A new early Pleistocene hominin mandible from Atapuerca-TD6, Spain

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Abstract
We present the description of a new mandibular specimen, ATD6-113, recovered in 2006 from the TD6 level of the Gran Dolina cave site in Sierra de Atapuerca, northern Spain. A detailed study of the lithostratigraphy of the top sequence of this level, the section from where all human remains have been recovered so far, is also presented. We have observed that the hominin stratum, previously defined as Aurora Stratum, represents a condensed deposit of at least six layers, which could not be distinguished in the test pit made in 1994–95. Therefore, the human fossil remains were probably deposited during a discrete and undetermined time period. The new mandibular fragment exhibits a very similar morphology to that of the most complete specimen, ATD6-96, which was recovered in 2003 from a different layer. This suggests that both specimens represent the same biological population. The two mandibles, as well as the small mandibular fragment ATD6-5 (which constitutes part of the holotype of Homo antecessor), present a morphological pattern clearly derived with regard to that of the African early Homo specimens usually included in H. habilis and H. rudolfensis, the mandibles D211 and D2735 from Dmanisi, and most of the early Pleistocene mandibles from Sangiran. The TD6 mandibles also exhibit some derived features with regard to the African early Pleistocene specimens included in H. ergaster (or African H. erectus). Thus, the TD6 hominins seem to represent a lineage different from other African and Asian lineages, although some (metric in particular) similarities with Chinese middle Pleistocene mandibles are noted. Interestingly, none of the apomorphic mandibular features of the European middle and early late Pleistocene hominins are present in the TD6 mandibles.

Introduction
The Gran Dolina (TD) cave is placed in the southwestern slope of the Sierra de Atapuerca (Burgos, Spain). The cave is completely filled by interior and exterior facies deposits, which are up to 18 meters thick. A British mining company exposed the TD infilling during the construction of a railway trench at the end of the nineteenth century. The main lithostratigraphic units that infill Gran Dolina were established by Gil et al. (1987), who described eleven different levels from TD1 (bottom) to TD11 (top) on the basis of the vertical distribution of facies and main unconformities along the N-S exposure of the TD sequence. The history of the archeological investigations in TD is reviewed in Carbonell et al. (1999a), and a detailed description of the lithostratigraphy of the site can be found in Parés and Pérez-González (1999).

The 1990s findings in TD6
During the 1994–1995 field seasons, about 90 early Pleistocene human fossil remains corresponding to a minimum of six individuals were obtained from the TD6 level (Carbonell et al., 1995). These finds were recovered during the excavation of a test pit of approximately seven square meters (m²), a survey that preceded the excavation of a larger area of about 80 m² (see Fig. 6 of Carbonell et al., 1999a). The west side of the pit corresponds to the ancient vertical and irregular section of the infilling left by the construction of the railway trench, modified by atmosphere over the decades. At the TD6 level, the pit involved the squares H16, H17, H16, H17, and part of the I18, H18, and G16, G17, G18 (Fig. 1, and see also Fig. 2 of Fernández-Jalvo et al., 1999).

The human remains, together with 268 lithic artifacts made of flint, quartzite, sandstone, limestone, and quartz classified as Mode 1 technology (Carbonell et al., 1999b) were recovered from...
a distinctive stratum of the unit TD6 named “Aurora”. A rich faunal assemblage of micro- and macrovertebrates was also recovered from this stratum, which has a thickness of approximately 25–30 cm. The 1994 findings include a mandibular fragment of a juvenile individual, ATD6-5 (Rosas and Bermúdez de Castro, 1999), which together with a set of isolated teeth constitutes the holotype of the species Homo antecessor (Bermúdez de Castro et al., 1997). The study of the arvicolids suggests that the TD6 level corresponds to the Biharian biochron (Cuenca-Bescós et al., 1999). The macro mammal assemblage (near one thousand fossil remains) is biochronologically consistent with the end of the early Pleistocene or early Cromerian (García and Arsuaga, 1999; van der Made, 1999). Paleomagnetic polarity places TD6 in the Matuyama reversed Chron, hence before 780 ka (Pares and Pérez-González, 1995, 1999). These paleomagnetic data combined with ESR and U-series results give an age range of between 780 and 857 ka for TD6 (Falguères et al., 1999). Pollen analysis suggests that the Aurora Stratum was deposited under wet, temperate conditions (García-Antón, 1995). Therefore, the Aurora Stratum possibly correlates to oxygen isotope stages 21 or 19.

