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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 archaeological 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 (m^2), a survey that preceded the excavation of a larger area of about 80 m^2 (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 I16, I17, 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

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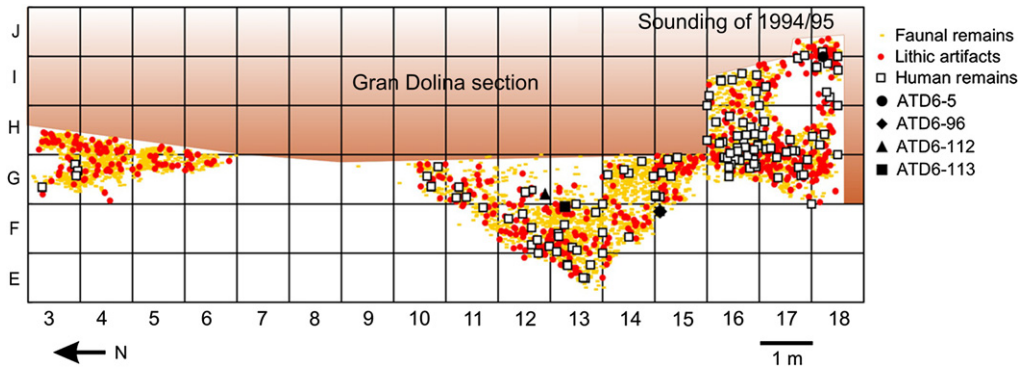

Fig. 1. Schematic plan of the TD6 level from south (squares E18 to J18) to north (squares E3 to J3), showing the situation (in projection) of the elements recovered in different field seasons. The test pit (south area) was excavated in 1994–95, whereas the excavations of the middle and north areas are in progress. The black square between G13 and F13 corresponds to the human mandible ATD6-113. Note that the mandible ATD6-112 was recovered from the upper layers of TD6, about 30 cm over the ATD6-113 specimen. The mandible ATD-96 come from the Jordi layer, and was recovered about 40 cm under the ATD6-113 specimen (see Fig. 2).

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 (Parés 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 m^2 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.

Litostratigraphy of TD6

Figure 2 shows the top sequence of unit TD6 at the level of the middle area (Squares G14 and G15: see Fig. 1). In this sector of the Gran Dolina section, a total of six well differentiated layers, which we have named "Aurora archaeostratigraphic set" (AAS), correlates with the Aurora Stratum defined in 1995 in the southern area. In other words, Aurora represents a condensed deposit of at least six layers, which could not be distinguished in the test pit made in 1994–95 because of the lateral variation of the sediments. All six layers contain either artifacts or hominin remains.

On top of TD6, a water channel is represented by some thin layers of gravel that are intercalated between thin clay and silt layers. A fragment of an infant mandible (ATD6-112) was recovered from the channel in 2006. The mandible is strongly cemented with matrix, and the delicate process of restoring is currently in

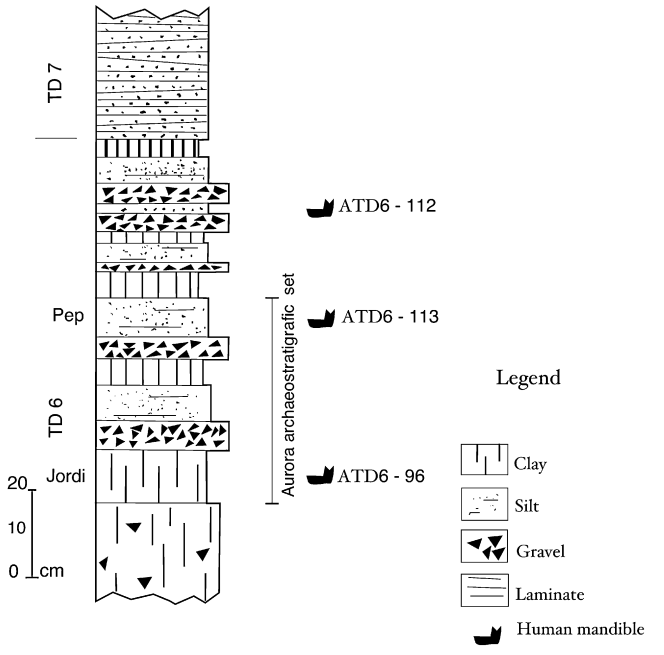

Fig. 2. Upper sequence of the lithostratigraphic unit TD6 from the Gran Dolina cave infilling (Matuyama Chron), which includes the "Aurora archaeostratigraphic set" (AAS). This sequence corresponds to the middle area of the Gran Dolina section, and the observations were made at the level of squares G14 and G15 (see text for additional information).

