a).

It is also possible to obtain certain taxonomic information from foot remains (Day and Napier 1964; Zipfel et al. 2011; Pablos et al. in press). Generally, however, taxonomic assignment is proposed only when the foot remains are associated with cranio-mandibular remains (Pearson et al. 2008; Zipfel et al. 2011; Pablos et al. in press), and this usually only occurs in Neandertals, Late Pleistocene *Homo sapiens* and at sites that are specially well preserved, such as at Dmanisi and Sima de los Huesos (Lordkipanidze et al. 2007; Arsuaga et al. 2014).

A complete review is provided below of the foot remains of the *Homo* fossil record throughout the world. The most important anatomical and metrical features describing each species or taxonomic group are discussed. Furthermore, a review of the estimations of body size and stature calculated with the foot remains is presented. Finally, the possible phylogenetic relationships within the genus *Homo* regarding the foot remains are discussed. This last point refers mainly to the last members of human evolution and the more abundant fossil record for this anatomical area.

In the *Homo* fossil record, more than two thousand foot fossils have been recovered prior to modern humans (Fig. 1 and Table 1). However, most of them belong to Neandertals and Late Pleistocene *Homo sapiens*. Here it is important to emphasize that more than 500 foot fossils have been recovered in a single site, the Middle Pleistocene site of Sima de los Huesos (SH) in Atapuerca (Spain). All the skeletal elements are represented at this site, including both cranial and postcranial bones, and even the ribs and tiny distal pedal phalanges, indicating that entire corpses were accumulated here (Arsuaga et al. 2014, 2015). Thus, the SH hominin sample has been proposed as an intentional accumulation of cadavers by other hominins (Sala et al. 2015).

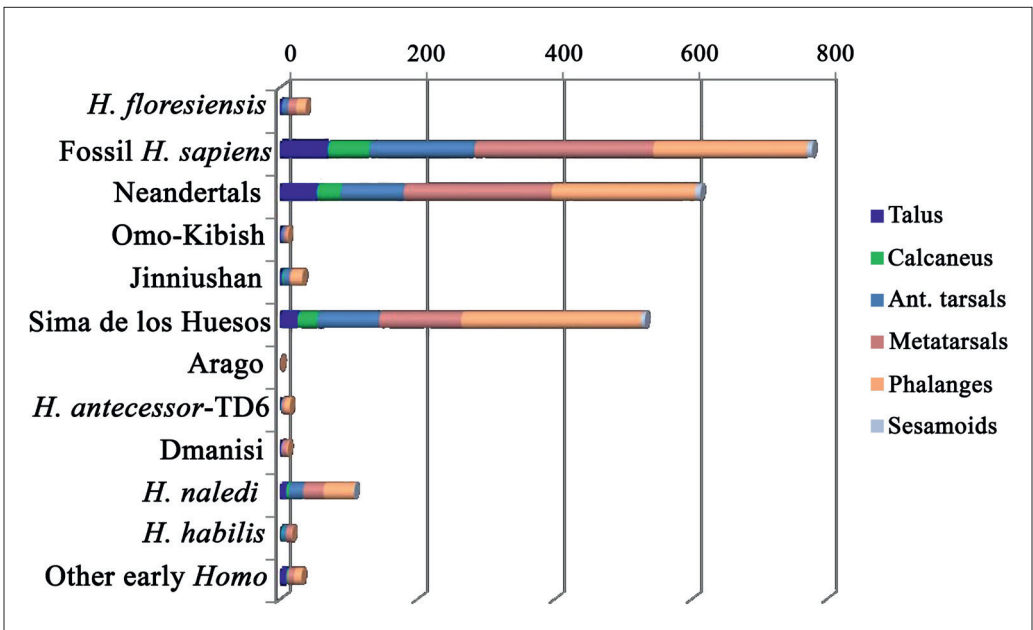


Fig. 1: Foot bones of the genus *Homo* excluding modern humans.

## Early Pleistocene African record

The earliest evidence of the genus *Homo* is represented by the mandible Ledi-Geraru LD 350-1 from Ethiopia, with a chronology of 2.75-2.8 myr (Villmoare et al. 2015). However, the oldest foot bones that could be assigned to Early *Homo* have a chronology of 2.2-2.36 myr (Deloison 1986, 1997; Gebo and Schwartz 2006). They include a talus (Omo 323-76-989) and a calcaneus (Omo 33-74-896) from the Early Pleistocene site of the Shungura formation from Omo (Ethiopia). The talus is similar to modern humans and KNM-ER 813 in total length, with a narrow trochlea, a short neck and a head absolutely and relatively narrow (Gebo and Schwartz 2006). A narrow head relative to talar length is also observed in this fossil, which could represent the primitive morphology in the genus *Homo* (Pablos et al. in press).

The calcaneus Omo 33-74-896 possesses a large and robust peroneal tubercle (Gebo and Schwartz 2006). It is slightly shorter than that in modern humans, and narrow with a narrow *sustentaculum tali* compared with Sima de los Huesos hominins and Neanderthals (Pablos et al. 2014). In both cases (the talus and the calcaneus from the Shungura Formation), we must keep in mind that they could belong to the genus *Paranthropus* (McHenry 1992, 1994).

Another important fossil in the *Homo* record of foot remains is the nearly complete foot OH 8 from bed 1 of Olduvai in Tanzania (Day and Napier 1964), with a chronology of around 1.8-1.9 myr (Walter et al. 1991). It consists of all the tarsals and metatarsals of the left foot from the same individual. The calcaneus and the metatarsals are eroded and lack some important parts. These fossils were originally described as paratypes of *Homo habilis* (Leakey et al. 1964), but currently several authors consider the taxonomic attribution of these fossils to *Homo* as unclear (Moyà-Solà et al. 2008; DeSilva 2009). This fossil belonged to a small-sized individual, which is reflected in the small size of all the bones of this foot.

A distal hallucal phalanx (OH 10) (Day and Napier 1966) and a couple of metatarsals (OH 43) from the third and fourth toes (Day 1973) were also discovered in the bed 1 at Olduvai. The phalanx OH 10 is shorter than the later taxonomic groups and slightly narrower than Neanderthals and the hominins from Sima de los Huesos (Pablos et al. in press).

If we assume that these fossils from Olduvai belonged to *Homo habilis*, it would confirm the small size of this species. These supposed *Homo habilis* foot fossils display some derived human-like characteristics, consistent with a bipedal biomechanical pattern and an adducted hallux (Day and Napier 1964; Berillon 2000; Harcourt-Smith and Aiello 2004).

There are some foot bones from Koobi Fora (Kenya), with chronologies between 2-1.5 myr (Day 1976; Lamy 1983). In this formation, it is not easy to associate cranial and postcranial elements. Moreover, they represent fossils from the genus *Homo*, *Paranthropus* and *Australopithecus*, with it not always being possible to assign the postcranial elements to a specific genus (Lamy 1983; Berillo, 2000; DeSilva 2009). Usually these foot bones reflect adaptations to habitual bipedalism, with a morphology similar to modern humans though smaller in size (Day and Leakey 1974; Wood 1976). This occurs especially with the talus KNM-ER 1476a, which is quite small. However, there is a talus

(KNM-ER 5428) of 1.5-1.6 myr that displays a similar morphology to that of modern humans, representing as well one of the biggest tali in the *Homo* fossil record (Boyle and DeSilva 2015). These size differences in the sample from Koobi Fora could be due to intraspecific variation (i.e., sexual dimorphism), or they could have belonged to a different species or probably even different genus (Lamy 1983, 1986; Gebo and Schwartz 2006; DeSilva 2009; Boyle and DeSilva 2015).

