

The Atapuerca Sites and Their Contribution to the Knowledge of Human Evolution in Europe

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Over the last two decades, the Pleistocene sites of the Sierra de Atapuerca (Spain) have provided two extraordinary assemblages of hominin fossils that have helped refine the evolutionary story of the genus *Homo* in Europe. The TD6 level of the Gran Dolina site has yielded about one hundred remains belonging to a minimum of six individuals of the species *Homo antecessor*. These fossils, dated to the end of the Lower Pleistocene (800 kyr), provide the earliest evidence of hominin presence in Western Europe. The origin of these hominins is unknown, but they may represent a speciation event from *Homo ergaster/Homo erectus*. The TD6 fossils are characterized by a significant increase in cranial capacity as well as the appearance of a “sapiens” pattern of craniofacial architecture. At the Sima de los Huesos site, more than 4,000 human fossils belonging to a minimum of 28 individuals of a Middle Pleistocene population (ca. 500–400 kyr) have been recovered. These hominins document some of the oldest evidence of the European roots of Neanderthals deep in the Middle Pleistocene. Their origin would be the dispersal out of Africa of a hominin group carrying Mode 2 technologies to Europe. Comparative study of the TD6 and Sima de la Huesos hominins suggests a replacement model for the European Lower Pleistocene population of Europe or interbreeding between this population and the new African emigrants.

Since the late 1980s, paleoanthropology has witnessed a paradigm shift in interpretation of the evolution of

the genus *Homo*.¹ The anagenetic evolutionary model, which postulate an unbroken lineal temporal succession of the reproductive continuity of *Homo habilis*, *Homo erectus*, and *Homo sapiens*, representing three evolutionary grades, is gradually being replaced by the cladogenetic model of speciation, which recognizes several speciation events throughout the evolution of the genus *Homo*. These events (cladogenesis) might have been favored by successive dispersals of hominins out of Africa and migratory movements between Africa and Eurasia during the Pleistocene, as well as events of reproductive isolation due to climatic and ecological changes.

The anagenetic model divides the fossil record, or the morphological space of the genus *Homo*, into three evolutionary grades. As the morphospace is filled with new findings, it is becoming increasingly difficult to agree on the exact boundaries between species. The difficulties of this model are exemplified by the frequent

use of terms such as “advanced,” “primitive,” “early archaic,” “archaic,” and “late archaic” to modify *Homo sapiens*. These terms and other similar ones^{2,3} have no taxonomical validity, but suggest a need to describe morphological diversity.

The cladogenetic model also has difficulties. Cladistics requires the establishment of character polarities (the phylogeny of the characters), the selection of independent traits, and the identification of homoplasies. These difficulties have opened several debates concerning the recognition of one or more species in a given hypodigm. One of the most prominent examples concerns the possible partition of a large portion of the Early Pleistocene fossil record into two species, *Homo erectus*, Dubois 1892, and *Homo ergaster*, Groves and Mazak 1975. *Homo ergaster* would be restricted to Africa (if we consider the hominins found in the Dmanisi site, Republic of Georgia, to belong to a different species⁴), while *Homo erectus* may have representatives in Asia and Africa.¹ The distinctions are based on the absence of some specific traits in the African fossils that are present in the Asian ones, to which the species name *erectus* applies. These include a midline keel on the vault, strong reduction of the postglenoid process, an angular torus at the posterior-inferior corner of the parietal bone, overall thickening of the braincase, and reduced superstructures in the temporal-occipital region. Moreover, *Homo erectus* ss exhibits a styloid process, as well as differences in the size and shape of the supraorbital torus.^{5–7} The debate about the partitioning of the fossil record is beyond the scope of this paper but, from this point on, we assign the specimens

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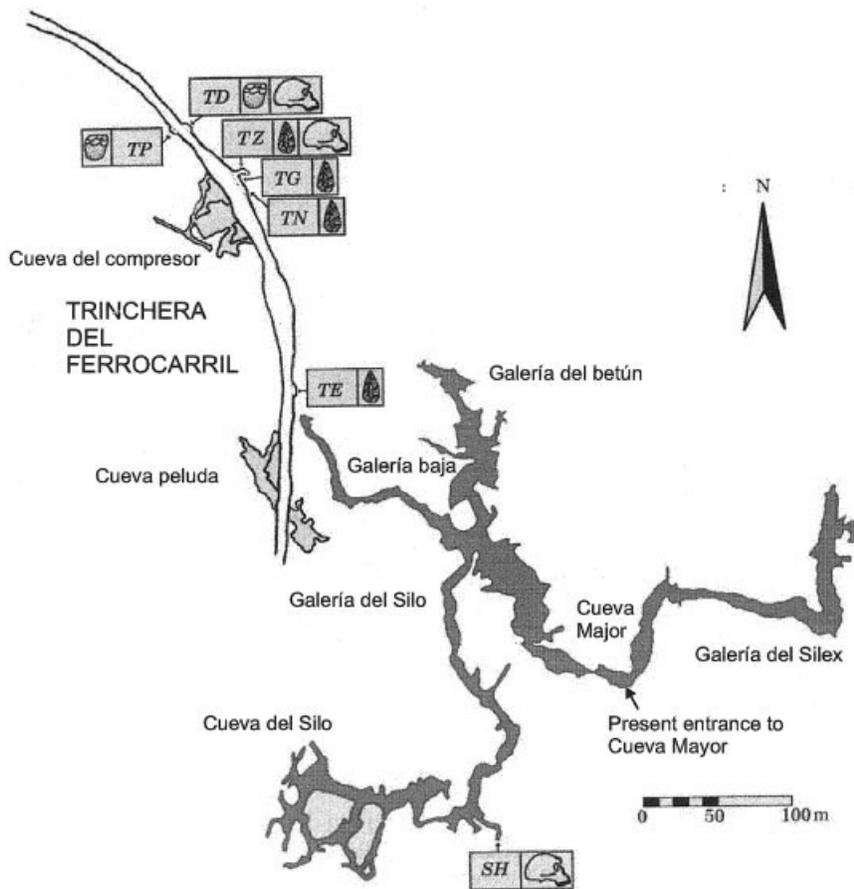


Figure 1. Map of the Trinchera del Ferrocarril and Cueva Mayor, showing the location of the main Atapuerca sites. TD: Gran Dolina; TG: Galería; TN: Trinchera Norte; TZ: Covacha de los Zarpazos; TE: Sima del Elefante; SH: Sima de los Huesos.

THE SIERRA DE ATAPUERCA SITES

The Sierra de Atapuerca is a small hill of about twelve square kilometers that rises 1,079 meters above sea level and approximately 100 meters above the alluvial flatness of the Arlanzón river. The Sierra de Atapuerca is located in northern central Spain (Duero Basin) fourteen kilometers east of the historical city of Burgos. It contains numerous karst cavities in Cretaceous limestones that are filled with Pleistocene sediments (Fig. 1).

The Sima de los Huesos is a blind cavity of $8 \times 4 \text{ m}^2$ located well inside the Cueva Mayor-Cueva del Silo cave system of the karst of Sierra de Atapuerca (Fig. 1). The access to this chamber is a vertical conduit 14 m deep, which ends with a steep inclined ramp about 9 m long. The first human remains, associated with a large assemblage of cave-bear (*Ursus deningeri*) fossils, were found here in 1976.¹² This site has been systematically excavated since 1984. Over several decades, tons of sediment were turned over by cavers hunting for cave-bear teeth.¹³ A meticulous and methodical excavation began in 1988.¹⁴ Arsuaga and coworkers¹⁴ described the stratigraphy and many other aspects of the Sima de los Huesos site and other nearby cavities. They also published cross-sectional diagrams of the Sima de los Huesos site and a map of the excavation grid. The stratigraphy, geological history, and preliminary dating of the site can be found in Bischoff and coworkers.¹⁵ All the human fossils were recovered from the same unit, which is shaped by breccias of clay-supporting bones, blocks, and clasts¹⁵ of varying thickness along the site's profile. Apparently, all fossils were deposited in the site during the same sedimentation period.¹⁵

Previous radiometric and paleomagnetic analyses, as well as biochronological data, pointed to an age of 200 to 320 kyr (oxygen isotope stages 7 to 9) for the Sima de los Huesos hominins.¹⁵⁻¹⁷ However, recent radiometric studies (U-series) of a 14-cm-thick in-situ speleothem overlying the mud-breccia containing the human bones has provided a minimum age of 350 kyr for these hominins.¹⁸ An esti-

of the African Early Pleistocene, including KNM-ER 992 (the holotype of the species), KNM-ER 3733, KNM-ER 3883, and KNW-WT 15000 (the Turkana boy) to the species *Homo ergaster*.

Most authors suggest the use of apomorphies (unique derived traits) for the recognition of a species in a strict application of the cladogenetic model.⁸ However, trait exclusiveness is not as common in the fossil record as it might seem. Given this situation, criteria that are less strict, such as the presence of a unique combination of apomorphic (derived) and plesiomorphic (primitive) traits frequently has been used.^{9,10} Furthermore, due to the difficulties we have noted, some authors consider that the species diagnosis does not need a cladistic basis, but can be made through the phenetic determination of a distinctive morphology.¹¹

Despite the internal debate generated by the cladogenetic model, most authors have abandoned the gradualist model for the "phylogenetic species concept" and the recognition of a larger number of species in the fossil record of the genus *Homo*. This situation has triggered an ongoing debate about the number of cladogenetic events, the nomenclature of the identified species, and possible evolutionary scenarios. For the past thirty years, the research team of the Sierra de Atapuerca sites (Spain) has contributed to this debate through the discovery of two hominin fossil assemblages from the Sima de los Huesos and Gran Dolina sites. These assemblages, as well as other specimens discovered in the last decade in Africa and Europe, give insight into the relationship between Early Pleistocene *Homo* and the lineage that gave rise to *Homo sapiens*.

mated age of 400 to 500 kyr (oxygen isotope stages 12 to 14) for these hominins is based on the rate of growth of the speleothem, correlation of the fauna (micro- and macro-mammals) at Sima de los Huesos with that at other Atapuerca sites (for example, TD6, TD8, TD10, and TD11 levels of Gran Dolina), and the normal magnetization of the Sima de los Huesos fossiliferous mud.¹⁸

The current hominin sample from Sima de los Huesos consists of more than 4,000 fossil remains. Considering all skeletal elements, it represents more than the 80% of the worldwide Middle Pleistocene record for the genus *Homo*.¹⁸ The relative homogeneity of the sample and the fact that all fossils were recovered from the same level strongly support the notion that all of these hominins belonged to the same biological population.

