

An Early Pleistocene hominin mandible from Atapuerca-TD6, Spain

E. Carbonell*, J. M. Bermúdez de Castro^{†‡§}, J. L. Arsuaga[¶], E. Allue*, M. Bastir[†], A. Benito^{||}, I. Cáceres*, T. Canals*, J. C. Díez^{**}, J. van der Made[†], M. Mosquera*, A. Ollé*, A. Pérez-González^{||}, J. Rodríguez[†], X. P. Rodríguez*, A. Rosas^{†‡}, J. Rosell*, R. Sala*, J. Vallverdú*, and J. M. Vergés*

*Àrea de Prehistòria, Universitat Rovira i Virgili, Plaza Imperial Tarraco, 1, 43005 Tarragona, Spain; [†]Departamento de Paleobiología, Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas, José Gutiérrez Abascal, 2, 28006 Madrid, Spain; [‡]Centro Nacional de Investigación Sobre Evolución Humana, 09001 Burgos, Spain; [§]Departamento de Paleontología, Universidad Complutense de Madrid-Instituto de Salud Carlos III, 28040 Madrid, Spain; [¶]Departamento de Geodinámica, Universidad Complutense de Madrid, 28040 Madrid, Spain; and ^{**}Departamento de Ciencias Históricas, Facultad de Humanidades, Universidad de Burgos, 09001 Burgos, Spain

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We present a mandible recovered in 2003 from the Aurora Stratum of the TD6 level of the Gran Dolina site (Sierra de Atapuerca, northern Spain). The specimen, catalogued as ATD6-96, adds to the hominin sample recovered from this site in 1994–1996, and assigned to *Homo antecessor*. ATD6-96 is the left half of a gracile mandible belonging to a probably female adult individual with premolars and molars in place. This mandible shows a primitive structural pattern shared with all African and Asian *Homo* species. However, it is small and exhibits a remarkable gracility, a trait shared only with the Early and Middle Pleistocene Chinese hominins. Furthermore, none of the mandibular features considered apomorphic in the European Middle and Early Upper Pleistocene hominin lineage are present in ATD6-96. This evidence reinforces the taxonomic identity of *H. antecessor* and is consistent with the hypothesis of a close relationship between this species and *Homo sapiens*.

human evolution

Between 1994 and 1996, during the excavation of a 7-m² test pit, a sample of ≈100 hominin fossil remains was found in the so-called Aurora Stratum of the stratigraphic unit TD6 of the Gran Dolina site in Sierra de Atapuerca, Burgos, northern Spain (1). The hominin remains were associated with 268 lithic artifacts made of flint, quartzite, sandstone, limestone, and quartz. This sample is characterized by the presence of small artifacts, and includes flakes, denticulates, notches, and side-scrapers and can be characterized as Mode 1 technology (2). The excavation of the Aurora Stratum also yielded a rich small mammal assemblage (26 species, including the water vole *Miomys savini*) as well as ≈1,000 large mammal fossil remains. The study of the arvicolid suggests that the TD6 level can be referred to the Biharian biochron (3). The macromammal assemblage is biochronologically consistent with the end of the Early Pleistocene or early Cromerian (4, 5). Paleomagnetic dating places TD6 in the Matuyama reversed Chron, hence, before 780 thousand years ago (6, 7). These paleomagnetic data combined with electron spin resonance and uranium series results give an age range of between 780 and 857 thousand years for TD6 (8). Pollen analysis suggests that the Aurora Stratum was deposited under wet, temperate conditions (9); thus, the Aurora Stratum possibly correlates to oxygen isotope stages 21 or 19.