The recent findings in TD6 (2003–2007)

At the end of the nineties, we began to homogenize the exposed section of TD by vertically cutting the different levels. The TD7 and TD6 levels presented marked projecting areas at the middle and the north end of the section (Fig. 1), which provided a new opportunity to excavate approximately 13 m² of the Aurora Stratum and to obtain additional information concerning the TD6 hominins. Currently, the excavation of the small northern area (squares G3 to G6) has just begun, whereas excavation of the middle area (squares G11 to G15) is more advanced and still in progress. In 2003, we found the fragment of a human parietal and the left half of a mandible (ATD6-96; Carbonell et al., 2005) in square G15, approximately at the same depth as the previous human finds. During the successive field seasons we have obtained more than 25 new human fossils. Among them, there is a fragment of the left half of a mandible, ATD6-113 recovered in 2006, whose descriptive and comparative study is the main purpose of this paper.

In contrast to what was observed in the 1994–1995 period, the middle area has yielded fossil human remains and artifacts in well-differentiated levels of moderate thickness. Therefore, we have made a detailed lithostratigraphic study of the upper part of unit TD6, which is presented in the next section.
progress. The AAS is 46 cm thick in this middle sector. The mandible ATD6-113 appeared between the squares G13 and F13 in a 9 cm thick bed of silt that we have named “Pep.” Below this layer, a sequence of gravels, clay, and silts layers can be identified. Finally, a 12-cm thick clay bed, that we have named “Jordi”, represents the bottom of the AAS. The mandible ATD6-96 was found in this layer.

The fact that the Aurora Stratum can now be interpreted as a sequence of different layers deposited during an undetermined period of time could have some interesting implications for the interpretation of human cannibalism that we presented in 1996 (Fernández-Jalvo et al., 1996; and see also Fernández-Jalvo et al., 1999). However, that topic is not the focus of this paper and we will go further into this matter when the excavation of the middle and northern areas is finished.

Methods

For comparative purposes, a large number of adult fossil Homo mandibles were included in our study. Observations and data were recorded on the following original fossil samples: Atapuerca-Sima de los Huesos, Arago, Atapuerca-TD6, Tighenif, Sangiran (6, 1B, and 5), and Dmanisi, as well as on some high-quality casts. Furthermore, features and data of several mandibular specimens were confirmed or obtained from Tables 5–7 of Rosas (2001), Table 2 of Rosas and Bermúdez de Castro (1999), Table 4 of Kauf et al. (2005), and Suwa et al. (2007).

Thickness of the mandibular body was measured at the M₃ and at the location of the lateral prominence (see Table 1). The measurements were taken between the external side of the mandibular body and the most prominent point of the lingual side (Table 2). Since the corpus is damaged at M₁ only an estimate of the thickness at the level of this tooth is possible. Height of the mandibular body at the M₃ was taken between the basal and superior alveolar border of the corpus, keeping the calipers parallel to the external side of the mandibular body. A table with data of other Homo specimens is provided for comparison (Table 3). Dental dimensions were measured to the nearest 0.1 mm following the methods of Flechier, Lefèvre, and Verdène (Lefèvre, 1973). This method can be identically applied to both isolated and in situ teeth. In addition, it has shown to have low intraobserver error since it employs a reference plane that can be easily identified between observers. With this technique we take a projected measure across the incisal/occlusal plane that can be easily identified between observers. With this technique we take the relevant maximum dimension of the tooth crown parallel to the occlusal plane. For this purpose, a special caliper with wide, flat, and thin tips, which allowed insertion between teeth still in situ, was used. For molars, the MD diameter is the maximum distance between the mesial and the distal faces, parallel to the occlusal surface. The reference plane for the placement of the fixed caliper tip is the mesial surface, since it is usually flatter than the distal surface. For the BL diameter of molars, we take the maximum width between the buccal and the lingual surfaces, parallel to the occlusal surface. The reference plane for this measurement is usually the lingual surface for the lower molars. Occlusal wear was scored following Molnar (1971).