The Sima de los Huesos hypodigm represents a minimum of 28 individuals. The most plausible explanation for this striking fossil accumulation is the use of this cavity by the human population of Atapuerca as a place to deposit corpses. The group may have died over a relatively short period or because of a catastrophic event.^{14,19} In 1998, the finding of a handaxe with exceptional characteristics provided the first evidence of lithic industry at this site.²⁰ In our opinion, this discovery reinforces the hypothesis of the anthropic accumulation of the hominin remains with possible symbolical rituals.

Near the end of the nineteenth century, a British mining company opened a railway trench in the southwestern slope of the Atapuerca Hill less than 1 km from the entrance of the Cueva Mayor. Since 1978, some of the exposed cave infillings along the now-abandoned railway trench have been systematically explored, sampled, and excavated. The vertical section of one of these deposits, Gran Dolina, is 18 m high, formed by 11 successive levels deposited from the late Early Pleistocene to the end of the Middle Pleistocene.²¹ The lowest stratigraphic levels (TD1 and TD2) contain sediments of interior facies typical of a closed cave. With the exception of TD9, the paleontological record (pollen and faunal remains) is

continuous from TD3 to TD11 and some levels (TD4, 5, 6, 7, 10, and 11) contain abundant stone tools.

In 1993, with the aim of performing a more detailed stratigraphic study of the Gran Dolina site, our team excavated an archeological survey pit of 6 m². In July 1994, the test pit reached level 6 (TD6). In one of its strata, known since then as the Aurora stratum, a rich assemblage of fossils and lithic industry was found.²² The excavation of this stratum was completed in 1996. The human sample recovered includes a total of 86 hominin remains, 250 lithic pieces, and hundreds of macrovertebrate remains.

The first paleomagnetic investigation of the Gran Dolina site was performed by Parés and Pérez-González.²³ They found a paleomagnetic

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inversion of the TD7 level 1 m above the Aurora stratum, which they identify with the Matuyama-Brunhes boundary. Another study by these authors²¹ confirmed that the lower levels (TD1–TD6) displayed reversed polarity, whereas the upper levels (TD7–TD11) were normal. At the bottom of the TD section, Parés and Pérez-González reported evidence of a short normal polarity event, which they interpreted as being the Jaramillo or Kamikatsura event. The electron spin resonance and U-series results obtained by Falguères and coworkers²⁴ also confirm an age range between 780 and 857 kyr for TD6.

Pollen studies of the Atapuerca sites by García Antón²⁵ suggest that the up-

per part of TD6, the Aurora stratum, corresponds to a Mediterranean forest composed of *Quercus* (oak, holm, gall-oak) and *Cupresaceae* (cypress), as well as *Olea*, *Celtis*, and *Pistacea*. The structure and composition of the mammals and avian paleocommunities is consistent with a Mediterranean climate similar to the present one.^{26,27} Therefore, the Aurora stratum could be correlated with the oxygen isotope stage 21 (warm). The TD6 macromammals include *Vulpes* sp., Canidae indet., Mustelidae indet., *Panthera* sp., *Felis silvestris*, *Ursus* sp., Proboscidea indet., *Equus* sp. *Stenonian*, *Stephanorhinus etruscus*, *Sus scrofa*, *Dama dama vallonensis*, *Cervus elaphus* cf. *acoronatus*, *Megaloceros* cf. *verticornis*, *Capreolus capreolus*.^{28,29} The fauna is considered typical of the end of the Early Pleistocene and beginning of the Middle Pleistocene. Among microvertebrates, the presence of *Mimomys savini*, also represented in TD7 and TD8,³⁰ is noteworthy, as this taxon persisted at other European sites until 450 kyr ago.^{31,32}

The TD6 human fossil record comprises more than 85 fragmented bones belonging to the cranial and postcranial skeleton. The sample includes more than 43 parts of clavicles, radii, femora, vertebrae, ribs, and patellae, metacarpal, and metatarsal bones, and pedal and manual phalanges. The cranial sample is represented by fragments of frontal, parietal, temporal, occipital, maxillary, zygomatic, sphenoid, and mandibular bones. A total of 30 deciduous and permanent teeth were identified as human. The human remains were assigned to a minimum of six individuals identified by the maxillae, mandibles, and teeth (Table 1). Two isolated lower incisors were attributed to two adult individuals whose age at death is difficult to assess, but were probably young adults.

THE ATAPUERCA HOMININS
Sima de Los Huesos

Study of the human fossils from Sima de los Huesos has revealed primitive features not found in Upper Pleistocene Neanderthals, transitional traits associated with the Neanderthal morphology, and some more derived

TABLE 1. Mesiodistal (MD) and Buccolingual (BL) Dimensions of the Canines and Postcanine Teeth of the Atapuerca Sima de los Huesos and TD6 Hominins

			Maxilla				Mandible			
			N	X	S.D.	Range	N	X	S.D.	Range
C	SH	MD	17	8.6	0.3	8.1–9.6	19	7.6	0.4	6.9–8.5
		BL	18	9.7	0.5	8.8–10.7	18	8.5	0.7	7.3–10.1
	TD6 H1	MD		8.9				8.1		
		BL		11.0				10.0		
P3	SH	MD	13	8.0	0.5	7.2–8.9	19	7.9	0.4	7.2–9.0
		BL	13	10.7	0.6	9.7–11.8	19	8.9	0.6	7.9–10.0
	TD6 H1	MD		8.4				8.8		
		BL		11.7				10.6		
TD6 H3	MD		8.8							
	BL		12.1							
P4	SH	MD	12	7.6	0.5	7.1–8.4	23	7.2	0.5	6.0–8.0
		BL	13	10.4	0.6	9.5–11.3	23	8.6	0.6	7.2–10.1
	TD6 H1	MD		8.0				8.2		
		BL		11.7				10.2		
TD6 H3	BL		11.6							
	MD		11.1	0.6	9.9–12.3	23	11.2	0.5	10.3–12.1	
M1	SH	BL	16	11.5	0.7	10.3–13.0	23	10.4	0.5	9.6–11.6
		MD		12.1				12.2		
	TD6 H1	BL		13.1				11.8		
		MD		11.9						
TD6 H3	BL		12.1							
	MD		9.9	0.9	8.1–11.6	26	11.0	0.5	9.9–12.1	
M2	SH	BL	17	12.1	0.8	11.0–13.8	26	10.2	0.5	9.3–11.5
		MD		12.1				13.5		
	TD6 H1	BL		13.7				12.0		

Neanderthal traits, especially in the supraorbital torus, facial skeleton, and mandible.^{33–36} The dental sample also displays a general morphology and proportions that are very similar to those observed in Neanderthals.^{37,38} Therefore, this sample supports the European roots of Neanderthals deep in the Middle Pleistocene. This lineage can be tracked through the specimens recovered at other Middle Pleistocene European sites such as Arago, Montmaurin, Petralona, Pontnewydd, Steinheim, and Swanscombe. In all these specimens, we can observe one or more Neanderthal apomorphies in combination with primitive traits lost in Upper Pleistocene Neanderthals.^{33,36,39}

According to Arsuaga and colleagues,³⁶ “Middle Pleistocene Europeans and Neanderthals represent the same ‘evolutionary’ species, an ancestral-descendant sequence of populations without rupture of the reproductive continuity.” However, these authors also state that the European Middle Pleistocene population can be defined by a combination of various plesiomorphies not found in later Neanderthals, Neanderthal apomor-

phies, and incipient Neanderthal-like traits, suggesting the inclusion of these specimens in the species *Homo heidelbergensis* as a chronospecies of the European-Neanderthal lineage.

This taxon was proposed by Otto Schoetensack⁴⁰ to name the mandible found in 1907 in the fluvial deposits of the Neckar river near the small German locality of Mauer, nor far from the city of Heidelberg. The Mauer mandible is probably the oldest specimen from the European Middle Pleistocene population. This mandible shows clear affinities to other European specimens such as Arago 2, Arago 13, and the first mandible discovered at Sima de los Huesos (Atapuerca 1).^{41,42} Rosas and Bermúdez de Castro⁴³ showed that the Mauer mandible displays a set of traits that form the structural basis through which Neanderthal apomorphies eventually were fully developed. Moreover, study of the Mauer mandible dental morphology and proportions reveals the proximity between it and the Sima de los Huesos and Neanderthal samples.^{43,44} It is clear that during the Middle Pleistocene an in-

dependent hominin clade evolved into the Neanderthal human population, which, according to several authors, should be included in the species *Homo heidelbergensis*.^{36,45,46}

Gran Dolina, TD6 Level

Studies of the TD6 human fossils reveal that most of the dental traits are plesiomorphic for the genus *Homo*, with a tendency toward enlarged anterior teeth. This appears to be a derived trait in *Homo ergaster* that is shared with European and African Middle Pleistocene populations. The TD6 mandible displays a generalized morphology in common with African, Early European, and Middle Pleistocene hominins. However, it does not demonstrate distinctive African traits such as corpus robustness and strong alveolar prominence.