In 1997, the TD6 hominins were attributed to *Homo antecessor*, a new European Lower Pleistocene species (10). On the basis of cranial and dental features, it was suggested that this species could be the common ancestor of modern humans (*Homo sapiens*) and Neandertals (*Homo neanderthalensis*). The new taxon was defined in part by using facial and mandibular traits observed in immature individuals. Although the TD6 remains were compared with those of individuals of the same dental age (e.g., KNM-WT 15000), it was clear that the credibility of the species would improve if new specimens corresponding to adult

individuals were found. In 2003, we obtained in the Aurora Stratum an excellently preserved mandible, whose description and comparative analysis is the subject of the present study.

Mandible ATD6-96

Preservation and Age at Death. The specimen catalogued as ATD6-96 was recovered in a planar section of <1 m², near the area excavated during the 1994–1997 field seasons (1). ATD6-96 is a left half of a gracile mandible of an adult individual (Hominid 7) with the premolars and molars in place (Fig. 1). The specimen is broken at the level of the lateral incisor–canine septum, and the left genial apophysis is preserved. Some post-mortem fractures are observed at the region between the corpus and ramus and near the neck of the condyle, but there is no noticeable distortion. Molar (M)3 is fully erupted and exhibits a minimal wear facet at the mesial marginal ridge. During restoration, the corpus and ramus were separated, and the roots of the M3 were observed directly. These roots are at stage Rc of tooth formation (11). Thus, according to modern human standards of dental development, the age at death of this probably female individual was 17–18 years. However, considering recent evaluations of dental development in *H. antecessor* (12) an age at death of 15–16 is more convincing.

Description (Figs. 1 and 2). In lateral view, the basal and alveolar margins of ATD6-96 are almost parallel. The height of the corpus decreases slightly from the level of the mental foramina to the level of the lateral prominence (Table 1). As in the specimen ATD6-5 (13) the mandibular body of ATD6-96 is gracile, and exhibits a smooth lateral prominence, that is placed at the level of M2. The swelling of the lateral prominence is greater at the middle area of the corpus, equidistant from the alveolar and basal margins. The posterior part of the lateral prominence is separated from the alveolar margin by a sulcus extramolaris. The sulcus extramolaris is 6.0 mm wide at the level of M3. The torus lateralis superior, torus marginalis, and tuberculum marginalis posterior are barely expressed and only perceived by touch. The tuberculum marginalis anterior is absent. Judging by the preserved portion of the mandibular body, it seems that no mentum osseum was developed in ATD6-96. Four mental foramina are present: The bigger one lies below the level of premolar (P)3 and approximately halfway between the alveolar and basal borders. This foramen opened laterally. The more distal foramen is located at the level of the interalveolar P4/M1 septum, 18.8 mm from the alveolar border, and is directed posteroinferiorly. Two smaller foramina lie below the P3/P4

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Abbreviations: Mn, molar n; Pn, premolar n.

[§]To whom correspondence should be sent at the † address. E-mail: jmbc@mncn.csic.es.

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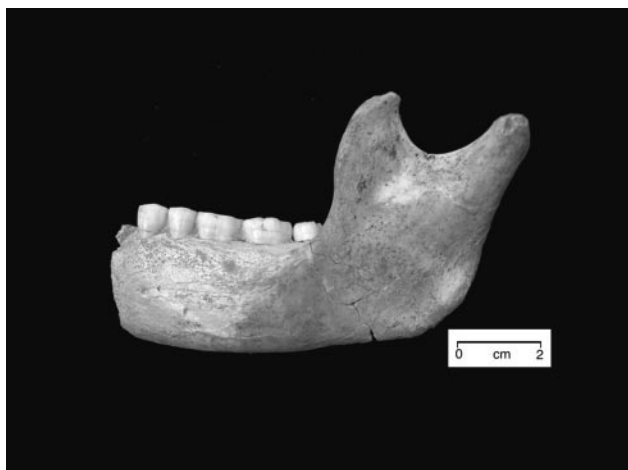


Fig. 1. Lateral view of ATD6-96.

interalveolar septum, 6.2 and 12.8 mm away from the alveolar border. Despite the small size of the M3 (Table 1) as seen in *norma lateralis*, the anterior border of the ramus rises at the level of the distal half of M3, and there is no retromolar space. The trigonum postmolare is oblique and measures 7.0 mm. The trigonum postmolare is clearly delimited by the crista pharyngea (or endoalveolaris) and by a less marked crista buccinatorix. The maximum width of the buccinator gutter (the insertion area of the anterior fasciculi of *musculus temporalis*) is 12.5 mm.