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 Kaifu et al. (2005), and Suwa et al. (2007).

Thickness of the mandibular body was measured at the M_1 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 M_1 only an estimate of the thickness at the level of this tooth is possible. Height of the mandibular body at the M_1 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, Lefêvre, and Verdéne (Lefêvre, 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 in both isolated and in situ teeth. Placing the fixed caliper tip on the reference plane 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).

Table 1
Horizontal position of the lateral prominence of the mandible in Pleistocene hominins

Distal M1	M1/M2	Mesial M2	Mid-M2	Distal M2	M2/M3	M3
Sangiran 9	UR 501	501[a]	OH 13	1805[a]	730[a]	Mauer
	D 211	1802[a]	OH 37	3734[a]	3734[a]	Arago 2
	D 2735	Sangiran 22	992[a]	OH 22	BK 67	Arago 89
	1502[a]		8518[a]	OH 37	KGA10-1	AT-1
	Sangiran 5		Tighenif 1	Tighenif 2	D 2600	AT-75
	Bk 7905			Sangiran 1b	Tighenif 3	AT-250
	Sangiran 6b			Sangiran 8	ZHD G1	AT-300
				ATD6-96	ZHD H1	AT-301
				ATD6-113	ZHD K1	AT-605
					Arago 13	AT-888
					AT-172	AT-950
					AT-505	
					AT-2193	

[a] KNM-ER.

Table 2
Corpus measurements of the TD6 mandibles

	ATD6-5[a]		ATD6-96		ATD6-113	
	Thickness	Height	Thickness	Height	Thickness	Height
Corpus at M1	16.3	26.7	16.6	28.5	19.0[b]	31.0[2]
Corpus at LP	–	–	18.6	27.5	20.0	32.0
Postmolar trigone	–		7.0		7.5	
Extramolar sulcus	–		6.0		4.7	
Angle between the mylohyoid groove and the alveolar margin	35		42		37	

[a] ATD6-5 is a juvenile individual. The M3 crown is completed, but the roots are at an early stage of formation. Rosas and Bermúdez de Castro (1999) have estimated an increase of about 3 mm for the corpus height, and between 1 and 3 mm for the corpus thickness in this individual, if she/he would have reached the time of M3 eruption.
[b] Estimated value.

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 3
Thickness and height of the corpus (mean and standard deviation) in some *Homo* samples and individual specimens[a]

Specimen/sample	Thickness	Height
ATD6-5	16.3	26.7
ATD6-96	16.6	28.5
ATD6-113	**19.0**	**31.0**
H. rudolfensis	23.1 ± 3.2	37.1 ± 2.8
H. habilis	19.7 ± 2.3	29.3 ± 2.2
H. ergaster	19.3 ± 0.4	28.4 ± 3.3
East Africa middle Pleistocene	20.1 ± 1.7	32.0 ± 2.8
North Africa middle Pleistocene	18.0 ± 1.1	35.8 ± 1.5
Dmanisi 211	18.5	25.0
Dmanisi 2600	22.0	42.0
Javanese *H. erectus*	19.8 ± 2.6	36.3 ± 1.1
Chinese *H. erectus*	16.5 ± 1.8	28.6 ± 3.3
H. heidelbergensis	17.9 ± 2.5	32.2 ± 2.6
Atapuerca-SH	15.6 ± 1.1	29.4 ± 3.4
H. neanderthalensis	15.3 ± 1.7	32.1 ± 3.3
H. sapiens	10.8 ± 1.2	28.0 ± 2.4

[a] With the excepcion of the TD6 and Dmanisi 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 8, Sangiran 9 (mandible C); **Chinese *H. erectus***: Zhoukoudian A, Zhoukoudian G, Zhoukoudian K, Zhoukoudian H, PA86, Lantian, Hexian; ***H. heidelbergensis***: Arago II, Arago XIII, Mauer, Montmaurin; **Atapuerca-SH**: AT-1, AT-2, AT-3, AT-75, AT-172, AT-250, AT-300, AT-505, AT-605, AT-607, AT-888, AT-950; ***H. neanderthalensis***: Krapina J, Krapina G, Krapina H, Krapina E, Krapina D, Vindija 20, Vindija 22, Vindija 23, La Chaise, Ehringsdorf, Amud 1, Tabun 1, Tabun 2, Spy 1, La Quina 9, Regourdou, Circeo III, Hortus 4, St Cesaire, Kebara, La Ferrassie. ***H. sapiens***: Modern human sample from Spitalfields.