In South Africa, in the site of Swartkrans, a few foot remains belonging to genus *Homo* have been recovered with a chronology of 1-1.8 myr (McHenry 1994; Susman and de Ruiter 2004; Balter et al. 2008). As is the case with fossils from Koobi Fora, in this Early Pleistocene site it is not always clear if the hominins belong to *Homo* or *Paranthropus*. The foot bones from the early Pleistocene of South Africa display the same pattern observed in the fossils from Koobi Fora. They belonged to bipedal individuals and show a mosaic of derived human-like features and primitive ape-like features (Susman 1989; McHenry 1994; Susman and de Ruiter 2004).

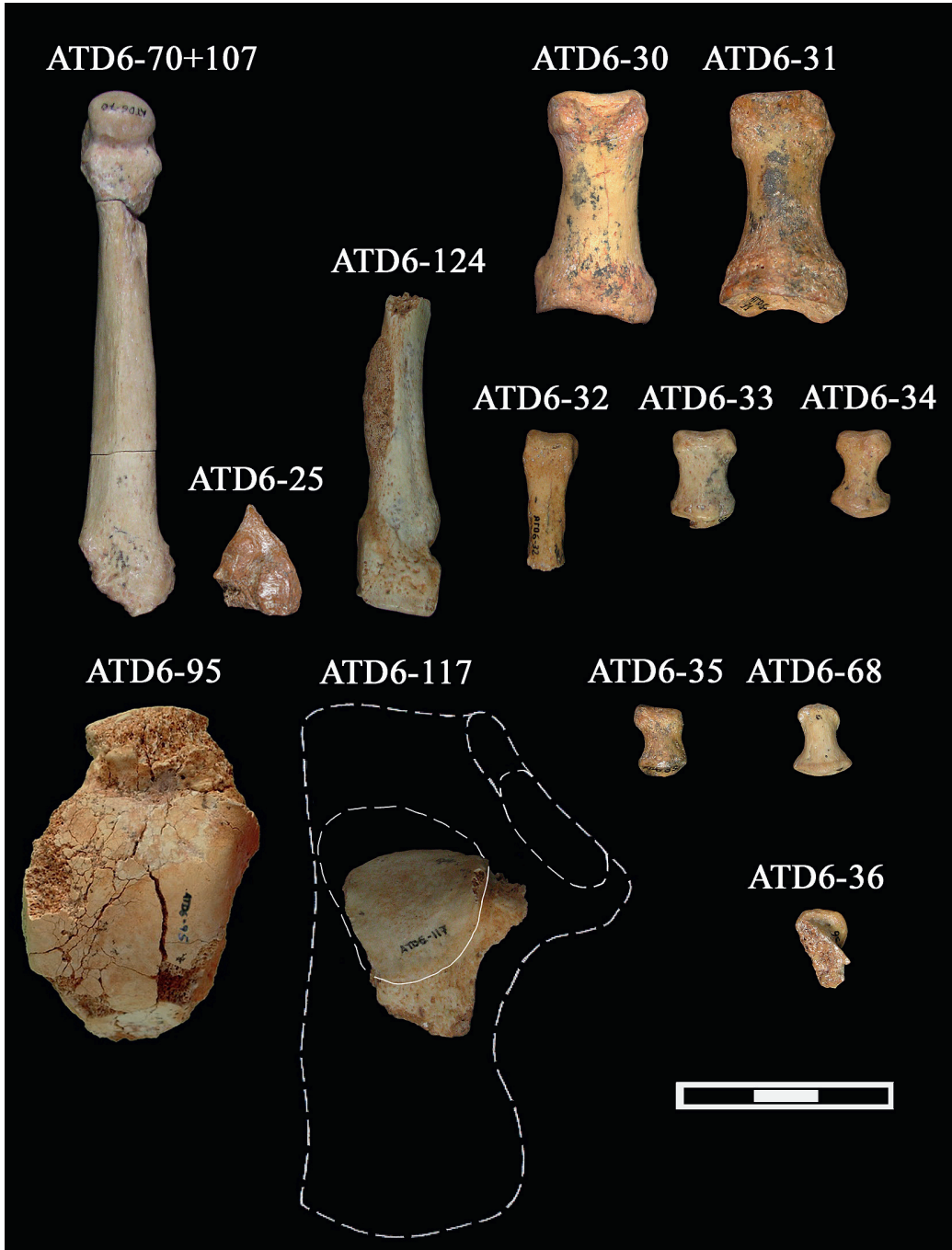
A new species from the genus *Homo* has recently been reported from the Dinaledi Chamber in South Africa (Berger et al. 2015). More than 100 foot fossils have been recovered from the species, which has been named *Homo naledi* (Harcourt-Smith et al. 2015). The *Homo naledi* foot is predominantly modern-like in morphology and inferred function, with an adducted hallux, elongated tarsus, derived ankle and calcaneocuboid joints. However, the *H. naledi* foot differs from modern humans with its reduced medial longitudinal arch (Harcourt-Smith et al. 2015). The feet of this species correspond to small-sized individuals similar to the supposed *Homo habilis* foot bones previously known. Unfortunately, a precise chronology for the new fossils has yet to be determined (Dirks et al. 2015). A reliable date is needed in order to make correct comparisons, mainly due to the fact that, with *Homo floresiensis*, another small-sized species exists in the *Homo* fossil record from the Late Pleistocene (Brown et al. 2004).

## Early Pleistocene Eurasian record

The oldest site with foot remains found outside of Africa is Dmanisi (Georgia), with a chronology of c. 1.8 myr (Gabounia and Vekua 1995). In this site, both cranial and postcranial hominin remains from different individuals assigned to *Homo georgicus* or *Homo erectus* have been recovered (Gabounia et al. 2002; Lordkipanidze et al. 2013). This site has yielded 11 hominin foot remains, including two tarsals, seven metatarsals and two foot phalanges (Lordkipanidze et al. 2007; Jashashvili et al. 2010; Pontzer et al. 2010). This sample represents an early presence of the genus *Homo* outside of Africa.

The morphology of the foot remains found in Dmanisi is human-like, but they belong to small-sized individuals. They show a longitudinal and transverse arch, an adducted hallux and a morphology of the ankle functionally similar to modern humans. However, the metatarsals display a configuration similar to early hominins, including OH 8 and *Australopithecus*. In general, the foot bones from Dmanisi are smaller than current populations, a point reflecting the small body size and stature of these individuals (Lordkipanidze et al. 2007; Pontzer et al. 2010).





**Fig. 2:** Foot remains from the Early Pleistocene TD6 level of Gran Dolina, Atapuerca (Spain).

The human fossils found in the Early Pleistocene TD6 level of Gran Dolina in Atapuerca (Spain) were described as a new species, *Homo antecessor* (Bermúdez de Castro et al. 1997). In this level, with a chronology of around 900-950 kyr (Berger et al. 2008; Cuenca-Bescós et al. 2015), cranial, dental and postcranial remains from at least 11 individuals have been recovered (Carbonell et al. 2005; Martínón-Torres et al. 2007; Bermúdez de Castro et al. 2010). In the TD6 sample, 14 foot remains have been identified (Fig. 2), which include a talus, a fragment of a calcaneus, four fragments of metatarsals and eight phalanges (Lorenzo et al. 1999; Pablos et al. 2012). The study of this material established that the morphology of the metatarsals and phalanges of *Homo antecessor* does not differ significantly from that of modern humans and the robust Neandertals (Lorenzo et al. 1999). The recent discovery of more foot bones promoted the detailed study of a talus and a fourth metatarsal, and the reconsideration of the second metatarsals that were previously published (Pablos et al. 2012).