The masseteric fossa is shallow, and the gonion profile is regular, following a smooth curve. The incisura semilunaris is 12.9 mm deep and describes an asymmetric trajectory, the posterior slope being longer and gentler than the anterior slope. The lowest point of the incisura semilunaris is located closer to the coronoid process. The crest defining the mandibular notch meets the condyloid process in the lateral part of the articular surface. The condyloid process is 22.3 mm long and 10.0 mm wide. In posterior view, this process shows a gentle medial lateral convexity. The neck is robust, and the fossa subcondylea is very broad but not especially deep. The posterior border of the ramus is medially flexed because of the action of the sphenoid mandibular ligament.

ATD6-96 lacks an alveolar prominence and a torus mandibularis. As in ATD6-5, the mylohyoid line is defined by a step between the flat and vertical subalveolar plane and a moderately hollowed subalveolar fossa. The mylohyoid line runs from just below the trigonum postmolare forwards and downwards to



Fig. 2. Medial view of ATD6-96.

Table 1. Measurements of the mandible and teeth of ATD6-96

Mandibular sections	Thickness, mm	Height, mm	Mesiodistal, mm	Buccolingual, mm
Corpus at M1	16.6	28.5	—	—
Corpus at LP	18.6	27.5	—	—
Ramus	60.0	40.6	—	—
P3	—	—	8.0	9.7
P4	—	—	7.6	9.4
M1	—	—	10.5	11.0
M2	—	—	12.3	11.0
M3	—	—	9.2	8.8

The ramus value under thickness represents breadth. Measurements for the ramus breadth and height were taken by following the methods in ref. 27. LP, Lateral prominence; —, not applicable.

disappear near the plane of M1. At the M3 level, this line is ≈ 9.0 mm below the alveolar margin and finishes 15.0 mm below this margin. At the canine level, the planum alveolare is almost vertical. At the level of M3, a smooth step of the basal margin marks the transition from the corpus to the ramus and the limits between the subalveolar fossa and the pterygoid fossa.

The mylohyoid groove is 20.0 mm long. A thin bony sheet bridges ≈ 4.5 mm of its middle section. The mesial end of this groove lies at the level of the trigonum postmolare, 16.4 mm from the alveolar margin and 10.2 mm from the basal margin. The mylohyoid groove forms an angle of 42° with the alveolar margin. A lingula mandibulae is present.

A photographic restoration of the entire ATD6-96 mandible (Fig. 3) shows an index of the alveolar arcade of ≈ 100 , thus clearly surpassing the highest values obtained in the Middle Pleistocene hominin sample and the Neandertals (14). The pterygoid fossa is shallow. Marked muscular impressions for the attachment of the pterygoid muscle are present at the angulus mandibulae. The medial pterygoid tubercle is well developed.

The posterior teeth are relatively small in comparison to those of Hominid 1 from TD6, the holotype of *H. antecessor* (15). ATD6-96 shows the P3 > P4 and M1 < M2 size sequences. The crown of P3 is asymmetrical and exhibits a vestige of buccal cingulum. P4 shows a moderately developed talonid. As seen in a computerized tomography scan, both premolars have a single



Fig. 3. Photographic restoration of ATD6-96: occlusal view. The original photograph was transformed into a drawing, manipulated in PHOTOSHOP (Adobe Systems, San Jose, CA), and then edited by DRAW (Corel, Ottawa, Canada).