The mandible ATD6-113

ATD6-113 cannot be assigned to any of the nine individuals of the TD6 hypodigm established so far (Bermúdez de Castro et al., 2006). Thus, this mandible has been attributed to a new individual of the hypodigm, identified as the Hominin 10.

Table 1

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<tr>
<td>ATD6-96</td>
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<td>ATD6-113</td>
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A With the exception of the TD6 and Dmanisian specimens, data were taken from Rosas and Bermúdez de Castro (1999). **H. rudolfensis:** KNM-ER 1483, KNM-ER 1801, KNM-ER 1802; **H. habilis:** KNM-ER 1501, KNM-ER 1805, OH 7, OH 13, OH 37; **H. ergaster:** KNM-ER 730, KNM-ER 731, KNM-ER 992, KNM-WT 15000; **East Africa middle Pleistocene:** OH 22, OH 23, OH 51, KNM-BK 67, KNM-BK 8518; **North Africa middle Pleistocene:** Tighenif 1, Tighenif 2, Tighenif 3, Sidi Abderraman; **Javanese H. erectus:** Sangiran 1B, Sangiran 5, Sangiran 6b; **Chinese H. erectus:** Zhoukoudian A1, Zhoukoudian G1, Zhoukoudian K1, Zhoukoudian H1, PAB6, Lantian, Hexian; **H. heidelbergensis:** Atapuerca II, Atapuerca XIII, Mauer, Montmaurin; **Atapuerca-SH:** AT-1, AT-2, AT-3, AT-75, AT-127, AT-250, AT-300, AT-505, AT-605, AT-607, AT-888, AT-996; **H. neanderthalensis:** Kratina J, Kratina G, Kratina H, Kratina E, Kratina D, Vindija 20, Vindija 22, Vindija 23, La Chaise, Ehringsdorf, Amud 1, Tabun 1, Tabun 2, Spy 1, La Quina 9, Regourdou, Crenece III, Hortus 4, St Césaire, Kebbara, La Ferrassie. **H. sapiens:** Modern human sample from Spitzalfields.
ATD6-113 is a fragment of the left side of the mandibular body and a part of the ramus, which retains the M\textsubscript{2} and M\textsubscript{3} in situ. The methods and techniques used to restore and preserve the TD6 human remains are presented in López-Polín et al. (2008). The preservation of the molar crowns is excellent. On the buccal side, the corpus exhibits an irregular fracture with two borders that intersect forming a vertex at the level of the P\textsubscript{4} (Fig. 3a). Lingually, the fracture is placed at the M\textsubscript{2} level (Fig. 3b). The interalveolar septa between the P\textsubscript{3}–M\textsubscript{1}, and M\textsubscript{1}–M\textsubscript{2} are missing. Only a part of the ramus is preserved and it extends upwards very close to the deepest point of the mandibular notch, but it lacks the condylar and coronoid processes, the gonial region, and most of the posterior margin. The anterior border of the ramus is also damaged, but it seems that the M\textsubscript{3} was partially covered by the ramus. The surface of the preserved bone exhibits numerous fissures and cracks with loss of cortical bone on both the buccal and lingual sides, as well as a probably circular depression 8 mm in diameter near the lateral prominence. Despite this damage some mandibular features of taxonomic interest can be observed.