The assessment of these traits, as well as the chronological and geographic situation of the TD6 level of Gran Dolina, initially led us to consider the Aurora stratum hominins as a representation of a primitive form of *Homo heidelbergensis*.²² However, the

1995 finding of several remains belonging to the facial skeleton drastically modified our original assessment. The most striking attribute of the find was the modern morphology in the facial skeleton, representing the earliest occurrence of a modern face in the fossil record. These TD6 human remains exhibit a unique combination of a modern face with a primitive dentition. They were subsequently attributed to a new species that the Atapuerca research team named *Homo antecessor*.⁴⁷ We further suggested that this species might represent the last common ancestor to both the Neanderthal and modern human lineages. This hypothesis implies that *Homo antecessor* had an ancestor-descendant relationship with both European and African Middle Pleistocene populations.

A SPECIATION EVENT IN THE LATE EARLY PLEISTOCENE?

In 1996, Rightmire⁴⁸ proposed that a speciation event occurred either in Africa or Western Eurasia early in the Middle Pleistocene or before. Rightmire reached this conclusion from his study of a cranium recovered in 1976 at the locality of Bodo, in the Middle Awash region of Ethiopia. The Upper Bodo Sand Unit, from which this specimen was collected, has been dated by the argon-argon method to about 640 kyr (Middle Pleistocene). This age was later ratified by archeological and paleontological evidence.⁴⁹ Rightmire⁴⁸ pointed to clear similarities between the Bodo cranium and the species *Homo erectus/Homo ergaster*, such as the great breadth and heavy buttressing of the face (massive zygomatic bones), very thick vault bones, the low and archaic appearance of the braincase, a flattened frontal profile, and a prominent angular torus. In combination with these primitive traits, Rightmire also described the Bodo cranium as having some synapomorphies with later Middle Pleistocene populations and modern humans. In particular, the cranial capacity of Bodo is around 1,300 cc, exceeding the upper limit of 1,100 cc in *Homo erectus*. The large capacity of the Bodo cranium, reflected in its broad midvault with signs of parietal

bossing, the high contour of its temporal squama, and the minimum and maximum dimensions of its frontal breadth, exceeds the values for *Homo erectus/Homo ergaster*. Furthermore, the crista nasalis falls vertically from the rhinion, projecting the nose in a way similar to that in modern populations. Nevertheless, the Bodo cranium shows a very inflated maxilla without a canine fossa. Finally, the incisive canal follows a nearly vertical trajectory, having an anterior position 6 to 8 mm behind the septum separating the central incisor sockets. The Bodo cranium shares this trait with

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Middle Pleistocene European hominins, Neanderthals, and modern humans.

Consequently, the speciation suggested by Rightmire⁴⁸ would be characterized by the appearance of some derived traits in both the face and the braincase. According to his view, the most appropriate interpretation of the data would be to include the Bodo specimen in the species *Homo heidelbergensis*, together with other Middle Pleistocene specimens such as those from Arago, Mauer, or Petralona in Europe,

Kabwe, Elandsfontein, and Ndotu in Africa, and maybe Dali, Jinniushan, and Yunxian in Asia. This fossil assemblage would represent the stem group for Neanderthals and modern humans. This model had been suggested previously by Stringer^{50,51} and Stringer and McKie,⁵² and defended by Tattersall,⁵³ reviving use of the designation *Homo heidelbergensis*.

The one-million-year-old specimen from Buia (Northern Danakil Depression, Eritrea), which was partially described by Abbate and coworkers,⁵⁴ displays primitive traits, including its 750 to 800-cc cranial capacity, that are characteristic of *Homo erectus/Homo ergaster*. However, this specimen also shows some "progressive traits," such as the high position of its greatest biparietal breadth. According to Abbate and colleagues,⁵⁴ the Buia cranium could provide the key to understanding the time, place, and model of the origins of *Homo sapiens*. Asfaw and coworkers⁵⁵ have recently described the calvarium recovered from the Dakanihylo Member of the Bouri Formation (Middle Awash, Ethiopia), which is from the same period as the Buia cranium. The Daka calvarium has a cranial capacity of 995 cc and has morphological similarities to the Buia specimen. Asfaw and associates⁵⁵ believe that this skull should be included in the species *Homo erectus*. They propose an evolutionary continuity in Africa, from fossils such as KNM-ER3733 and KNM-ER3883 to OH9, Daka/Buia, and Bodo, but suggest that a speciation event in Africa may have taken place approximately one million years ago. Manzi, Bruner, and Passarello⁵⁶ agree that the Daka calvarium should be considered as part of an African evolutionary lineage spanning the interval from approximately 1,800 kyr up to about 1,000 kyr. However, these authors do not believe that the Bodo and Kabwe Middle Pleistocene specimens indicate a continuation of the same African lineage.

The common idea underlying these studies is the presence of one or more evolved forms of *Homo erectus/Homo ergaster* having derived traits pointing to the origin of modern populations. This idea was proposed some years ago with the notion of "archaic"

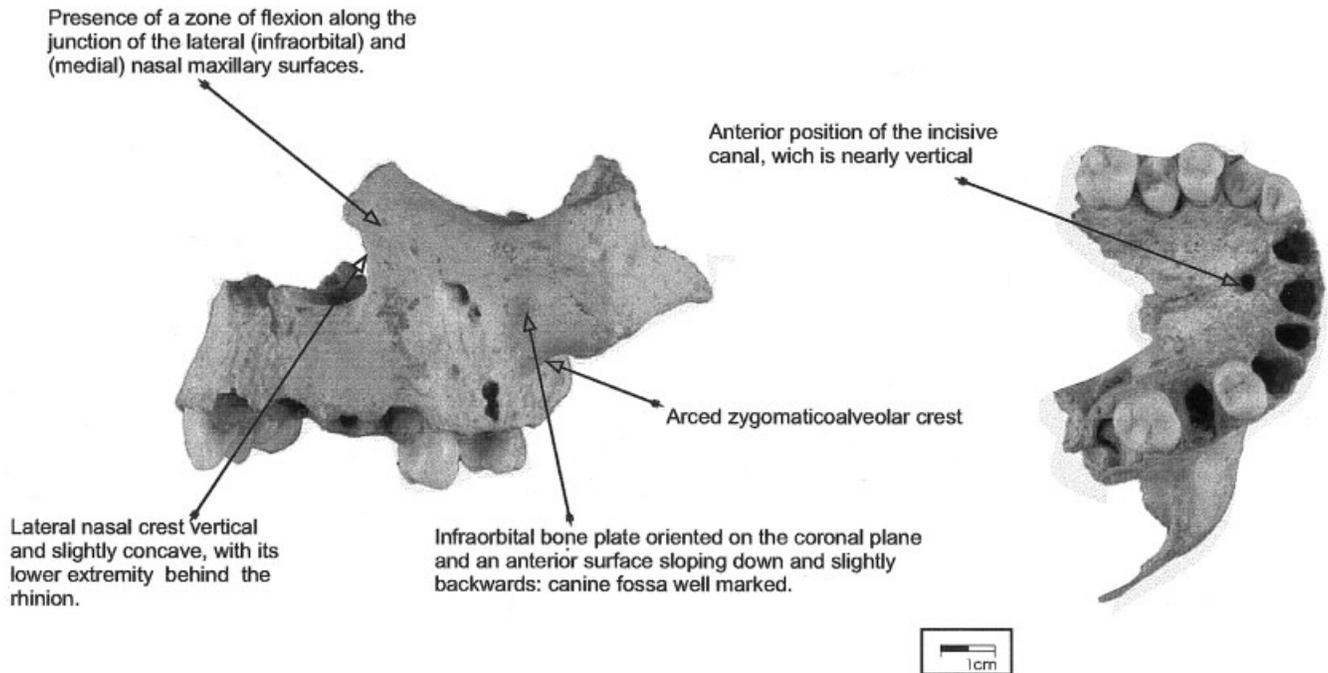


Figure 2. The partial face ATD6-69 (Hominid 3 from TD6) exhibits a completely modern pattern of midfacial topography. ATD6-69 shares with Neanderthals and modern humans an anterior position of the incisive canal, which has a nearly vertical course.

Homo sapiens (see, for instance, Wood², Stringer, Howell, and Melentis,⁵⁷ and Rightmire.⁵⁸ Following the concept of “evolutionary grade,” this suggested a progression toward *Homo sapiens* and the Neanderthals. The TD6 hominin findings are crucial in solving this problem. The ATD6-69 maxilla (Hominid 3) has a fully modern pattern of midfacial morphology⁵⁹ (Fig. 2). Clearly, this specimen belonged to an adolescent⁴⁷ with incomplete facial growth. However, ATD6-19 and ATD6-58, which represent two adults, also exhibit modern traits (see Figs. 3d and 3e in Arsuaga and coworkers⁵⁹). ATD6-58 shows expansion of the maxillary sinus that reduces expression of the canine fossa.⁵⁹ From this evidence, we suggest that the face of *Homo sapiens* may have appeared by a pedomorphic process in which adults retained the facial developmental rate of juveniles.

Another derived trait of the TD6 hominins with respect to *Homo erectus/Homo ergaster* is the shape of the squamosal suture, which depicts a high arch (ATD6-20 specimen). Although there are no tools robust

enough for precise estimation of the cranial capacity of the TD6 hominins, the estimated minimum frontal breadth of the ATD6-15 frontal bone (around 100 mm) suggests a cranial capacity greater than 1,000 cc for Hominid 3.²² The TD6 hominins share three derived traits with modern humans, Neanderthals, and African and European Middle Pleistocene populations⁵⁹; these are a convex superior border of the temporal squama, an anterior position of the incisive canal, and a marked nasal prominence. As a result, *Homo antecessor* appears to be the common ancestor of all of them.⁵⁹ With regard to the postcranial skeleton, Carretero, Lorenzo, and Arsuaga⁶⁰ and Lorenzo, Arsuaga, and Carretero⁶¹ concluded that the more completely preserved specimens, which include clavicles, radii, a femur, vertebrae, and hand and foot bones, display morphological traits that resemble modern humans more than they do either Middle Pleistocene hominins or the Neanderthals.