The foot remains from TD6 belong to bipedal individuals, with transverse and longitudinal arches, and human-like in morphology. Moreover, the talus ATD6-95 belonged to a large-sized individual with large articular surfaces (Pablos et al. 2012), likely similar in size to the Early Pleistocene talus KNM-ER 5428 from Koobi Fora (Boyle and DeSilva 2015). The association between the talus ATD6-95 and the second metatarsal ATD6-70+107 has allowed us to estimate a body mass of 76 kg and a stature of around 173 cm for the supposed male individual to whom these foot fossils belonged (Pablos et al. 2012, in press). Finally, the study of the fourth metatarsal ATD6-124 has established a broad base in the fourth metatarsal as a likely shared derived trait in the evolutionary line of Sima de los Huesos and Neandertals (Pablos et al. 2012, in press; Arsuaga et al. 2015).

## The Middle Pleistocene African record

The main site containing a Middle Pleistocene foot record in Africa is the Kamoya's Hominid site, in the Omo River Valley (Ethiopia) (Day 1969). In this site, three partial skeletons have been recovered (Omo-Kibish 1, 2 and 3), and their chronology is around 195 kyr (McDougall et al. 2008). Omo-Kibish 1 corresponds to an individual that is most likely female with preserved cranial and postcranial elements (Day 1969; Pearson et al. 2008). These fossils were assigned to Early *Homo sapiens* (Day 1969). However, some primitive traits in the cranium and the postcranial skeleton call into question the taxonomic affinity of these individuals, and they are considered as a morphological gap between late archaic and early modern humans (Arsuaga et al. 1997b; Pearson et al. 2008; Pablos et al. 2012).

The studies carried out on the foot remains of Omo-Kibish 1 indicate that it is modern-like biped (Pearson et al. 2008). However, it is morphologically different from Neandertals, modern humans and the Middle Pleistocene population of Sima de los Huesos (Pearson et al. 2008; Pablos et al. 2012, 2013b, in press). In general, the Omo-Kibish 1 foot belonged to a small individual with small articular surfaces and with the anatomical traits required for bipedalism. Nevertheless, certain anatomical features differentiate it from Neandertals and modern humans. The body mass estimate for this individual using the talus is 54.1 Kg (Pablos et al. in press).



## The Middle Pleistocene Eurasian record

Unlike in Africa, there are several Middle Pleistocene sites in Europe and Asia that have yielded hominin foot remains. The oldest one is located close to the village of Tautavel (France). In the cave of Arago, situated in the French Pyrenees, abundant human fossils belonging to several individuals have been recovered (Lumley and Lumley 1971), with a chronology of 400-600 kyr (Falguères et al. 2004). These fossils were considered to be of the species *Homo heidelbergensis* (Lumley 2010), but a recent study has classified them as *Homo erectus tautavelensis* (Lumley 2015). Among the human fossils discovered in Arago, just one foot bone, Arago 43, which is a fragmentary left second metatarsal, has been recovered. It is human-like in morphology, but it is not very robust (Lamy 1982).

The Sima de los Huesos (SH) site in Atapuerca, Burgos (Spain), has yielded the largest collection of human bones in a single site. The SH site is located deep inside the Cueva Mayor-Cueva del Silo karstic system (Arsuaga et al. 1997a). To date, more than 6800 human fossils have been recovered in this site (Sala et al. 2015), belonging to a minimum of 28 individuals (Bermúdez de Castro et al. 2004). All of the human bones in SH come from the Lithostratigraphic Unit 6-LU6, and are dated to c. 430 kyr (Arsuaga et al. 2014; Aranburu et al. in press). In SH, both cranial (Arsuaga et al. 2014) and post-cranial remains (Arsuaga et al. 2015) have been identified, belonging to the Neandertal clade (Arsuaga et al. 2014).

More than 500 foot remains have been collected from SH (Pablos et al. in press). They represent nearly the same specimens comprising the entire Neandertal record in the world, and there are many more than what are found in the entire record of *Homo* fossils previous to those of *Homo sapiens* and Neandertals (Fig. 1). In the SH sample, all skeletal parts of the foot are represented (tarsals, metatarsals and phalanges).

All the *Homo* fossil tali, including those from SH, display short necks compared to modern humans. It was argued that a short neck is the product of an inverse relationship between the length of the neck and the trochlea (Rhoads and Trinkaus 1977), which indicates an increase in the articular surfaces and, hence, an increase in the body mass. The SH tali and calcanei show some variables similar to Neandertals. However, there are a few features that differentiate the foot from SH and Neandertals. SH and Neandertal tali share a broad lateral malleolar facet, which is even broader in SH than in Neandertals (Pablos et al. 2013b). The calcanei from SH are broad and robust as those in Neandertals, but the SH calcanei display a very projected *sustentaculum tali*, even more so than found in Neandertals (Pablos et al. 2014).

One trait clearly allows us to distinguish between the Neandertal and SH foot: the breadth of the head of the talus. The Neandertal tali have broad heads, while the SH tali have narrow heads. If this variable is compared to the talar length, as a proxy of general size, there are significant differences between Neandertals and the SH population (Pablos et al. in press). In SH, the longer the talus is, the narrower the head. However, in Neandertals, the longer the talus is, the broader the head.

Regarding the rest of the foot elements, the naviculars from SH are broader than those of modern humans, and equally as broad as those of Neandertals. The intermediate cuneiforms from SH are shorter than those of Neandertals and modern humans. The first metatarsals from SH are significantly broader than those of Neandertals (Pablos et

al. in press), and the lateral metatarsals (III-V) are broader than those found in modern humans and Late Pleistocene *Homo sapiens* (Arsuaga et al. 2015; Pablos et al. in press). The existence of a narrow fourth metatarsal (ATD6-124) in the Early Pleistocene TD6 level of Gran Dolina, also in Atapuerca, indicates that a broad fourth metatarsal could represent a derived trait in the evolutionary line of Neandertals and SH (Pablos et al. 2012). Finally, the phalanges of the hallux from SH are broad and robust, as in Neandertals (Pablos et al. in press).

In summary, the foot remains from SH are similar to Neandertals in having a broad navicular and broad lateral metatarsals and phalanges. Most of these features are related to the large corporal size of both populations, that of Sima de los Huesos and Neandertals (Arsuaga et al. 1999). This robusticity pattern in SH and Neandertals possibly constitutes the primitive condition, as was previously proposed (Arsuaga et al. 1999; Lorenzo et al. 2015). However, there are a few traits that clearly differentiate SH from Neandertals: the SH foot remains have a very broad lateral malleolar facet and a narrow head in the talus, a very broad *sustentaculum tali* in the calcaneus, a short intermediate cuneiform and a broad first metatarsal.