Fig. 3. Mandible ATD6-113. (a) buccal aspect; (b) lingual aspect; (c) occlusal aspect.

Buccally, the lateral prominence is weakly expressed with its maximum swelling halfway between the alveolar and basal borders of the corpus. The lateral prominence is placed at the level of the talonid of the M\textsubscript{2}. The position of the lateral prominence is variable in the current Homo mandibular fossil sample and the expression of the feature is probably continuous (Table 1). A similar position for the lateral prominence is observed in some East African specimens, Tighenif, and Sangiran (1b and 8), as well as in ATD6-96. The preserved portion of the mandibular body of ATD6-113 exhibits parallel alveolar and basal borders. The marginal torus is weakly expressed and delimits a shallow intertoral sulcus. The superior lateral torus is not present, at least in the preserved portion of the corpus. Buccally, the masseteric fossa is shallow but deeper than in ATD6-96. The anteroinferior portion of this fossa is well delimited by the bulge that is formed by the prolongation of the anterior edge of the ramus and the lateral eminence of the ramus. The concavity of the superior portion of the fossa is deep and well delimited by the ectocoronoid crest and a smooth ectocondylar crest. Finally, on the lateral surface of the ramus, the vertical portion of the fossa is also deep, but only a small area is preserved.

According to the criteria of Franciscus and Trinkaus (1995: 577) and Rosas (2001: 78), no retromolar space is present in ATD6-113. Indeed, the M\textsubscript{3} appears to be partially covered by the mandibular ramus, a derived condition with regard to the genus Homo (Rosas, 2001). The postmolar trigone is well delimited by the endoalveolar crest and by a less marked buccinator crest, and is 7.5 mm long from the distal face of the M\textsubscript{3} to the vertex. The trigone exhibits a certain inclination and continues with the triangular torus and a short stretch of the endocondylar crest. Thus, ATD6-113 deviates from the primitive condition, in which the postmolar trigone is vertical (Rosas, 2001). The extramolar sulcus is narrow and measures 4.7 mm at the level of M\textsubscript{2}.

Lingually, a portion of the mylohyoid line is present, and it is defined by a step between the subalveolar plane and the subalveolar fossa. The mylohyoid line runs from the pharyngeal crest and it is placed about 9 mm from the alveolar border at the M\textsubscript{3}. The line descends about 13 mm from this border at the level of M\textsubscript{2}. From this point, the line seems to follow a subparallel trajectory to the alveolar border. The subalveolar plane is well delimited from the subalveolar fossa. The mylohyoid line runs from the pharyngeal crest and it is placed about 9 mm from the alveolar border at the M\textsubscript{3}. The line descends about 13 mm from this border at the level of M\textsubscript{2}. From this point, the line seems to follow a subparallel trajectory to the alveolar border. The subalveolar plane is well delimited from the subalveolar fossa. The mylohyoid groove is present. The angle between the mylohyoid groove and the alveolar margin is 37° (see Table 2).

Table 2 shows the measurements of the corpus of the three mandibles. If we consider the estimations made by Rosas and Bermúdez de Castro (1999) for the expectations of growth of the juvenile mandible ATD6-5, this specimen could have reached similar dimensions to those estimated for ATD6-113 and slightly greater than those of ATD6-96. So, although both sexes may be represented in the TD6 sample, the metric variability is not great.