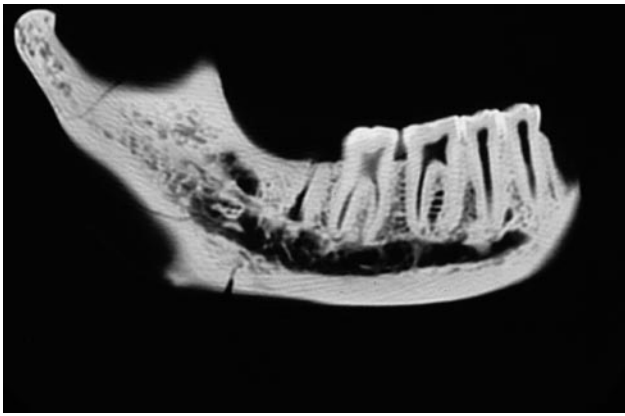


Fig. 4. Computerized tomography scan image of ATD6-96. The slice concerns the premolars and first and second molars.

root (Fig. 4), the one of P3 showing a bifurcation (Tomes' root) of the lower half, with buccal and lingual components. The upper half of the root of the third molar is fused and exhibits an expanded single canal (mesotaurodontism).

As additional evidence of cannibalism in the Aurora Stratum (16), ATD6-96 shows seven clear, subparallel cut marks on the external aspect of the coronoid apophysis, probably for detaching the mandible from the skull.

Comparative Analysis

Before comparing the dimensions of the TD6 mandibles with those of other specimens, it is necessary to note that judging by the remarkable size difference between the teeth of ATD6-5 (Hominid 1) and ATD6-96 (Hominid 7), the former was probably a male, whereas the latter mandible belonged to a female. The dimensions of the upper canine of Hominid 1 are at the high end of the range of the genus *Homo*, which supports the sex status of this individual. On the other hand, the mandible ATD6-5 belonged to an adolescent whose M3 was at the gingival stage of eruption. According to the Rosas and Bermúdez de Castro estimates (13), this mandible could have reached a height at M1 of ≈ 30 mm, whereas its corpus thickness would have remained similar. In *H. sapiens*, adult corpus thickness is reached

at the time of M2 eruption, which means that in *H. antecessor* both males and females probably had small mandibles (low and narrow) in comparison with *Homo ergaster* (East African Early and Middle Pleistocene specimens), *Homo mauritanicus*, and *Homo erectus* (Table 2). Especially high are the mandibles from the North African sites of Tighenif and Sidi Abderrahman. *Homo heidelbergensis* males also have mandibles higher than those of *H. antecessor*, whereas only the height of the Chinese Middle Pleistocene specimens (mean value) is similar to that of the TD6 mandibles. The width of the Chinese mandibles from Zhoukoudian, Lantian, or Hexian is also comparable with that of the TD6 mandibles, and *H. antecessor* and *Homo pekinensis* share a similar robustness index.

H. antecessor exhibits a primitive structural pattern in the mandible that is shared with all African and Asian *Homo* species (Tables 3 and 4). Some features of the TD6 mandibles, such as the position of the M3 in relation to the ramus, the inclination of the retromolar area, or the gonion profile, are slightly derived from the primitive status, as is also seen in some specimens assigned to *H. ergaster*, *H. mauritanicus*, *H. pekinensis*, and *H. heidelbergensis*. From the taxonomic and phylogenetic points of view, these traits are only useful in distinguishing *H. antecessor* from the Java specimens (*H. erectus* in our narrow vision of this taxon), which maintained a primitive pattern in the mandible. The low angle of inclination of the mylohyoid groove in Sangiran 9 might be an exception. The interpretation of this feature is, however, difficult. In the TD6 mandibles, the angle is small (35° in ATD6-5), thus differentiating these individuals from most hominins except for the Sangiran specimen and the immature individual KNM-WT 15000 (13).

The absence of an alveolar prominence, the almost vertical inclination of the planum alveolare, and the moderately hollowed posterior subalveolar fossa are signs of the gracility of the TD6 mandibles, contrasting with the robustness of the African specimens and some European mandibles, such as Mauer and Arago 13.