The foot remains from SH have been used to estimate the body mass and the stature using different modern regression formulae (McHenry 1992; Pablos et al. 2013a). The body mass, based on the medio-lateral breadth of the trochlea in the talus, has provided a mean of  $69.7 \pm 10.0$  kg for the SH hominins. The estimated mean stature, based on the total length of the talus, provided an estimate of  $173.9 \pm 1.4$  cm for males and  $161.9 \pm 2.3$  cm for females (Pablos et al. in press). These estimates are similar to those obtained using other postcranial bones, although the body mass calculated with the bi-iliac breadth is higher (Bonmatí et al. 2010), and the stature estimated with long bones is slightly lower (Carretero et al. 2012).

In the Liaoning Province (China), in level 7 of the Middle Pleistocene site of Jinniushan, a most likely female individual has been recovered that preserves both cranial and postcranial remains (Lu 2003; Rosenberg et al. 2006). The chronology of this site is around 200 kyr or older (Chen et al. 1994), and most of both feet are represented (Lu et al. 2011). The foot of Jinniushan reveals a robusticity pattern that clearly distinguishes it from modern humans, and it is similar to the robust Neandertal foot (Lu et al. 2011). This foot offers evidence of stabilized longitudinal and transversals arches, while at the same time retaining primitive features and characteristics of robust hominins, such as a robust calcaneus, large trochlea of the talus and robust hallucal phalanges (Lu et al. 2011). The estimate of body mass (78.6 kg) with the pelvic remains reveals a broad individual (Rosenberg et al. 2006). Furthermore, the body mass calculated with the talus (74.4 kg) (Pablos et al. in press) is similar to that obtained with the pelvis (Rosenberg et al. 2006).

## Neandertals

Based on the study of the Neandertal foot from more than a century ago, several features have been established as different from that of modern humans. In general, Neandertal tarsals tend to be large, robust and have relatively large articular surfaces (Trinkaus 1975, 1983a; Rhoads and Trinkaus 1977; Harvati et al. 2013). However, the



*Fig. 3: Foot of the La Ferrassie 2 Neandertal (France).*

feet of Neandertals are indistinguishable from modern humans in the implied locomotor capabilities, and similar in general dimensions and proportions (Fig. 3). These traits have usually been associated with a high level of biomechanical stress and a greater robusticity of the postcranial skeleton (Trinkaus 1975, 1983b; Rhoads and Trinkaus 1977; Vandermeersch 1981; Harvati et al. 2013).

There are a few traits that are exclusive to the Neandertal feet, although their ancestors, the hominins from Sima de los Huesos, share some of these traits. The Neandertals present a relatively large trochlea of the talus, especially its lateral malleolar facet, and a broad calcaneus with broad *sustentaculum tali* (Trinkaus 1975; Rhoads and Trinkaus 1977; Vandermeersch 1981). These traits (the lateral malleolar facet of the talus and the *sustentaculum tali* of the calcaneus) are broader in Neandertals than in modern humans, but narrower than those of their ancestors, the hominins from Sima de los Huesos (Pablos et al. 2013b, 2014). The naviculars of Neandertals, like those from Sima de los Huesos, are broad, robust and have a great navicular tuberosity, which could represent a derived trait in this evolutionary line (Trinkaus 1975; Harvati et al. 2013; Pablos et al. in press). The lateral metatarsals and the phalanges of Neandertals are wider than those of modern humans (Trinkaus 1975, 1983a, b; Trinkaus and Hilton 1996; Pablos et al. in press). As was previously noted, in the case of the fourth metatarsals, a broad base probably represents a shared derived trait in the evolutionary line of Sima de los Huesos and Neandertals (Pablos et al. 2012, in press).

Several foot traits associate Neandertals with the Sima de los Huesos population. However, there are some metric and morphological features that differentiate these two samples/populations (Pablos et al. 2013b, 2014, in press). In sum, the Neandertal feet are essentially robust in their articular surfaces when compared to modern humans.

The estimations of body size for Neandertals based on foot remains were calculated with the formulae provided by McHenry (McHenry 1992). Using the talus trochlear breadth, a mean body mass of  $67.4 \pm 8.7$  kg has been calculated for Neandertals (Pablos et al. in press). This value is slightly lower than that obtained using the talus from Sima de los Huesos (Pablos et al. in press), which could indicate a gracilization process in the evolutionary Neandertal line, parallel to what occurs in modern humans (Ryan and Shaw 2015).

## Late Pleistocene *Homo sapiens*

The foot remains of the Late Pleistocene *Homo sapiens* are morphologically and functionally quite similar to, but more robust than, modern humans. However, these specimens display tali with short necks, as is the case for all *Homo* fossils, and probably the result of a long trochlea (Rhoads and Trinkaus 1977; Vandermeersch 1981; Pablos et al. in press). Moreover, tali of the populations from the Late Pleistocene that belong to *Homo sapiens* display a trochlea of the talus with wedged sides (Pablos et al. in press).

## *Homo floresiensis*

To the South of the Wallace line, no other hominin other than *Homo sapiens* was known until 2004. In this year, a new species was discovered in the cave of Liang Bua (Flores Island, Indonesia): *Homo floresiensis* (Brown et al. 2004). These findings include several cranial and postcranial human bones belonging to a small-bodied species. The chronology of the site is between 17 kyr and 95 kyr (Roberts et al. 2009). Among the enormous quantity of human fossils, a partial skeleton from a female adult individual (LB1) with more than 30 foot bones and several unassociated foot remains stands out (Jungers et al. 2009a, b). The foot of *Homo floresiensis* is long in relation to the femur and the tibia when compared with modern humans. However, the human-like robusticity pattern of

the metatarsals and a short and adducted hallux indicate a bipedal pattern for this hominin (Jungers et al. 2009a). The size of the talus and the foot of LB1 are comparable to the *Australopithecus afarensis* specimen AL 288-1. The feet from Flores are similar to modern humans with regard to some features. But they are considered intermediate between humans and African apes in other respects, such as, for example, the primitive navicular or the poorly developed longitudinal arch (Jungers et al. 2009a, b).

## Discussion and conclusions

Despite the paucity of human foot remains from the genus *Homo*, even if the fossils with uncertain taxonomic affinity are included, it is possible to establish that most of them display some characteristics related to bipedalism, i.e., the presence of both longitudinal and transverse arches, an adducted hallux and a robusticity pattern of metatarsals similar to modern humans (Day and Napier 1964; Trinkaus 1983a; Deloison 1997; Berillon 2000; Lordkipanidze et al. 2007; Boyle and DeSilva 2015; Pablos et al. in press).

From the first representatives of the genus *Homo*, it can be said that there are two morphotypes or bauplans. There are a few Early *Homo* remains that belonged to small-sized individuals (Day and Napier 1964; Day and Leakey 1974; Day 1976; Lordkipanidze et al. 2007), with other foot bones belonging to modern-like individuals in terms of size having been identified (Deloison 1986, 1997; Gebo and Schwartz 2006; DeSilva 2009; Boyle and DeSilva 2015; Arsuaga et al. 2015). This could be explained by intraspecific variation in Early *Homo* (e.g., sexual dimorphism) or the fact that they belonged to different species, or even different genus, as was previously proposed (Day 1976; Berillon 2000; Gebo and Schwartz 2006; Moyà-Solà et al. 2008).