**Dental description**

ATD6-113 retains the left M\textsubscript{2} and M\textsubscript{3}. On the M\textsubscript{2} (Fig. 4) occlusal wear has produced wide enamel facets on all cusps, but no dentine is exposed; the main fissure pattern and some secondary fissurations remain visible. Thus, M\textsubscript{2} exhibits a degree of wear of stage 3 according to Molnar’s classification. On the M\textsubscript{3} (Fig. 5) occlusal wear had just commenced (degree 2), yielding small enamel facets on the protoconid, metaconid, and the mesial marginal ridge. In
respectively). However, the M3 is the largest of the TD6 sample. Like the largest and the smallest values of the sample (Hominid 1 and 7, respectively (Table 4)), Sangiran (1B, 5, 8, and 9), Olduvai (OH 23 and 51), as well as KNM-BK 67, and especially D2600 are substantially taller than that of ATD6-113. In contrast, the thickness of the corpus at M1 in ATD6-113 clearly surpasses that of all European middle Pleistocene mandibles, with the exception of Arago XIII. It is remarkable that the thickness of the smallest mandible ATD6-96 is similar to that of the larger specimens of the Atapuerca-Sima de los Huesos mandibular sample. The height of ATD6-113 is only slightly greater than the mean value of the Sima de los Huesos sample. It is interesting to note that the measurements of the mandibular body in Chinese H. erectus mandibles are very similar to those of TD6 specimens (Carbonell et al., 2005).

Morphological comparisons and affinities

The morphology of ATD6-113 is virtually identical to that of the adult ATD6-96 specimen (Carbonell et al., 2005). Both mandibles show the same location of the lateral prominence, position of mylohyoid line in relation to the alveolar margin, relief of the pterygoid fossa, position of the plane of the postmolar trigone, relief of the masseteric fossa, depth of the posterior subalveolar fossa, and spatial relationship between the M3 and the ascending ramus. These observations suggest that both specimens belong to the same biological population, even though they were deposited at different times in the TD6 level.

To establish the affinities of the TD6 sample, we compare them below to other members of the genus Homo. The primitive pattern for the genus includes, among other features: a narrow and broadly U-shaped arcade, large size of the mandibular corpus, well-developed lateral prominence at the level of M2, no retromolar space, but a wide extramolar sulcus, and a M3 totally covert by the ramus (see Chamberlain and Wood, 1985; Tobias, 1991; Wood, 1991; Rosas and Bermúdez de Castro, 1998, 1999; Brauer and Schultz, 1996; Rosas, 2001; Antón, 2003; Kaifu et al., 2005; Suwa et al., 2007, for a discussion of these features).

A lateral prominence placed at the level of M3 is the primitive condition of Homo (see also Tobias, 1991; Rosas, 2001; Antón, 2003;
Kaifu et al., 2005; Suwa et al., 2007). Thus, ATD6-113 would be plesiomorphic for this trait, and would share it with other African and Asian early Pleistocene specimens such as OH 7, OH 13, OH 37, UR 501, and KNM-ER 992 (Table 1). Nevertheless, it is interesting to note that in the Dmanisi mandibles (D211 and D2735), as well as in some of the mandibles from Sangiran (9 and 5), and in KNM-ER 1502 the lateral prominence is placed at the M₁ or M₁–M₂ level. Furthermore, the sagittal plane of the corpus and the sagittal plane of the ramus of ATD6-113 are almost in line with one another; in contrast to what is observed in other early hominins such as those from Dmanisi (D211 and D2735), Sangiran (9 and 5), KNM-ER 1502, and OH 13. These latter specimens are characterized by a buccal position of the sagittal plane of the ramus in relation to the sagittal plane of the corpus. The anterior border of the ramus of these specimens grows anteriorly reaching a forward position and forming a conspicuous lateral prominence and a wide extramolar sulcus. This configuration is not present in the TD6 mandibles so, definitively, their architecture is derived with regard to these early specimens.