The calvarium found in 1994 near the Italian locality of Ceprano has provided relevant information. The geostatigraphy and biostratigraphy

of the Ceprano basin, as well as the available K/Ar dating, give an age to this fossil or more than 700 kyr, probably 800 to 900 kyr.⁶² The first study of the Ceprano calvarium revealed similarities to *Homo erectus*, although some general traits related to the large cranial capacity of this specimen, estimated at 1,185 cc, suggested the need for prudence in its taxonomic assignment.⁶² Later, Ascenzi and associates⁶³ assigned the specimen to late *Homo erectus*. A new reconstruction of the Ceprano calvarium by R. J. Clarke, M. A. de Lumley, and F. Mallegni confirmed the previous taxonomic assessment.^{63,64} More recently, Manzi, Mallegni, and Ascenzi⁶⁵ performed a comparative study of the Ceprano calvaria. They obtained a matrix of Manhattan phenetic distances. The unrooted trees generated from this matrix show that the Ceprano specimen occupies an intermediate position between *Homo erectus/Homo ergaster* specimens and the African and European Middle Pleistocene ones. Consequently, these investigators conclude that “Ceprano represents a unique morphological bridge between the clade *Homo ergaster/*

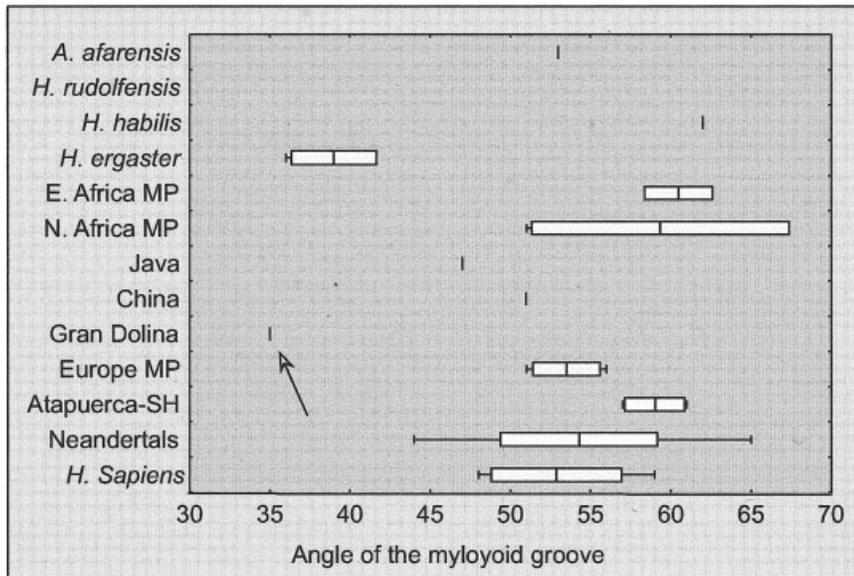


Figure 3. The angle of inclination of the mylohyoid groove in relation to the alveolar margin at the level of M1 and M2 is compared in different hominid samples. The mylohyoid groove in the ATD6-5 mandible forms a 34° angle and can be traced to the level of M2/M3. No other *Homo* mandible shows a mylohyoid groove located in such an extreme position. In OH13, attributed to *Homo habilis*, the mylohyoid groove is more vertical (about 60°), and ends at the distal end of the M3. Similar inclinations are found in African Middle Pleistocene mandibles such as Tighenif II and III, OH22, and BK67. However, in all of them the groove fails to reach M3. In the European hominids, the mylohyoid groove is more posterior and less inclined ($\bar{x} = c. 55^\circ$, $n = 12$). Thus, with regard to this feature, the Gran Dolina specimen is clearly different from the African and European Middle Pleistocene mandibles. Three mandibles in the fossil sample resemble ATD6-5: KNM-WT 15000, mandible C from Sangiran, and an Upper Palaeolithic specimen from Arene Candide (Italy).

Homo erectus and later Middle Pleistocene specimens commonly referred to *Homo heidelbergensis* (and/or to *Homo rhodesiensis*).” Manzi, Mallegni, and Ascenzi⁶⁵ subscribe to the notion of attributing the Ceprano calvarium to the species *Homo antecessor*, although this adult specimen cannot be directly compared to the immature TD6 hominins.

The TD6 hominins represent the earliest evidence of clear and unquestionable modern traits in the fossil record. These hominins, together with the Ceprano calvarium, are older than the Bodo cranium and more recent than the Buia and Daka specimens. Consequently, the appearance of *Homo antecessor* appears to be the best candidate for the speciation event that, around one million years ago, preceded the origin of later hominin lineages. Given this framework, several questions arise: Where did this speciation event take place? What is the origin of *Homo antecessor*? What are the possible evolutionary scenar-

ios for the phylogenetic position of this species?

THE ORIGIN AND PHYLOGENETIC RELATIONSHIPS OF *HOMO ANTECESSOR*

Different evolutionary scenarios can be considered to explain the origins of the European Early Pleistocene population. One is the possibility that TD6 and the Dmanisi hominins are phylogenetically related. At the Dmanisi site, located in the Republic of Georgia, the entrance to Europe, the earliest evidence of hominins out of Africa has been recovered, dated to the Pliocene-Pleistocene boundary.^{4,66–69} Perhaps this first dispersal out of Africa, which may have occurred at the end of the Pliocene, also reached southwestern Europe, but this has yet to be determined. The oldest archeological evidence of the presence of hominins in Europe comes from three Spanish localities: Sima

del Elefante, also located in the railway trench of the Sierra de Atapuerca, and Barranco León and Fuente Nueva 3, in the Guadix-Baza basin (Andalucía). The lower levels of Sima del Elefante (E8-E12) give a reverse polarity. The micromammal association of these levels is consistent with the Matuyama cron, suggesting an age of about 1,000 kyr for a small sample of flint flakes recovered from the E11 level.⁷⁰ With regard to the paleomagnetic data and the faunal assemblages recovered from Barranco León and Fuente Nueva 3, the lithic artifacts (Mode 1) may be older than 1,070 kyr.⁷¹

The metrical and morphological differences between the hominins from Dmanisi and TD6 are remark-

. . . the appearance of *Homo antecessor* appears to be the best candidate for the speciation event that, around one million years ago, preceded the origin of later hominin lineages. Given this framework, several questions arise. . .

able,⁶⁶ a fact that could weaken this scenario. However, it is necessary to bear in mind that these hominins are one million years apart. This first scenario would explain the presence of Mode 1 in all of the European Early and early Middle Pleistocene sites.⁷² Moreover, in this evolutionary scenario *Homo antecessor* would represent a speciation event in Eurasia after the first hominin dispersal out of Africa. This species could have disappeared or been absorbed by the subsequent arrival of an “Acheulean” population that originated in Africa. In this case, we should consider that the expression of “modern” traits in the skull happened more than once, in