Through the evolution of the feet in the genus *Homo*, it can be observed that an increase in body size, robusticity and stature has taken place in the later stages of human evolution, similarly to *Homo ergaster*, *Homo antecessor*, Neandertals and the hominins from Sima de los Huesos (Trinkaus 1983a; Arsuaga et al. 1999, 2015; Gebo and Schwartz 2006; Lu et al. 2011; Pablos et al. 2012, in press; Boyle and DeSilva 2015). However, in the early specimens of the genus *Homo*, there are feet belonging to small-sized individuals (Day and Napier 1964; McHenry 1994; Lordkipanidze et al. 2007) and large-sized individuals (Wood 1976; Gebo and Schwartz 2006; Boyle and DeSilva 2015). In this context, it is important to emphasize the small size of the feet from the Late Pleistocene species *Homo floresiensis* (Jungers et al. 2009a, b), especially because all the other foot bones belonging to the genus *Homo* from the Middle Pleistocene are large-sized individuals. This could be related to an evolutionary relationship between *Homo floresiensis* and earlier hominins such as *Homo habilis*, or even *Australopithecus* (Jungers et al. 2009a).

Although it is difficult to establish phylogenetic relationships based solely on foot remains, it is possible to make an approximation with the current data. This is true especially for the evolutionary line that gave place to Neandertals due to the Atapuerca discoveries. The studies of Neandertal feet have proposed several traits exclusive to this group/population (Rhoads and Trinkaus 1977; Vandermeersch 1981; Trinkaus 1983a; Harvati et al., 2013; Pablos et al. 2013b, in press). Most of these Neandertal features are associated with a large corporal size and increased biomechanical stress (Trinkaus 1975, 1983a; Rhoads and Trinkaus 1977; Vandermeersch 1981; Harvati et al. 2013). Some of



the traits characteristic of Neandertals are similar to those found in the hominins from Sima de los Huesos, such as, for example, the robust naviculars and lateral metatarsals (Pablos et al. 2013b, 2014, in press; Arsuaga et al. 2015). This broad, large and robust morphotype found in Neandertals as compared with their ancestors, the hominins from Sima de los Huesos, could be explained by the phylogenetic relationship between these two populations (Arsuaga et al. 2014, 2015). However, there are a few traits exclusive to Neandertals (e.g., a broad head of the talus), and others exclusive to the hominins from Sima de los Huesos (e.g., a relative and absolutely narrow head of the talus, very broad lateral malleolar facet in the talus and very broad *sustentaculum tali* in the calcaneus) (Pablos et al. 2012, 2013b, 2014, in press; Arsuaga et al. 2015). As mentioned above, Neandertals are, in some of these characteristics, broad, while at the same time narrower than the hominins from Sima de los Huesos (e.g., lateral malleolar facet in the talus and *sustentaculum tali* in the calcaneus). This suggests a gracilization process in Neandertals.

In summary, the morphology of the foot is similar throughout the genus *Homo*, but several bauplans could be proposed. In the first stages of the genus *Homo*, there were biped individuals, with both large- and small-sized individuals. Later, a group of archaic *Homo* existed, which were tall, broad and robust (e.g., *Homo erectus/ergaster*, *Homo antecessor*, the hominins from Sima de los Huesos and Neandertals). And finally, modern humans appeared, who were tall hominins, though narrow and gracile (Trinkaus 1975; McHenry 1994; Lordkipanidze et al. 2007; Boyle and DeSilva 2015; Arsuaga et al. 2015; Pablos et al. in press). Modern humans were more gracile than their ancestors, but Neandertals were also more gracile than their own ancestors, the hominins from Sima de los Huesos. Hence, a parallel gracilization process occurred in both the Neandertal and modern human lineages.

## Acknowledgements

The results and conclusions of this paper derived mainly from the bibliography and the published results of my PhD thesis. For this, I would especially like to acknowledge my advisors, Juan Luis Arsuaga, Ignacio Martínez and Carlos Lorenzo. I am grateful for the many constructive and fruitful discussions I have had with my advisors, my colleagues from the Centro Mixto UCM-ISCIH from Madrid and for the critical comments provided by Asier Gómez-Olivencia. Most of these results would not have been possible without the effort and dedication of the Atapuerca excavation team, especially those from Sima de los Huesos and the TD6 level. Many curators permitted me access to some important skeletal collections and fossil specimens; I extend my most heartfelt gratitude to all of them for their assistance. Part of this investigation was funded through the following: the Spanish Ministry of 'Economía y Competitividad' (Project number CGL2012-38434-C03-01), a postdoctoral fellowship from the "Universidad de Alcalá" (Spain), the SYNTHESYS project (<http://www.Synthesys.info/>), which is financed by the European Community Research Infrastructure Action under the FP7 integrating Activities Programme, and the seventeenth annual research prize for Early Prehistory and Quaternary Ecology of the University of Tübingen (Germany). Special thanks go to Nicholas Conard, Katerina Harvati, Michael Bolus and the BBP and R<sup>3</sup> groups. Lauren Ames kindly reviewed the English of a previous version.