In relation to this, the M₃ is only partially covered by the ramus in the TD6 specimens, whereas in OH 7, OH 13, OH 37, D211, D2735, KNM-ER 1501, and Sangiran 9 the M₃ is totally covered, thus showing the primitive condition (Tobias, 1991; Franciscus and Trinkaus, 1995; Rosas and Bermúdez de Castro, 1998). The oblique inclination of the postmolar trigone in the TD6 mandibles is another consequence of the changes in the spatial relationship between the corpus and ramus with regard to the older Homo specimens. Furthermore, the TD6 mandibles are derived for the depth of the masseteric fossa and the posterior subalveolar fossa, as well as for the absence/presence of the alveolar prominence with regard to the African hominins included in H. habilis and H. rudolfensis, the mandibles D211 and D2735 from Dmanisi, and the oldest Sangiran specimens (early Javanese H. erectus; Rosas and Bermúdez de Castro, 1998). Interestingly, although the Zhoukoudian hominins are generally included in H. erectus as well, they exhibit a morphological pattern clearly derived with regard to that of the Sangiran hominins and, in some aspects, more derived than that of the TD6 hominins. Thus, the lateral prominence is placed at the M₂/M₃ level and the M₃ is sometimes not covered by the ramus. Furthermore, the alveolar prominence is generally absent and the alveolar plane is much less developed than in the early and middle Pleistocene African specimens. In ATD6-96 the alveolar plane exhibits a minimum inclination at the canine level (Carbonell et al., 2005).

The African Pleistocene mandibles usually included in H. ergaster (or African H. erectus) are also derived for the spatial configuration and relationship between the corpus and the ramus and associated features and, therefore, they approach the morphology of the TD6 mandibles. Nevertheless, in KGA10-1 and KNM-ER 992 the lateral prominence is well-developed and the extramolar sulcus is broad (9.0 and 8.5 mm, respectively: Suwa et al., 2007], thus suggesting that the sagittal plane of the ramus is placed in a buccal position in relation to the corpus in these mandibles. Furthermore, the African specimens preserve the primitive condition for the deepness of the masseteric fossa and have a conspicuous alveolar prominence, which contributes to an increase in the thickness of the corpus, and which is absent in the TD6 mandibles. In addition, in these African mandibles, the symphyseal condition for the depthness of the masseteric fossa and have a conspicuous alveolar prominence, which contributes to an increase in the thickness of the corpus, and which is absent in the TD6 mandibles. Furthermore, the Neandertal lineage shows a diagonal trajectory of the mylohyoid line, a medial position of the intersection between the mandibular notch and condyle, or a deeply excavated pterygoid fossa (see other traits and references in Table 4 of Rosas, 2001). Finally, the so-called horizontal-oval type mandibular foramen has been considered as a very frequent trait (46.2%) of Neandertals (Smith, 2005). Both the ATD6-96 and ATD6-113 specimens show the V-shaped morphology of this foramen not the horizontal oval.

Metrically, it is difficult to establish a clear differentiation between the TD6 sample and other groups. Nevertheless, the corpus height and thickness of the African specimens attributed to H. rudolfensis, most East African middle Pleistocene specimens, the Sangiran mandibles, and Dmanisi D2600 are much greater than those of the TD6 mandibles. The same applies for the corpus height of the North African middle Pleistocene mandibles from Tighenif and Sidi Abderraman which is considerably greater than that of the TD6 mandibles.

It is noteworthy that, with the exception of the Arago XIII specimen, the thickness of ATD6-113 is greater than that of all European middle Pleistocene specimens and the Neandertals. The height of ATD6-113, however, is in the range of variability of these hominins. Chinese H. erectus mandibles resemble the TD6 sample in their low height and moderate width, with comparable values for both measurements.

Overall, the new evidence represented by the ATD6-113 specimen confirms previous observations in other TD6 mandibles, and helps to deepen the understanding of the phylogenetic position of the TD6 hominins. These hominins seem to represent a European lineage different from other African and Asian lineages (Bermúdez de Castro et al., 1997), although some similarities are noteworthy between the TD6 and Chinese middle Pleistocene mandibles (Carbonell et al., 2005). The TD6 mandibular evidence does not provide data in favor of the continuity in Europe between this early Pleistocene lineage and the Neanderthal lineage. Nevertheless, the dental evidence seems to support this continuity (Gómez-Robles et al., 2007; Martínón-Torres et al., 2006, 2007) and this matter will be the subject of future studies.

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