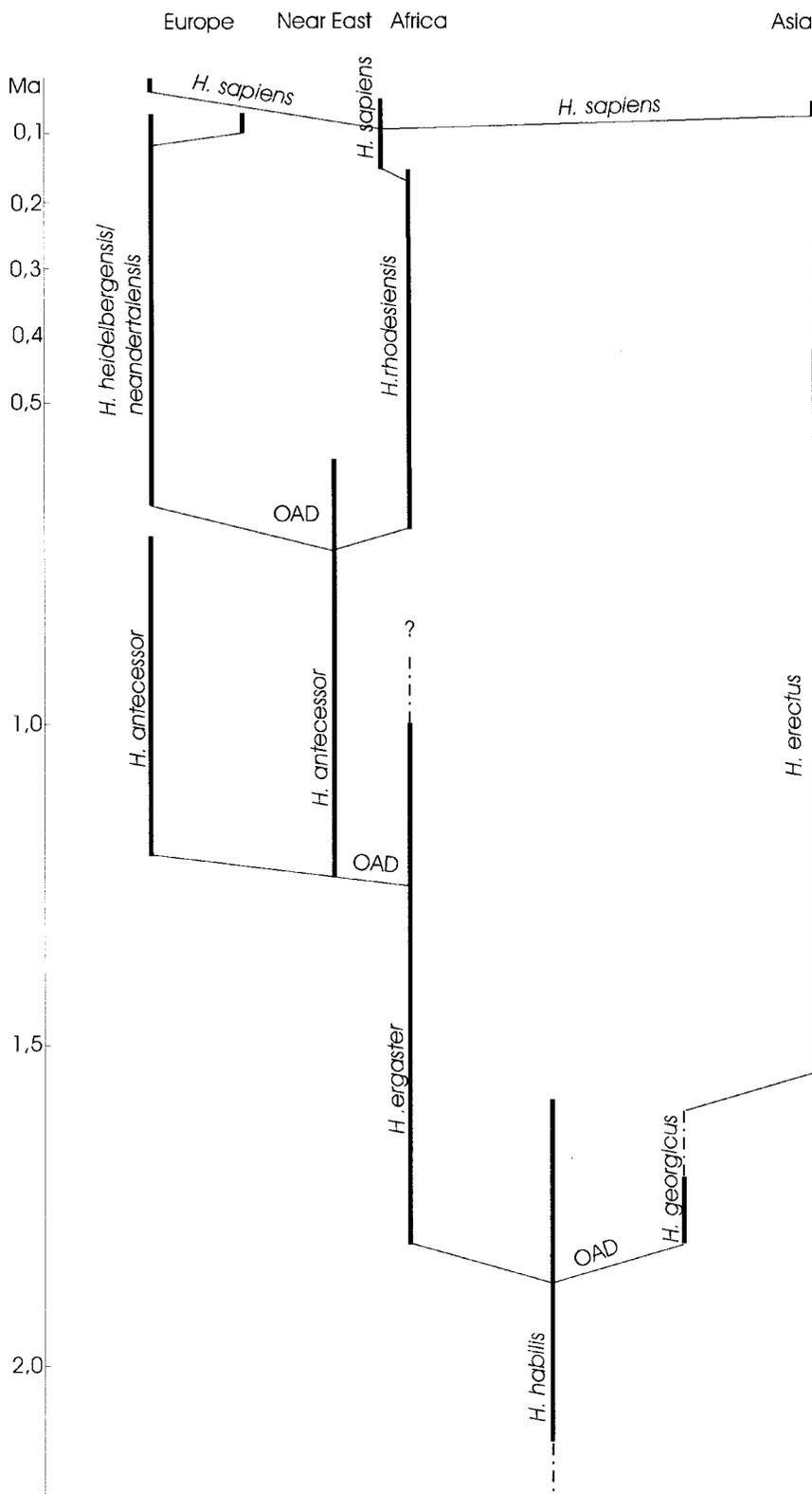


Figure 4. In this scheme, we assume that the Dmanisi hominins represent a distinct species, *Homo georgicus*,¹⁰² and that this species shares a common ancestor with *Homo ergaster*. A candidate for this common ancestor is *Homo habilis*. Although *Homo erectus* appears as a long-lasting lineage in China and Southeast Asia, the large variability of this species needs to be revised. Theoretically, the distribution of the species *Homo antecessor* would include Southern Europe, the Near East, and Africa. OAD = Out of Africa dispersal.

both Africa and Europe, and in populations that had been separated for almost one million years.

In relation to this first scenario, it is known that before 1,200 kyr a series of dispersals started in Eurasia, mainly involving mammals of Asiatic origin and probably related to climatic change.^{73,74} More than 25 species of large mammals dispersed from Asia into western and central Europe in the next 500 kyr, many more than in any period of comparable length since the early Miocene.

A second scenario postulates a second major dispersal of hominins out of Africa across the Levant toward southwestern Europe at the end of the Early Pleistocene, around one million years ago or earlier. In this context, it is important to remember that the main dispersals of mammals from Africa to Europe during the Pleistocene occurred around 1,200, 900, and 500 to 600 kyr.^{74–75} In this scenario, *Homo antecessor* could represent a speciation event that occurred either in Africa or Eurasia after the second major dispersal. If this event occurred in Africa, *Homo antecessor* would have persisted in Africa to originate the evolutionary lineage of *Homo sapiens*. If the species originated in Eurasia, or perhaps in the Near East, *Homo antecessor* must have gone back to the African continent to give rise to our species.

This second scenario is strengthened by the morphological similarities between the TD6 hominins and certain African hominins and hominins of Africa origin. Thus, the mandibular specimen ATD6-5 displays a remarkable position of the mylohyoid groove, comparable only to that found in immature specimens of *Homo ergaster* and, very rarely, in adult *Homo sapiens* (Fig. 3). Furthermore, as stated earlier, the TD6 hominins share three derived traits with modern humans, Neanderthals, and African and European Middle Pleistocene hominins. Considering either of the two possibilities that might be expected in this second scenario, we would still need to know why this expansion occurred with Mode 1 technology when Mode 2 was already present in Africa and the Near East. According to suggestions made by Stringer and

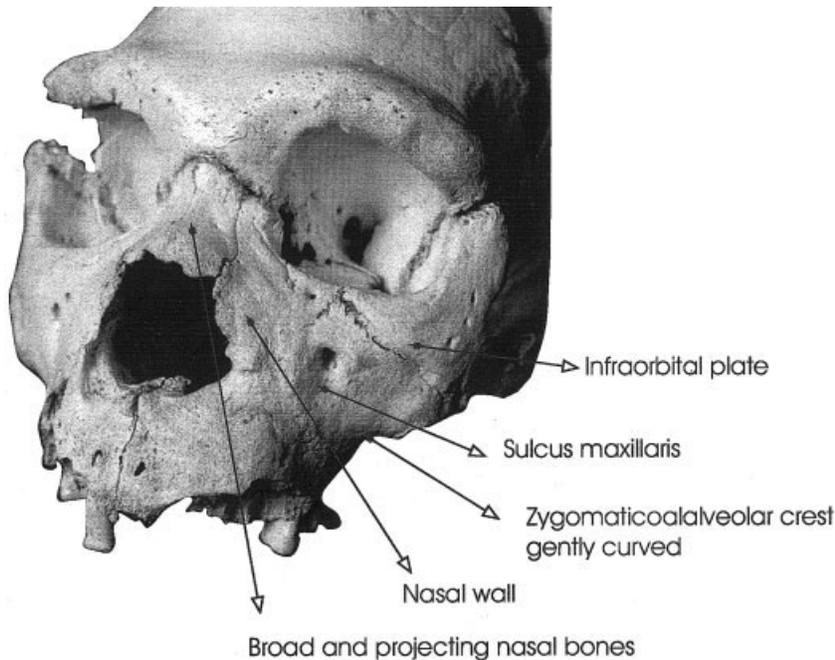


Figure 5. Partial view of Cranium 5 from Sima de los Huesos (Individual XXI). This specimen exhibits midfacial prognathism. The infraorbital plate and the nasal wall do not form a uniplanar surface as they do in classic Neanderthals, but they meet at a wide angle. The zygomaticoalveolar crest is gently curved instead of straight and oblique as in classic Neanderthals.

McKie,⁵² Rightmire,⁴⁸ and Tattersall,⁴⁶ the origin of the European Middle Pleistocene population may be related to the dispersal toward Europe of an African Middle Pleistocene population that probably resembled the Bodo specimen. In this way, Mode 2 might have been carried to Europe by these new emigrants,^{22,65} resulting in replacement of the autochthonous populations or, more likely, crossbreeding between them.⁷⁶

If this is correct, then it is necessary to assume that another cladogenetic event took place in Africa at the beginning of the Middle Pleistocene, initiating the geographic split between the European lineage, which then dispersed out of Africa, and the African lineage, which subsequently gave rise to *Homo sapiens*. This cladogenetic event could have been from the African population of the species *Homo antecessor*, if we accept that this species is the common ancestor of the Neanderthals and modern humans (Fig. 4). For climatic and geographical reasons, the European lineage might have evolved during the Middle Pleistocene almost without genetic ex-

change with other people outside Europe, culminating in the “classic” Neanderthals of the early Upper Pleistocene. The appropriate name for this lineage is *Homo neanderthalensis* if we acknowledge that the Neanderthals do not represent a cladogenetic event in Europe but, instead, are the result of an evolutionary process of morphological “accretion” of the Neanderthal features.^{36,45,77,78} For practical reasons, we can consider two chronospecies, *Homo heidelbergensis* and *Homo neanderthalensis* in this European lineage.³⁶ The Middle Pleistocene African fossils could be grouped in *Homo rhodesiensis* (see Stringer⁴⁵). The African lineage followed a different trajectory that culminated in the last speciation event, which gave rise to the species *Homo sapiens* (Fig. 4).

HOMO ANTECESSOR AND THE EUROPEAN MIDDLE PLEISTOCENE POPULATION

In both of the scenarios outlined, an essential question is whether or not there is an ancestor-descendant relationship between the European Early

Pleistocene population, represented by TD6 and Ceprano, and the European Middle Pleistocene population. In other words, did *Homo antecessor* evolve in Europe into the Neanderthal lineage?

One of the most striking Neanderthal features is midfacial prognathism.^{79,80} In these hominins, the infraorbital bone plate is not orientated in the coronal plane, as it is in modern populations, but rather exhibits a coronal-sagittal (or parasagittal) orientation, conforming to uniplanar surface with the lateral nasal wall. This surface lacks a canine fossa and maxillary flexion. The zygomatico-alveolar crest is straight and oblique with its

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root low in the maxilla. Finally, the zygomatic bone is located at the M2 or M2–M3 level.⁸⁰ Midfacial prognathism, a derived trait of the Neanderthal facial skeleton, was already present in its Middle Pleistocene ancestors. According to Arsuaga and co-workers,³⁶ Arago 21, Petralona, and Cranium 5 of Sima de los Huesos also show midfacial prognathism (Fig. 5), although differences from the classic Neanderthal pattern are still distinguishable.⁷⁹

The TD6 Hominid 3 face is categorically modern, bearing no resemblance to the derived face of Neander-