## References

- Aranburu, A., Arsuaga, J. L., Sala, N. in press: The stratigraphy of the Sima de los Huesos (Atapuerca, Spain) and implications for the origin of the fossil hominin accumulation. *Quaternary International*. DOI: 10.1016/j.quaint.2015.02.044.
- Arsuaga, J. L., Martínez, I., Gracia, A., Carretero, J. M., Lorenzo, C., García, N., and Ortega, A. I. 1997a: Sima de los Huesos (Sierra de Atapuerca, Spain). The site. *Journal of Human Evolution* 33, 109–127.
- Arsuaga, J. L., Martínez, I., Gracia, A., and Lorenzo, C. 1997b: The Sima de los Huesos crania (Sierra de Atapuerca, Spain). A comparative study. *Journal of Human Evolution*, 219–281.
- Arsuaga, J. L., Lorenzo, C., Carretero, J.-M., Gracia, A., Martínez, I., García, N., Bermúdez de Castro, J.-M., and Carbonell, E., 1999: A complete human pelvis from the Middle Pleistocene of Spain. *Nature* 399, 255–258.
- Arsuaga, J. L., Martínez, I., Arnold, L. J., Aranburu, A., Gracia-Téllez, A., Sharp, W. D., Quam, R. M., Falguères, C., Pantoja-Pérez, A., Bischoff, J., Poza-Rey, E., Parés, J. M., Carretero, J. M., Demuro, M., Lorenzo, C., Sala, N., Martínón-Torres, M., García, N., Alcázar de Velasco, A., Cuenca-Bescós, G., Gómez-Olivencia, A., Moreno, D., Pablos, A., Shen, C.-C., Rodríguez, L., Ortega, A. I., García, R., Bonmatí, A., Bermúdez de Castro, J. M., and Carbonell, E. 2014: Neandertal roots: Cranial and chronological evidence from Sima de los Huesos. *Science* 344, 1358–1363.
- Arsuaga, J. L., Carretero, J.-M., Lorenzo, C., Gómez-Olivencia, A., Pablos, A., Rodríguez, L., García-González, R., Bonmatí, A., Quam, R. M., Pantoja-Pérez, A., Martínez, I., Aranburu, A., Gracia-Téllez, A., Poza-Rey, E., Sala, N., García, N., Alcázar de Velasco, A., Cuenca-Bescós, G., Bermúdez de Castro, J. M., and Carbonell, E. 2015: Postcranial morphology of the middle Pleistocene humans from Sima de los Huesos, Spain. *Proceedings of the National Academy of Sciences of the U.S.A.* 112, 11524–11529.
- Balter, V., Blichert-Toft, J., Braga, J., Telouk, P., Thackeray, F., and Albarède, F. 2008: U–Pb dating of fossil enamel from the Swartkrans Pleistocene hominid site, South Africa. *Earth and Planetary Science Letters* 267, 236–246.
- Berger, G. W., Pérez-González, A., Carbonell, E., Arsuaga, J. L., Bermúdez de Castro, J.-M., and Ku, T.-L. 2008: Luminescence chronology of cave sediments at the Atapuerca paleoanthropological site, Spain. *Journal of Human Evolution* 55, 300–311.
- Berger, L. R., Hawks, J., de Ruiter, D. J., Churchill, S. E., Schmid, P., Deleuzene, L. K., Kivell, T. L., Garvin, H. M., Williams, S. A., DeSilva, J. M., Skinner, M. M., Musiba, C. M., Cameron, N., Holliday, T. W., Harcourt-Smith, W., Ackermann, R. R., Bastir, M., Bogin, B., Bolter, D., Brophy, J., Cofran, Z. D., Congdon, K. A., Deane, A. S., Dembo, M., Drapeau, M., Elliott, M. C., Feuerriegel, E. M., Garcia-Martinez, D., Green, D. J., Gurtov, A., Irish, J. D., Kruger, A., Laird, M. F., Marchi, D., Meyer, M. R., Nalla, S., Negash, E. W., Orr, C. M., Radovic, D., Schroeder, L., Scott, J. E., Throckmorton, Z., Tocheri, M. W., VanSickle, C., Walker, C. S., Wei, P., and Zipfel, B. 2015: *Homo naledi*, a new species of the genus *Homo* from the Dinaledi Chamber, South Africa. *eLife* 4, e09560.
- Berillon, G. 2000: Le pied des hominoïdes miocènes et des hominidés fossiles. Architecture, locomotion, évolution. *Cahiers de paléanthropologie*. Paris: CNRS Editions.
- Bermúdez de Castro, J. M., Arsuaga, J. L., Carbonell, E., Rosas, A., Martínez, I., and Mosquera, M., 1997. A Hominid from the Lower Pleistocene of Atapuerca, Spain: Possible Ancestor to Neandertals and Modern Humans. *Science* 276, 1392–1395.
- Bermúdez de Castro, J. M., Martínón-Torres, M., Lozano, M., Sarmiento, S., and Muela, A. 2004: Paleodemography of the Atapuerca-Sima de los Huesos hominin sample: a revision and new approaches to the paleodemography of the European Middle Pleistocene population. *Journal of Anthropological Research* 60, 5–26.
- Bermúdez de Castro, J. M., Martínón-Torres, M., Prado, L., Gómez-Robles, A., Rosell, J., López-Polín, L., Arsuaga, J. L., and Carbonell, E. 2010: New immature hominin fossil from European Lower Pleistocene shows the earliest evidence of a modern human dental development pattern. *Proceedings of the National Academy of Sciences of the U.S.A.* 107, 11739–11744.
- Bonmatí, A., Gómez-Olivencia, A., Arsuaga, J.-L., Carretero, J. M., Gracia, A., Martínez, I., Lorenzo, C., Bermúdez de Castro, J. M., and Carbonell, E. 2010: Middle Pleistocene lower back and pelvis from an aged human individual from the Sima de los Huesos site, Spain. *Proceedings of the National Academy of Sciences of the U.S.A.* 107, 18386–18391.
- Boyle, E. K. and DeSilva, J. M. 2015: A Large *Homo erectus* Talus from Koobi Fora, Kenya (KNM-ER 5428), and Pleistocene Hominin Talar Evolution. *PaleoAnthropology* 2015, 1–13.
- Brown, P., Sutikna, T., Morwood, M. J., Soejono, R. P., Jatmiko, Wayhu Saptomo, E., and Awe Due, R. 2004: A new small-bodied hominin from the late Pleistocene of Flores, Indonesia. *Nature* 431, 1055–1061.

- Carbonell, E., Bermúdez de Castro, J. M., Arsuaga, J. L., Allue, E., Bastir, M., Benito, A., Cáceres, I., Canals, A., Díez, J. C., van der Made, J., Mosquera, M., Ollé, A., Pérez-González, A., Rodríguez, J., Rodríguez, X. P., Rosas, A., Rosell, J., Sala, R., Vallverdú, J., and Vergés, J. M. 2005: An Early Pleistocene hominin mandible from Atapuerca-TD6, Spain. *Proceedings of the National Academy of Sciences of the U.S.A.* 102, 5674–5678.
- Carretero, J.-M., Rodríguez, L., García-González, R., Arsuaga, J.-L., Gómez-Olivencia, A., Lorenzo, C., Bonmatí, A., Gracia, A., Martínez, I., and Quam, R. 2012: Stature estimation from complete long bones in the Middle Pleistocene humans from the Sima de los Huesos, Sierra de Atapuerca (Spain). *Journal of Human Evolution* 62, 242–255.
- Chen, T., Yang, Q., and Wu, E. 1994: Antiquity of *Homo sapiens* in China. *Nature* 368, 55–56.
- Cuenca-Bescós, G., Blain, H.-A., Rofes, J., Lozano-Fernández, I., López-García, J. M., Duval, M., Galán, J., Núñez-Lahuerta, C. 2015: Comparing two different Early Pleistocene microfaunal sequences from the caves of Atapuerca, Sima del Elefante and Gran Dolina (Spain): Biochronological implications and significance of the Jaramillo subchron. *Quaternary International* 389, 148–158.
- Day, M. H. 1969: Omo human skeletal remains. *Nature* 222, 1135–1138.
- Day, M. H. 1973: Locomotor features of the lower limb in hominids. *Symposia of the Zoological Society of London* 33, 29–51.
- Day, M. H. 1976: Hominid postcranial remains from the East Rudolf succession. In: Y. Coppens, F. C. Howell, G. L. Isaac, and R. E. F. Leakey (eds.), *Earliest Man and environments in the Lake Rudolf Basin*. Chicago: University of Chicago Press, 507–521.
- Day, M. H. and Leakey, R. E. F. 1974: New evidence of the genus *Homo* from East Rudolf, Kenya (III). *American Journal of Physical Anthropology* 41, 367–380.
- Day, M. H. and Napier, J. R. 1964: Hominid fossils from Bed I, Olduvai Gorge, Tanganyika: Fossil Foot Bones. *Nature* 201, 969–970.
- Day, M. H. and Napier, J. R. 1966: A hominid toe bone from bed I, Olduvai Gorge, Tanzania. *Nature* 211, 929–930.
- Deloison, Y. 1986: Description d'un calcaneum fossile de Primate et sa comparaison avec des calcaneums de Pongidés, d'Australopithèques et d'*Homo*. *Comptes Rendus de l'Académie des Sciences Paris*, s. III, 302, 257–263.
- Deloison, Y. 1997: Description d'un astragale fossile de primate et comparaison avec des astragales de chimpanzées, d'*Homo sapiens* et d'hominidés fossils: Australopithèques et *Homo habilis*. *Comptes Rendus de l'Académie des Sciences Paris*, s. III, 324, 685–692.
- DeSilva, J. M. 2009: Functional morphology of the ankle and the likelihood of climbing in early hominins. *Proceedings of the National Academy of Sciences of the U.S.A.* 106, 6567–6572.
- Dirks, P. H. G. M., Berger, L. R., Roberts, E. M., Kramers, J. D., Hawks, J., Randolph-Quinney, P. S., Elliott, M., Musiba, C. M., Churchill, S. E., de Ruiter, D. J., Schmid, P., Backwell, L. R., Belyanin, G. A., Boshoff, P., Hunter, K. L., Feuerriegel, E. M., Gurtov, A., Harrison, J. d. G., Hunter, R., Kruger, A., Morris, H., Makhubela, T. V., Peixotto, B., and Tucker, S. 2015: Geological and taphonomic context for the new hominin species *Homo naledi* from the Dinaledi Chamber, South Africa. *eLife* 4, e09561.
- Elliott, M., Kurki, H., Weston, D. A., and Collard, M. 2015: Estimating body mass from postcranial variables: an evaluation of current equations using a large known-mass sample of modern humans. *Archaeological and Anthropological Sciences*. DOI: 10.1007/s12520-015-0251-6.
- Falguères, C., Yokoyama, Y., Shen, G., Bischoff, J. L., Ku, T.-L., and Lumley, H. de 2004: New U-series dates at the Caune de l'Arago, France. *Journal of Archaeological Science* 31, 941–952.
- Gabounia, L. and Vekua, A. K. 1995: La mandibule de l'homme fossile du Villafranchien supérieur de Dmanissi (Géorgie orientale). *L'Anthropologie* 99, 29–41.
- Gabounia, L., Lumley, M.-A. de, Vekua, A., Lordkipanidze, D., and Lumley, H. de 2002: Découverte d'un nouvel hominidé à Dmanissi (Transcaucasie, Géorgie). *Comptes Rendus Palevol* 1, 243–253.
- Gebo, D. L. and Schwartz, G. T., 2006. Foot Bones From Omo: Implications for Hominid Evolution. *American Journal of Physical Anthropology* 129, 499–511.
- Harcourt-Smith, W. E. H. and Aiello, L. C. 2004: Fossils, feet and the evolution of human bipedal locomotion. *Journal of Anatomy* 204, 403–416.
- Harcourt-Smith, W. E. H., Throckmorton, Z., Congdon, K. A., Zipfel, B., Deane, A. S., Drapeau, M. S. M., Churchill, S. E., Berger, L. R., and DeSilva, J. M. 2015: The foot of *Homo naledi*. *Nature Communications* 6, 8432.
- Harvati, K., Darlas, A., Bailey, S. E., Rein, T. R., El Zaatari, S., Fiorenza, L., Kullmer, O., and Psathi, E. 2013: New Neanderthal remains from Mani peninsula, Southern Greece: The Kalamakia Middle Paleolithic cave site. *Journal of Human Evolution* 64, 486–499.