The TD6 and Chinese mandibles show some minor differences, which might disappear with more representative samples. The lateral prominence is stronger in the Zhoukoudian specimens, which also exhibit a mandibular angle that is clearly everted and forms a prominent crest, which is especially marked in the male mandible GI (17). In the Lantian mandible, the torus

Table 2. Measurements of the mandibular body at the level of M1 in some *Homo* species

Species	Thickness, mm (n)	Height, mm (n)	Robustness (n)
<i>Homo habilis</i>	19.7 \pm 2.3 (5)	29.3 \pm 2.2 (4)	64.5 \pm 5.3 (4)
<i>H. ergaster</i> *	19.8 \pm 1.4 (8)	31.2 \pm 2.8 (8)	63.8 \pm 5.0 (8)
<i>H. erectus</i> †	19.8 \pm 2.6 (4)	36.3 \pm 1.1 (4)	54.7 \pm 7.4 (4)
<i>H. mauritanicus</i> ‡	18.0 \pm 1.1 (4)	35.8 \pm 1.5 (4)	50.2 \pm 1.8 (4)
<i>H. pekinensis</i> §	16.5 \pm 1.8 (7)	28.6 \pm 3.3 (7)	58.0 \pm 5.6 (7)
<i>H. antecessor</i>	16.4 (2)	27.6 (2)	62.6 (2)
<i>H. heidelbergensis</i>	16.4 \pm 1.7 (16)	30.8 \pm 3.4 (16)	53.4 \pm 5.1 (16)
<i>H. neanderthalensis</i>	15.3 \pm 1.7 (21)	32.1 \pm 3.3 (21)	47.9 \pm 5.1 (21)

Data are given as means \pm SD.

*Includes East African Early and Middle Pleistocene adult specimens KNM-ER 730, KNM-ER 731, KNM-ER 992, KNM-BK 67, KNM-BK 8518, OH 22, OH 23, and OH 51.

†We consider that the taxon *H. erectus* should be restricted to the Javanese specimens. This sample includes the Sangiran mandibles 1B, 5, 8, and 9.

‡There is a recent trend to classify the North African Middle Pleistocene specimens as *H. mauritanicus* (32), using the specific name proposed by C. Arambourg in 1963 (33). This sample includes the specimens from Tighenif and Sidi Abderrahman.

§The idea that the taxon *H. erectus* should be restricted to the fossils from Java was proposed in 1977 by Aguirre and de Lumley (34). Furthermore, some authors have observed that the Zhoukoudian and Nanjing specimens exhibit a unique cranial metric pattern not shared by African and Indonesian specimens assigned to *H. erectus* (35). For this reason we prefer to use the specific name *H. pekinensis* for the Chinese specimens. This sample includes the mandibles from Zhoukoudian, Lantian, Hexian, and PA86.

Table 3. State of mandibular features analyzed in Table 4 [partially modified from Rosas (17)]

Mandibular features	State A	State B	State C
1. Position of mental foramen	P3–P4	P4–M1	M1
2. Position of the anterior marginal tubercle	P3–P4	P4–M1	M1
3. Position of the lateral prominence	M2	M2–M3	M3
4. M3 in relation to ramus (retromolar space)	Covert	Partially covert	Uncover
5. Inclination of the retromolar area	Vertical	Oblique	Horizontal
6. Position of mylohyoid line in relation to alveolar margin at M3 level	Low	Medium	High
7. Trajectory of mylohyoid line in relation to alveolar margin	Parallel	Intermediate	Diagonal
8. Relief of masseteric fossa	Deep	Shallow	Flat
9. Relief of pterigoyd fossa	Shallow	Deep	—
10. Gonion profile	Expanded	Regular	Truncated
11. Intersection between mandibular notch and condyle	Lateral	Medial	—
12. Posterior subalveolar fossa	Shallow	Moderately hollowed	Deep
13. Alveolar prominence	Present	Absent	—
14. Angle of inclination of mylohyoid groove, °	<60	59–50	>49

—, not applicable.

lateralis superior and torus marginalis are more conspicuous, and the alveolar prominence is slightly developed (17). It is also interesting to mention the presence of multiple foramina in the Chinese specimens, as in ATD6-96. Nevertheless, this feature is also present in specimens like Mauer or the Tighenif mandibles (18). As in ATD6-96, the planum alveolare is much less conspicuous in the Zhoukoudian and Lantian mandibles than in the Early and Middle Pleistocene European and African specimens.