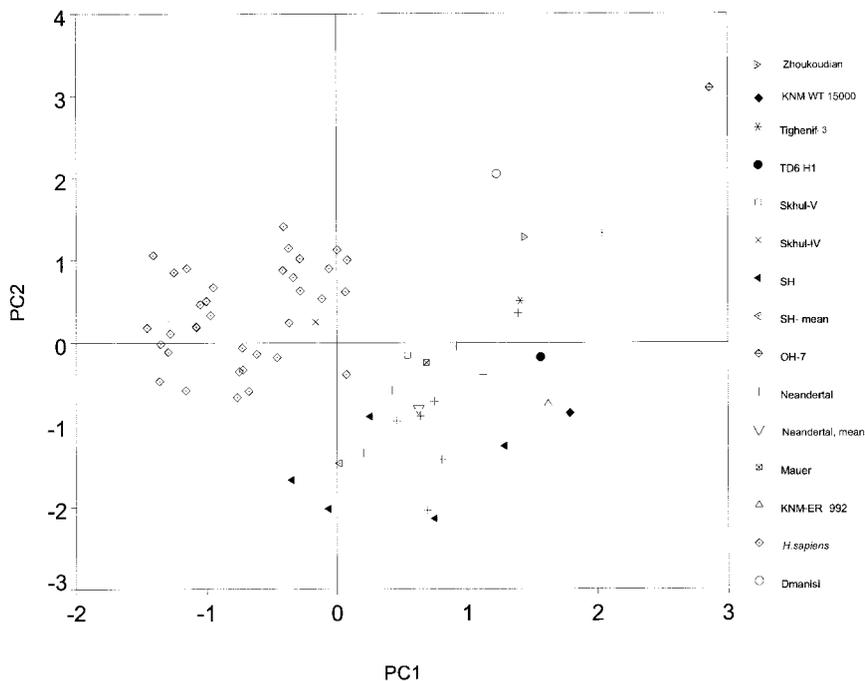


Figure 6. Scatter diagram for the first and second principal components of dental variables: mesiodistal and buccolingual diameters of the mandibular I2-M2. *Homo sapiens*: Aborigines from Gran Canaria, Canary Islands and individuals II, XII, and XXIII from the Atapuerca-Sima de los Huesos sample. (2): Individuals from the Neanderthal sample: Arcy II, Genay, Le Moustier, Ehringsdorf N, Spy II, Krapina D, Krapina E, Krapina H, Krapina L, and Valdegoba.

thals. ATD6-58 does not share any common trait with these hominins either.⁵⁹ However, Arsuaga and colleagues⁵⁹ believe that the Neanderthal face could be derived from a face like that of the TD6 hominin. According to these authors, specimens from Sima de los Huesos (AT-404) and Steinheim point to that possibility,⁵⁹ showing an intermediate morphology between the generalized midface⁷⁹ observed in certain hominins and modern populations and the derived midface of Neanderthals. They also point to the fact that the AT-404 and Steinheim specimens are clearly derived toward the Neanderthal direction.

The internal nasal cavity of ATD6-69 lacks the three Neanderthal apomorphies described by Schwartz and Tattersall⁸¹: development of an internal nasal margin bearing a well-developed and vertically oriented medial projection, swelling of the posterior-lateral wall of the nasal cavity as a result of a medially expanded maxillary sinus, and lack of an ossified roof over the lacrimal groove. Furthermore, nasal crests of ATD6-69 are

similar to those of modern humans and lack the typical Neanderthal sharp lower margin formed by the lateral crest.⁵⁹

Metric and shape features of the Early Pleistocene mandible specimen from TD6 show that ATD6-5 had a generalized morphology largely shared with both African and European Early and Middle Pleistocene samples.⁸² However, distinctive African traits such as corpus robustness and strong alveolar prominence are absent in the Gran Dolina specimen. At the same time, none of the apomorphic features that characterize Middle and early Upper Pleistocene European hominins can be recognized in ATD6-5.

Study of the size, proportions, and morphology of the TD6 and Sima de los Huesos dental samples also provide important data. Due to their highly conserved genetic component, teeth are considered a valuable and reliable source of characters for phylogenetic analysis.^{83,84} The sample for this analysis comprises the TD6 hypodigm, composed of 28 permanent

and 2 deciduous teeth and the Sima de los Huesos sample, with 467 permanent and 8 deciduous teeth.

The relative size of the second premolar (P4) and the molars (M1–M3) is a remarkable feature characterizing the Sima de los Huesos sample. The mean mesiodistal and buccolingual diameters of the crowns are similar to those in modern populations.⁸⁵ Considering the reduced size of these teeth in other Middle Pleistocene fossils such as those from Steinheim, Pontnewydd, and Mauer, as well as some of the Arago specimens, the general trend toward posterior tooth reduction (except the first premolar, P3) in the European Middle Pleistocene is clear. This could represent a case of parallelism between the Middle Pleistocene populations and the lineage leading to modern populations.⁸⁵ In contrast, the mesiodistal and buccolingual dimensions of the TD6 posterior teeth are large and comparable to those of the African and Asian Early and Middle Pleistocene specimens.⁴⁷ As shown in Table 1, some of the dimensions of the Gran Dolina-TD6 posterior teeth are beyond the Sima de los Huesos range of variation. This is true of the buccolingual dimension of the maxillary C mandibular and maxillary P3, and maxillary P4 and M1; the mesiodistal and buccolingual dimensions of mandibular P4, M1, and M2; and the mesiodistal dimension of maxillary M2. However, it is important to note that some specimens from Arago, such as Arago 13,

TABLE 2. Principal Component Analysis of the Mandibular Dental Variables

		Factor 1	Factor 2
I2	MD	0.853	-0.257
	BL	0.805	-0.424
C	MD	0.912	-0.222
	BL	0.901	-0.246
P3	MD	0.936	-0.007
	BL	0.902	-0.239
P4	MD	0.842	0.340
	BL	0.906	-0.003
M1	MD	0.798	0.460
	BL	0.728	0.483
M2	MD	0.884	0.131
	BL	0.897	0.199
% of variance:		74.9	8.6
Cumulative variance:		74.9	83.5

TABLE 3. Comparison of the State of Dental Features in the Gran Dolina-TD6 and Sima de los Huesos Hominins From the Sierra de Atapuerca

Dental Traits	TD6	SH
Shovel-shaped upper incisors	Present	Present
Relative buccolingual dimension of the mandibular incisors with regard to the posterior teeth dimensions	Intermediate	Broad
Relative buccolingual dimension of the maxillary incisors with regard to the posterior teeth dimensions	Intermediate	Broad
Cingulum in mandibular canines and premolars	Present	Absent
Crown shape of the mandibular third premolar (P3)	Strongly asymmetrical	Symmetrical or moderately asymmetrical
Relative buccolingual dimension of the mandibular P3 with regard to the mesiodistal dimension	Broad	Broad/narrow
Talonid of the mandibular P3	Well developed	Small or absent
Mandibular premolar root morphology	2 roots: MB + DL ^a	1 Root
Mandibular P3/P4 size sequence for the crown area	P3 > P4	P3 > P4
Mandibular M1/M2 size sequence for the crown area ^b	M1 < M2	M1 > M2
Maxillary M1/M2 size sequence for the crown area	M1 < M2	M1 > M2
Hypoconulid in the mandibular M1 and M2 ^b	Present and well developed	Frequently absent in M2, and less so in M1
Relative buccolingual dimension of the mandibular M1 with regard to the mesiodistal dimension	Broad	Broad
Taurodontism ^c	Hypotaurodontism	Hypo- to hypertaurodontism

^a The TD6 premolars have two roots; the distolingual root is shorter than the plate-like mesiobuccal root. The dominant buccal component and the shorter and narrower mesial components of the mesiobuccal root have independent root canals.

^b The Montmaurin mandible also exhibits the M1 > M2 size sequence. No hypoconulid is present in the M2 of this specimen or in the Arago 5 (M2) and Arago 6 (M2) specimens (personal observation of the originals by first author).

^c Classification of Shaw (1928).

have posterior teeth that are as large as or even larger than those of TD6.

The anterior teeth (incisors, canines, and the P3) from Sima de los Huesos are relatively large in comparison to the P4 and molars. The size imbalance of I1-P3 versus P4-M3 is an important trait that can be used to establish affinities and phylogenetic relationships among hominins.^{38,44} As far as the mandibular dentition is concerned, some *Homo* specimens such as Dmanisi, OH7, or Zhoukoudian (mean values of this sample) show predominance of the posterior dentition over the anterior teeth. Hominid 1 from TD6 and other *Homo* specimens such as Mauer and Tighenif 3 show a balanced relationship between

the size of the anterior and posterior dentitions. Finally, in the Sima de los Huesos hominins and most Neanderthals, anterior teeth are clearly larger than posterior teeth. Figure 6 and Table 2 show the results of an analysis of principal components (factors 1 and 2) illustrating this size relationship between anterior and posterior dentitions. It is important to highlight the fact that the size and shape of the dentition of the Mauer specimen (the holotype of *Homo heidelbergensis* Schoetensack, 1908) are very similar to those of the Neanderthal and Sima de los Huesos samples.^{43,44}

With regard to the dental morphology and interdental indices (Table 3), we selected a total of 14 features that

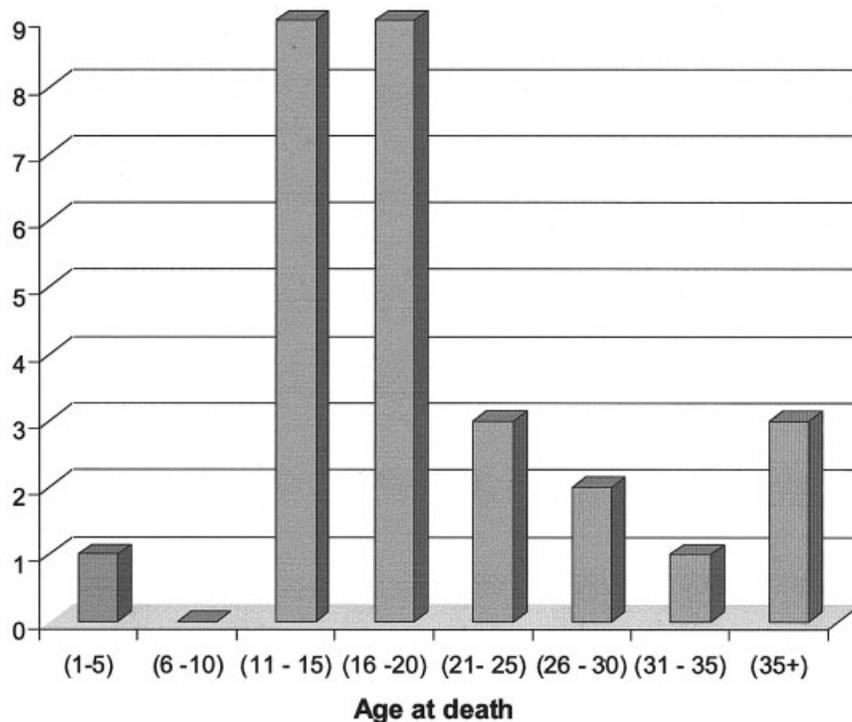
show the clear differences between the TD6 and Sima de los Huesos samples. The two samples share some traits, but these traits do not necessarily imply a phylogenetic relationship between the TD6 and Sima de los Huesos populations. For example, shovel-shape, a plesiomorphic trait for the *Homo* clade, is present in all *Homo* species, including some *Homo sapiens* populations. The P3 dominating P4 (P3 > P4) sequence is also shared by the African Early and Middle Pleistocene hominins and the Neanderthals. Finally, the relatively broad M1, common in TD6 and the Sima de los Huesos hominins, is also present in African and Asian Middle Pleistocene hominins.