- Jashashvili, T., Ponce de León, M. S., Lordkipanidze, D., Zollikofer, C. P. E. 2010: First evidence of a bipartite medial cuneiform in the hominin fossil record: a case report from the Early Pleistocene site of Dmanisi. *Journal of Anatomy* 216, 705–716.
- Jungers, W. L., Harcourt-Smith, W. E. H., Wunderlich, R. E., Tocheri, M. W., Larson, S. G., Sutikna, T., Awe Due, R., and Morwood, M. J. 2009a: The foot of *Homo floresiensis*. *Nature* 459, 81–84.
- Jungers, W. L., Larson, S. G., Harcourt-Smith, W. E. H., Morwood, M. J., Sutikna, T., Awe Due, R., and Djubiantono, T. 2009b: Descriptions of the lower limb skeleton of *Homo floresiensis*. *Journal of Human Evolution* 57, 538–554.
- Lamy, P. 1982: Le métatarsien Arago XLIII. In: H. de Lumley (ed.), *Congrès International de Paléontologie Humaine. L'Homo erectus et la Place de l'Homme de Tautavel parmi les Hominidés Fossiles*. Union Internationale des Sciences Préhistoriques et Protohistoriques, Nice, 319–336.
- Lamy, P. 1983: Le système podal de certains Hominidés fossiles du Plio-Pléistocène d'Afrique de l'Est: Etude morpho-dynamique. *L'Anthropologie* 87, 435–464.
- Lamy, P. 1986: The settlement of the longitudinal plantar arch of some African Plio-Pleistocene hominids: a morphological study. *Journal of Human Evolution* 15, 31–46.
- Leakey, L. S. B., Tobias, P. V., and Napier, J. R. 1964: A new species of the genus *Homo* from Olduvai Gorge. *Nature* 202, 7–9.
- Lordkipanidze, D., Jashashvili, T., Vekua, A., Ponce de León, M. S., Zollikofer, C. P. E., Rightmire, G. P., Pontzer, H., Ferring, R., Oms, O., Tappen, M., Bukhsianidze, M., Agusti, J., Kahlke, R., Kiladze, G., Martínez-Navarro, B., Mouskhelishvili, A., Nioradze, M., and Rook, L. 2007: Postcranial evidence from early *Homo* from Dmanisi, Georgia. *Nature* 449, 305–310.
- Lordkipanidze, D., Ponce de León, M. S., Margvelashvili, A., Rak, Y., Rightmire, G. P., Vekua, A., and Zollikofer, C. P. E. 2013: A Complete Skull from Dmanisi, Georgia, and the Evolutionary Biology of Early *Homo*. *Science* 342, 326–331.
- Lorenzo, C., Arsuaga, J. L., and Carretero, J. M. 1999: Hand and foot remains from the Gran Dolina Early Pleistocene site (Sierra de Atapuerca, Spain). *Journal of Human Evolution* 37, 501–522.
- Lorenzo, C., Pablos, A., Carretero, J. M., Huguet, R., Vallverdú, J., Martín-Torres, M., Arsuaga, J. L., Carbonell, E., and Bermúdez de Castro, J. M. 2015: Early Pleistocene human hand phalanx from the Sima del Elefante (TE) cave site in Sierra de Atapuerca (Spain). *Journal of Human Evolution* 78, 114–121.
- Lu, Z.-E. 2003: The Jinniushan Hominid in anatomical, chronological, and cultural context. In: C. Shen and S. G. Keates (eds.), *Current Research in Chinese Pleistocene Archaeology*. British Archaeological Reports International Series 1179, Oxford, 127–136.
- Lu, Z., Meldrum, D. J., Huang, Y., He, J., and Sarmiento, E. E. 2011: The Jinniushan hominin pedal skeleton from the late Middle Pleistocene of China. *Homo* 62, 389–401.
- Lumley, H. de and Lumley, M.-A. de 1971: Découverte de restes humains anténéandertaliens datés du début de Riss à la Caune de l'Arago (Tautavel, Pyénées-Orientales). *Comptes Rendus de l'Académie des Sciences Paris* 272, 1739–1742.
- Lumley, M.-A. de 2010: Relations between *Homo heidelbergensis* from the Caune de l'Arago at Tautavel and the *Homo erectus* from the Asian continent, India, China, Indonesia. *Communication on Contemporary Anthropology* 4, 195–196.
- Lumley, M.-A. de 2015: L'homme de Tautavel. Un *Homo erectus* européen évolué. *Homo erectus tautavelensis*. *L'Anthropologie* 119, 303–348.
- Martín-Torres, M., Bermúdez de Castro, J. M., Gómez-Robles, A., Bastir, M., Sarmiento, S., Muela, A., and Arsuaga, J. L. 2007: Gran Dolina-TD6 and Sima de los Huesos dental samples: Preliminary approach to some dental characters of interest for phylogenetic studies. In: S. E. Bailey and J.-J. Hublin (eds.), *Dental Perspectives on Human Evolution: State of the Art Research in Dental Paleoanthropology*. Dordrecht: Springer, 65–79.
- McDougall, I., Brown, F. H., and Fleagle, J. G. 2008: Spropels and the age of hominins Omo I and II, Kibish, Ethiopia. *Journal of Human Evolution* 55, 409–420.
- McHenry, H. M. 1992: Body size and proportions in Early Hominids. *American Journal of Physical Anthropology* 87, 407–431.
- McHenry, H. M. 1994: Early hominid postcrania. Phylogeny and function. In: R. S. Corruccini and R. L. Ciochon (eds.), *Integrative Paths to the Past. Paleoanthropological advances in Honor of F. Clark Howell*. New Jersey: Prentice Hall, 251–268.
- Meyer, M., Fu, Q., Aximu-Petri, A., Glocke, I., Nickel, B., Arsuaga, J.-L., Martínez, I., Gracia, A., Bermúdez de Castro, J. M., Carbonell, E., and Pääbo, S. 2014: A mitochondrial genome sequence of a hominin from Sima de los Huesos. *Nature* 505, 403–406.