Discussion

The differences in dimensions and robustness between the TD6 mandibles and the East and North African mandibles cast doubt on the African origin of *H. antecessor*. In contrast, our comparative analysis suggests looking toward the Asian continent. In this respect, it is relevant to mention some data that remained unpublished in 1997, when the new species was named (10), and that are relevant to this discussion. The partial cranium Nanjing I, recovered in 1993–1994 from the Hulu Cave (Tangshan Hill, eastern central China), shows clear modern midfacial traits similar to those observed in the specimen ATD6-69 (19). Wang and Tobias (20) also found similarities between Nanjing I and the Zhoukoudian hominins. Geochronological dates, combined with

ecological and paleoclimatic evidence, indicate that the Nanjing skull is ≈600 thousand years old (21). Furthermore, the Locality 1 levels at Zhoukoudian, which yielded most hominin specimens, are now considered at least 800 thousand years old (22). Thus, these Chinese hominins may be contemporaneous with or slightly younger than the TD6 hominins. If the Gran Dolina and Chinese populations are phylogenetically related, they should share a common ancestor that also had a modern midfacial pattern and a gracile mandible. In the cranium, this hypothetical common ancestor would have had a low and flat temporal squama, and an unfused styloid process. These traits would have been retained in the Asian hominins but lost in the TD6 hominins, who exhibit a fused styloid process, a convex temporal squama, and probably a significant increase in cranial capacity (19). The Ceprano calvaria (Italy), which has been tentatively assigned to *H. antecessor* (23), exhibits a convex temporal squama and a cranial capacity of about 1,057 ml (24). Interestingly, TD6 and Zhoukoudian are the only hominins that have a zygomaxillary tubercle before the Upper Pleistocene (19).

On the other hand, none of the mandibular features considered apomorphic of the European Middle and Early Upper Pleistocene hominin lineage (25) are present in ATD6-96. This

Table 4. State of the mandibular features listed in Table 3 in different *Homo* species

Mand. features	<i>habilis</i>	<i>ergaster</i>	<i>erectus</i>	<i>mauritanicus</i>	<i>antecessor</i>	<i>pekinensis</i>	<i>heidelbergensis</i>	<i>neanderthalensis</i>
1	A	A, B	A	A, B	A	A, B	B, C	C
2	A, 0	A, 0	A	A, 0	0	A, 0	A, B, C	A, B, C
3	A	A, B	A	A, B, C	A	B	C	C
4	A	A, B	A	B	B	B, C	B, C	C
5	A	A, B	A	B, C	B	A, B	B, C	C
6	A, B	A, B	A	A	A	A	A	A, B, C
7	A	A, B	A	A, B	A	A	A, B	B
8	A	A, B, C	A	A	B	A	A, B, C	B, C
9	—	A	A	A	A	A	A, B	B
10	—	A, B	—	A, B	B	A, B	B, C	B, C
11	—	A	—	A	A	A	A, B	B
12	A	A	A	A	B	C	B, C	C
13	A	A	A	A	B	A, B	A, B	B
14	A	A, B	C	A, B	C	B	A, B	A, B

Numbers in the mandibular (Mand.) features column represent the numbers given for the traits in the same column in Table 3. A, B, and C represent states A, B, and C of the mandibular features, respectively, also in Table 3. 0, Absence of the trait; —, no specimens available for that mandibular feature.