Box 1. The Origin of the Sima de los Huesos Hominin Assemblage

Including all the skeletal elements, the Sima de los Huesos hominin sample currently comprises more than 4,000 fossil remains. The minimum number of individuals was assessed through analysis of the maxilla, mandibles, and isolated teeth. The Sima de los Huesos hypodigm includes more than fifty remains of maxillas and mandibles. Some of these bones are nearly complete; others are less so. Moreover, the current sample includes a total of 479 teeth, 109 in situ and 370 isolated. The MNI evaluation has continued from the first excavation seasons.^{86–88} At this moment, we have determined a MNI of 28.

Data obtained from the Sima de los Huesos hominins suggest that the time and pattern of dental development in the population represented by these hominins were similar to those in modern human populations.⁸⁹ Thus, we have used modern standards of human dental development to assess the relative mineralization stage of developing teeth in the immature individuals and to estimate their age at death. According to these standards, the third molars (M3) of the hominins appear systematically advanced in their formation as compared to second molars (M2), from 1.5 years in individual XVIII to 3.4 years in individual XXV. This observation implies that in these Middle Pleistocene populations M3s had their gingival eruption approximately at the age of 15 years, whereas the occlusal eruption occurred at about the age of 16 years.⁹⁰

In order to estimate the age at death of the Sima de los Huesos adults we have applied the tooth-wear-based method developed by Miles⁹¹ to the canines, premolars, and molars. This method takes as reference a group of individuals with estimated sex and incompletely developed dentitions. The degree of wear on a particular tooth is calculated in a qualitative way and applied to adult specimens. This method has the advantage of obtaining an internal variable for the population, in this case the wear rate, which is supposed to be similar for all individuals belonging to that population. (See Bermúdez de Castro and Nicolás⁸⁷ for a discussion of this method). In our opinion, this method offers reasonable results for



Age-at-death distribution of the 28 individuals identified in the Atapuerca-Sima de los Huesos fossil hominin sample.

adults under the age of 30 years although, as tooth wear increases, its accuracy decreases. Nevertheless, only 3 individuals in the Sima de los Huesos sample are over 30 years old, so that the lack of precision at this stage does not really influence our mortality distribution assessment. Moreover, we have quantified the tooth-wear rate of lower incisors in immature individuals,⁹² which allows us higher reliability and precision up to the age of about 35 years. Concerning sex, the metrical and morphological variability of the Sima de los Huesos mandibles,⁹³ and the extremes of variability of dental size⁸⁸ suggest that 12 individuals are females and 8 are males, while sex determination for 8 individuals is inconclusive.

Figure 1 illustrates the age-at-death distribution for the Sima de los Huesos hominin sample. The most noteworthy results are the presence of a single individual under the age of 10, represented by a deciduous canine; the high percentage of those under the age of 20 years (64.3%); and the low percentage of individuals who died after the age of 35 years (10.7%).

When this mortality distribution is compared with theoretical models based on demographic parameters estimated for Middle Pleistocene populations,⁹⁴ we find that the peculiar Sima de los Huesos distribution fits neither an attritional profile nor a catastrophic one. The main reason is that this sample almost completely lacks infants and children, and has an abnormally high percentage of adolescents and prime-age adults. Also, the number of adults over the age of 20 years is lower than expected in these models.

The testimonial presence of only one individual under the age of 10 years in the Sima de los Huesos site could be explained by the action of taphonomic agents. The fragile and delicate remains of infants and children are more severely affected by the action of biostratinomic and fossil-diagenetic agents than are bones from adolescents and adults.⁹⁵ Andrews and Fernández-Jalvo⁹⁶ have observed the presence of carnivore marks of a big felid, probably *Panthera leo fossilis*, and small scavengers, probably *Vulpes vulpes* on more than 50% of the human remains at Sima de los Huesos. These authors

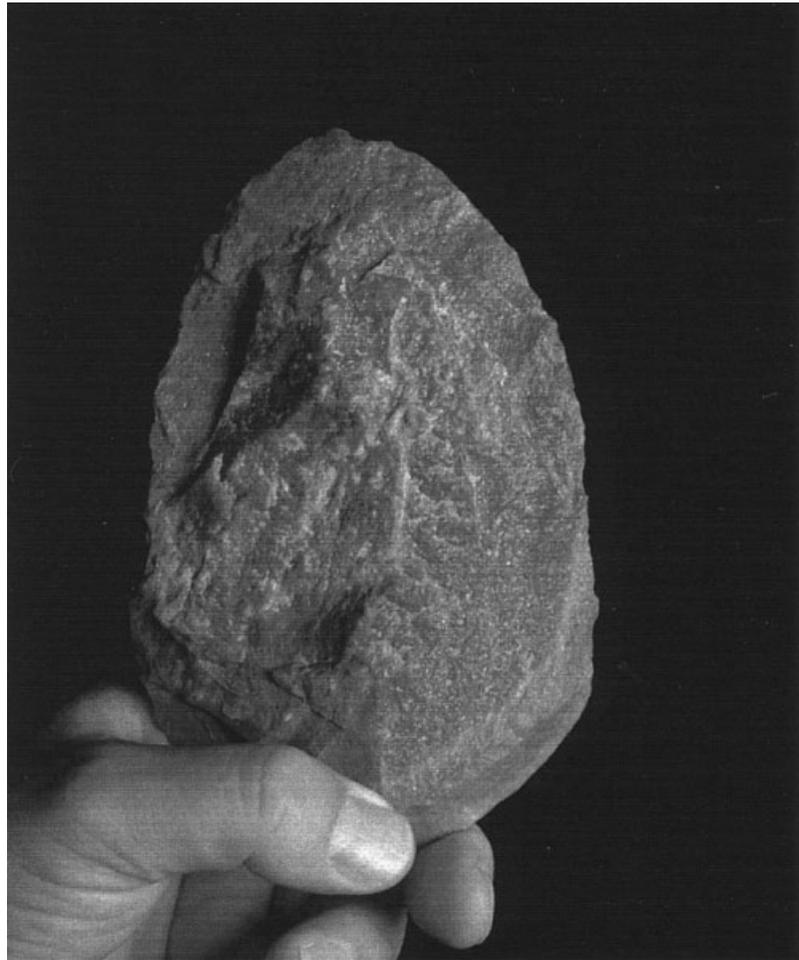
Box 1. The Origin of the Sima de los Huesos Hominin Assemblage (continued)

suggested that there was an initial anthropic accumulation of human corpses and that later the action of these animals eliminated all vestiges of the individuals younger than 10 years. However, very delicate bones have been recovered at the site, including small ear bones, as well as eight perfectly preserved deciduous teeth. This suggests extraordinary preservation conditions at the site. Consequently, it seems difficult to accept the idea that almost all evidence of infants, children, and juveniles disappeared in the manner suggested.

The presence of a high percentage of individuals under the age of 20 years is not expected in a mortality distribution of attritional type, where all individuals who died across a long period for diverse reasons are represented. In a distribution of this kind, we should expect a high number of individuals close to the age of the maximum longevity of that population.^{97,98} In all populations, it is normal to find a certain number of adolescents who have died of different causes, generally accidental death or first births. However, adolescents and young adults represent the sector of the population that is most resistant to illness, which is a major cause of death for infants, children, and elderly members of the population.

Arsuaga and coworkers¹⁴ also considered an anthropic origin for the accumulations, postulating that they were the result of a kind of mortuary practice because of the large minimum number of individuals. In a later work, Bocquet-Appel and Arsuaga⁹⁹ discarded the hypothesis that the site was a primitive cemetery, suggesting instead that the mortality distribution could be the result of a catastrophe, although they did not specify the origin of the accumulation.

The recent finding of a handaxe of exceptional characteristics provides



Frontal surface view of the handaxe found at Sima de los Huesos (Atapuerca Hill).

the first evidence of lithic industry in this site.²⁰ The tool is made of good-quality, reddish to light-brown veined quartzite, a raw material not commonly found among the thousand stone tools recovered so far from the Pleistocene sites of Atapuerca. It has an amygdaloid shape, and one of its sides is flat while the other is convex. It seems to have been made by means of soft hammer percussion after an initial reduction sequence of two main phases. The first phase was devoted to forming the volume,

through flat, invasive extractions around both of its surfaces. The second phase was implemented by shaping the edges of the biface to achieve a convex distal conformation and a straight, sharp perimetral edge (Fig. 2). Traceology studies reveal that the handaxe does not show use-wear traces. The finding of this unique stone tool together with the corpses of 28 individuals is difficult to explain as a natural accumulation, that occurred without human intervention.