- Moyà-Solà, S., Köhler, M., Alba, D. M., and Almécija, S. 2008: Taxonomic attribution of the Olduvai hominid 7 manual remains and the functional interpretation of hand morphology in robust australopithecines. *Folia Primatologica* 79, 215–250.
- Pablos, A., Lorenzo, C., Martínez, I., Bermúdez de Castro, J. M., Martínón-Torres, M., Carbonell, E., and Arsuaga, J. L. 2012: New foot remains from the Gran Dolina-TD6 Early Pleistocene site (Sierra de Atapuerca, Burgos, Spain). *Journal of Human Evolution* 63, 610–623.
- Pablos, A., Gómez-Olivencia, A., García-Pérez, A., Martínez, I., Lorenzo, C., and Arsuaga, J. L. 2013a: From toe to head: Use of robust regression methods in stature estimation based on foot remains. *Forensic Science International* 226, 299.e1–299.e7.
- Pablos, A., Martínez, I., Lorenzo, C., Gracia, A., Sala, N., and Arsuaga, J. L. 2013b: Human talus bones from the Middle Pleistocene site of Sima de los Huesos (Sierra de Atapuerca, Burgos, Spain). *Journal of Human Evolution* 65, 79–92.
- Pablos, A., Martínez, I., Lorenzo, C., Sala, N., Gracia-Téllez, A., and Arsuaga, J. L. 2014: Human calcanei from the Middle Pleistocene site of Sima de los Huesos (Sierra de Atapuerca, Burgos, Spain). *Journal of Human Evolution* 76, 63–76.
- Pablos, A., Pantoja-Pérez, A., Martínez, I., Lorenzo, C., and Arsuaga, J. L. in press: Metric and morphological analysis of the foot in the Middle Pleistocene population of Sima de los Huesos (Sierra de Atapuerca, Burgos, Spain). *Quaternary International*. DOI: 10.1016/j.quaint.2015.08.044.
- Pearson, O. M., Royer, D. F., Grine, F. E., and Fleagle, J. G. 2008: A description of the Omo I postcranial skeleton, including newly discovered fossils. *Journal of Human Evolution* 55, 421–437.
- Pontzer, H., Rolian, C., Rightmire, G. P., Jashashvili, T., Ponce de León, M. S., Lordkipanidze, D., and Zollikofer, C. P. E., 2010. Locomotor anatomy and biomechanics of the Dmanisi hominins. *Journal of Human Evolution* 58, 492–504.
- Rhoads, J. G. and Trinkaus, E. 1977: Morphometrics of the Neandertal talus. *American Journal of Physical Anthropology* 46, 29–43.
- Roberts, R. G., Westaway, K. E., Zhao, J. X., Turney, C. S. M., Bird, M. I., Rink, W. J., and Fifield, L. K. 2009: Geochronology of cave deposits at Liang Bua and of adjacent river terraces in the Wae Racang valley, western Flores, Indonesia: a synthesis of age estimates for the type locality of *Homo floresiensis*. *Journal of Human Evolution* 57, 484–502.
- Rosenberg, K. R., Zúñe, L., and Ruff, C. B. 2006: Body size, body proportions, and encephalization in a Middle Pleistocene archaic human from northern China. *Proceedings of the National Academy of Sciences of the U.S.A.* 103, 3552–3556.
- Ryan, T. M. and Shaw, C. N. 2015: Gracility of the modern *Homo sapiens* skeleton is the result of decreased biomechanical loading. *Proceedings of the National Academy of Sciences of the U.S.A.* 112, 372–377.
- Sala, N., Arsuaga, J. L., Pantoja-Pérez, A., Pablos, A., Martínez, I., Quam, R. M., Gómez-Olivencia, A., Bermúdez de Castro, J. M., and Carbonell, E. 2015: Lethal Interpersonal Violence in the Middle Pleistocene. *PLoS ONE* 10(5), e0126589.
- Susman, R. L. 1989: New Hominid Fossils From the Swartkrans Formation (1979–1986 Excavations): Postcranial Specimens. *American Journal of Physical Anthropology* 79, 451–474.
- Susman, R. L. and de Ruiter, D. J. 2004: New hominin first metatarsal (SK 1813) from Swartkrans. *Journal of Human Evolution* 47, 171–181.
- Trinkaus, E. 1975: A functional analysis of the Neandertal foot. Ph.D. Dissertation, University of Pennsylvania.
- Trinkaus, E. 1983a: Functional aspects of Neandertal pedal remains. *Foot Ankle* 3, 377–390.
- Trinkaus, E. 1983b. *The Shanidar Neandertals*. New York: Academic Press.
- Trinkaus, E. and Hilton, C. E. 1996: Neandertal pedal proximal phalanges: diaphyseal loading patterns. *Journal of Human Evolution* 30, 399–425.
- Vandermeersch, B. 1981: *Les hommes fossiles de Qafzeh (Israël)*. Cahiers de Paléontologie. Paris: Editions du CNRS.
- Villmoare, B., Kimbel, W. H., Seyoum, C., Campisano, C. J., DiMaggio, E. N., Rowan, J., Braun, D. R., Arrowsmith, J. R., and Reed, K. E. 2015: Early *Homo* at 2.8 Ma from Ledi-Geraru, Afar, Ethiopia. *Science* 347, 1352–1355.
- Walter, R. C., Manega, P. C., Hay, R. L., Drake, R. E., and Curtis, G. H. 1991: Laser-fusion  $^{40}\text{Ar}/^{39}\text{Ar}$  dating of Bed I, Olduvai Gorge, Tanzania. *Nature* 354, 145–149.
- Wood, B. 1976: Remains attributable to *Homo* in the East Rudolf succession. In: Y. Coppens, F. C. Howell, G. L. Isaac, and R. E. F. Leakey (eds.), *Earliest Man and Environments in the Lake Rudolf Basin*. Chicago: University of Chicago Press, 490–506.
- Zipfel, B., DeSilva, J. M., Kidd, R. S., Carlson, K. J., Churchill, S. E., and Berger, L. R. 2011: The Foot and Ankle of *Australopithecus sediba*. *Science* 333, 1417–1420.