The Arago hominins display a set of dental traits that deserves special mention. Most Arago permanent teeth are large, especially those of the Arago 13

mandible. In this specimen, the crown of the P3 is symmetrical and lacks a cingulum and talonid. However, the apical fourth part of the root is divided

into two components, mesiobuccal and buccolingual, each with a single canal (observable on CT scans). The crown of the P4 exhibits a well-developed tal-

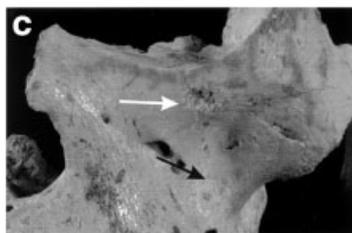
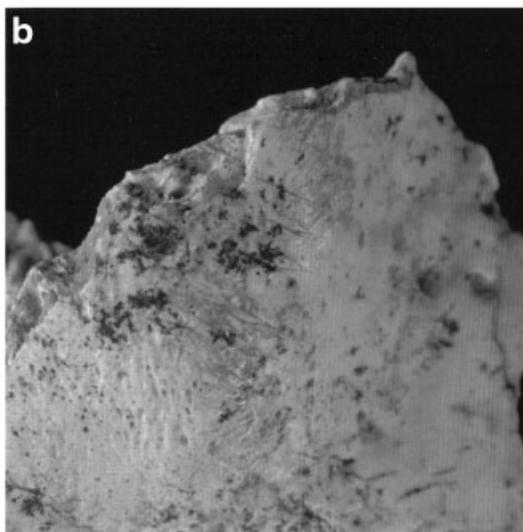
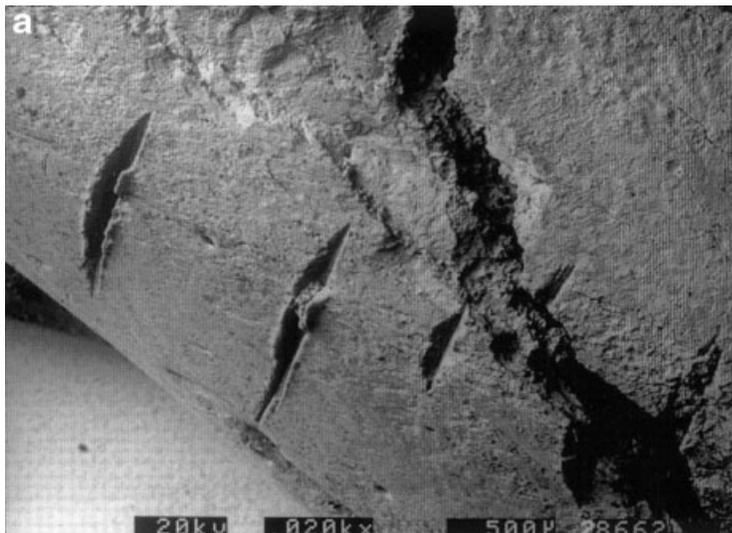
Box 2. Human Cannibalism in the Aurora Stratum

One of the most interesting results of study of the Aurora stratum of the TD6 level has been the conclusion that the hominin assemblage originated through the practice of cannibalism.¹⁰⁰ It thus represents the oldest evidence of cannibalism recorded so far in hominin evolution.

The 30-cm deep Aurora stratum contained a large number of human and nonhuman remains, and stone tools. The distribution of the human remains, excavated in 1994 and 1995, seems to be random in the 7 m² area. There is not a clear pattern in the distribution of the different human skeletal parts, which are mixed with the faunal remains and stone tools. Furthermore, a random arrangement characterizes the distribution of the human and nonhuman fossil remains. Most of these remains show human-induced damage. Tool-induced surface modifications in the sample include frequent cutmarks; scraping marks resulting from the removal of periosteum and muscle by scraping the bone surface; and percussion marks, which indicate the use of a stone hammer to smash the bones (Fig. 1). Adhered bone flakes are also frequent in the human and nonhuman remains. Such flakes are produced by striking bones with artifacts. Peeling is especially frequent in the remains of humans and small animals (roe deer, wild boars, and fallow deer). Peeling is defined as a roughened surface with parallel grooves or fibrous texture produced by bending the fresh bones between the hands.

All these butchering techniques were aimed at meat and marrow extraction. The presence of human remains in the assemblage suggests cannibalism for nutritional purposes. The species diversity recorded in the Aurora stratum is the richest found at any level in the Sierra de Atapuerca sites. The temperate climate inferred from the fossil record (pollen and mammal community) for TD6, as well as the abundance of hunting available to hominins, make it improbable that humans ate other humans as a survival strategy. Rather, it seems that the TD6 hominins consumed other members of their species as part of their regular diet (dietary or gastro-nomic cannibalism).

On the other hand, the skeletal-el-



a: Scanning electron microscope image of the immature clavicle ATD6-55 exhibiting parallel cutmarks and a transversal fracture made when the bone was still fresh. b: Fragment of human temporal ATD6-16 showing numerous more-or-less parallel cutmarks affecting the area where the sternocleidomastoid muscle is attached. c: The face ATD6-69 shows an impact produced with a stone tool near the infraorbital border (white arrow), as well as some slicing and sawing marks near the zygomaticoalveolar crest (black arrow).

ement representation in the Aurora stratum suggest that the small animals, including humans, were transported complete into the cave.¹⁰¹ In contrast, the anatomical representation of large animals, which is biased in favor of elements rich in fat and

marrow, suggests transport selection by hominins. Pending future excavations over the whole TD6 level, the Aurora stratum can be interpreted as a consumption site, whether it was a preferential central place or an occasional refuge.

onid, while the apical third of the root is also divided in two components, mesio-buccal and distolingual, as in the TD6 sample. Also, the mesio-buccal component has two-rooted canals. Hence, the root morphology of this tooth is similar to that of the corresponding tooth of Hominid 1 from TD6. On the other hand, Arago 13 and Arago 21 show a clear $M1 < M2$ size sequence; the $M2$ and $M3$ of Arago 13 are hypotaurodont and mesotaurodont, respectively. Arago 13 shows a combination of the Gran Dolina and Sima de los Huesos dental traits (see Table 1).

Since the 1997 publication regarding the species *Homo antecessor* and its possible phylogenetic position,⁴⁷ there have been new findings in Africa and Eurasia. Moreover, the question of the persistence of Mode 1 technology in Eurasia or, if preferred, the late arrival of Mode 2 to this continent, has been a source of debate in the scientific community. Given this context, we find it appropriate to review the Atapuerca evidence. The study of the skull, mandibles, and dental remains of TD6 has not revealed any Neanderthal apomorphic trait. Moreover, the size and shape differences between the TD6 and Sima de los Huesos specimens, as well as between TD6 and other specimens from the European Middle Pleistocene, are remarkable. Hence, the hypothesis of an ancestral-descendant sequence of populations without rupture of the reproductive continuity between the late early Pleistocene and the Middle Pleistocene in Europe does not seem clear. However, some of the Arago specimens might represent cross-breeding between the two populations.

CONCLUSIONS

The scattered nature of the fossil record has long undermined studies of human evolution in the period between 1,200 and 500 kyr. For Asia, there is a general consensus about the evolutionary continuity of the populations assigned to *Homo erectus*, probably from the beginning of the Early Pleistocene to the end of the Middle Pleistocene, seemingly with no cladogenetic events. However, it has been proposed that in Africa, or maybe in Western Asia, a speciation event mod-

ified the evolutionary landscape of the genus *Homo* around one million years ago.^{7,48} This speciation event implied the origin of the hominin population that derived toward the “sapiens” pattern but retained plesiomorphic traits of its ancestral species *Homo ergaster* (or *Homo erectus*, if we accept the scheme of those who consider *Homo ergaster* to be the African form of a polytypic species distributed throughout Africa and Eurasia). The “sapiens” pattern is characterized by a substantial increase in the cranial capacity with subsequent modifications of the cranial vault and the appearance of certain modern traits in the facial skeleton. According to anagenetic and gradualist vision of human evolution, the presence of this hominin population was established in the Middle Pleistocene of Africa, Asia, and Europe. In the last decade of the twentieth century, along with the move toward a cladogenetic understanding of human evolution, these hominins have been grouped as *Homo heidelbergensis*.

This model is not totally satisfactory, especially to those who see consistent and clear differences among the specimens assigned to *Homo heidelbergensis*, differences which seem sufficient for distinguishing two or more lineages within the group.³⁶ The excavations in the Pleistocene sites of Sierra de Atapuerca have yielded significant data to contribute to this debate. First, the study of the extraordinary human fossil assemblage recovered in the Sima de los Huesos site has undoubtedly shown that Europe was the home of the local evolution of a lineage that subsequently gave rise to the so-called “classic” Neanderthals. This lineage started at least half a million years ago, probably originating in a hominin dispersal out of Africa that brought the Mode 2 to Europe. The most appropriate name for this lineage is *Homo neanderthalensis*, although it is also possible to admit, only for practical reasons, the succession of two chronospecies, *Homo heidelbergensis* and *Homo neanderthalensis*. In Africa, a different lineage gave rise to the species *Homo sapiens*. These two lineages probably shared a common ancestor, from which they increasingly differ-

entiated during the Middle and early Upper Pleistocene.

At the point of origin of these two lineages, we should, according to protagonists of the previously mentioned speciation event, expect an ancestral species from the Early Pleistocene that fulfills the requirements of combining plesiomorphic *Homo ergaster*/*Homo erectus* traits with derived traits toward the “modern” pattern. Surprisingly, the first evidence of such morphology was discovered outside of Africa. The Gran Dolina site in the Sierra de Atapuerca and the Ceprano site¹⁰³ have provided fossils of a new species, *Homo antecessor*, which may represent the common ancestor of Neanderthals and modern populations. Different scenarios have been proposed to complete the puzzle of the available fossil record. However, there are still missing pieces waiting to be uncovered. These pieces undoubtedly would allow a more precise approach to the evolutionary history of the genus *Homo* and the origin of our species.

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