Preservation

ATD6-113 is a fragment of the left side of the mandibular body and a part of the ramus, which retains the M_2 and M_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_4 (Fig. 3a). Lingually, the fracture is placed at the M_2 level (Fig. 3b). The interalveolar septa between the P_4–M_1, and M_1–M_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_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.

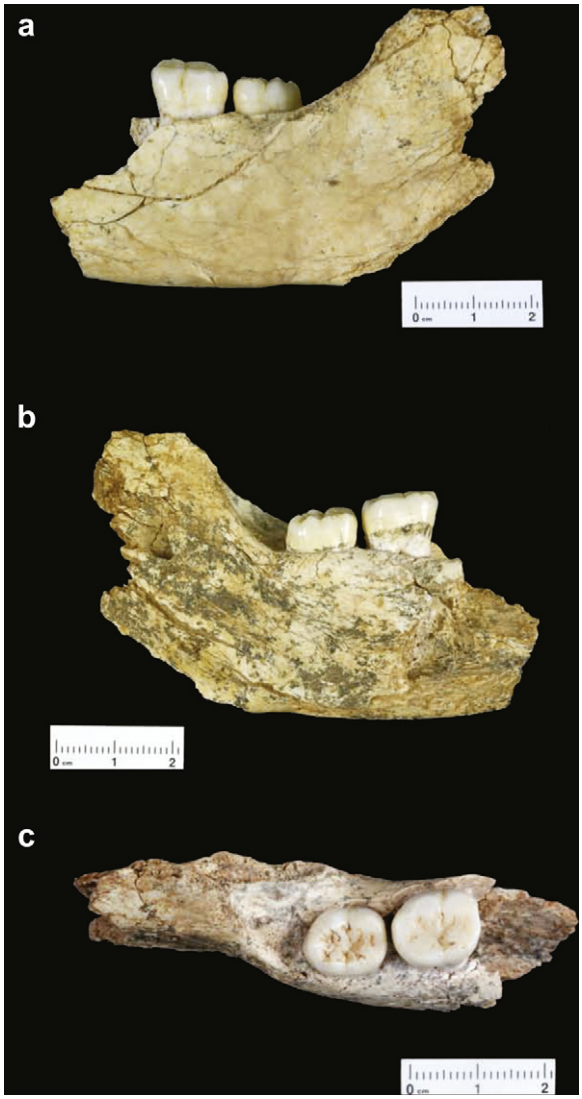

Fig. 3. Mandible ATD6-113. (a) buccal aspect; (b) lingual aspect; (c) occlusal aspect.

Mandibular description

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_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_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_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_3.

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_3. The line descends about 13 mm from this border at the level of M_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 pterygoid fossa is shallow, thus preserving the primitive condition for *Homo* (Rosas, 2001). A part of the sulcus colli is preserved. The sulcus is 8.4 mm wide and constitutes a strong depression on the internal face of the ascending ramus, where opens the conspicuous hollow of the dental channel. The mandibular foramen is V shaped. Partial bony bridging of 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_2 and M_3. On the M_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_2 exhibits a degree of wear of stage 3 according to Molnar's classification. On the M_3 (Fig. 5) occlusal wear had just commenced (degree 2), yielding small enamel facets on the protoconid, metaconid, and the mesial marginal ridge. In

Fig. 4. Detail of the occlusal face of the M_2 of ATD6-113.

this tooth, a complicated system of crenulations and secondary fissuration is present.

The M_2 exhibits five major cusps arranged in a Y-pattern. The hypoconulid occupies a distobuccal position. Occlusal wear obscures the presence or absence of the C6, although the distal bifurcation of the central fissure may indicate a C6. A deep, short linear anterior fovea is present. A mesial trigonid crest is expressed but interrupted by the central fissure. Also, a slight distal trigonid crest can be identified involving the protoconid. The mesiodistal (MD) and bucolingual diameters of the M_2 are 13.0 mm and 11.6 mm, respectively (Table 4).

The M_3 also exhibits five main cusps arranged in a Y-pattern. In this tooth, the hypoconulid occupies a more distal than buccal location. A small C7, but no C6, is present. As in the M_2, a deep, short linear anterior fovea, an interrupted mesial trigonid crest, and a slight distal trigonid crest can be identified. The secondary fissuration differentiates two small cuspules between the entoconid and the hypoconulid at the distobuccal corner of the crown. The M_3 MD is 12.1 mm and the M3 BL is 10.4 (Table 4).

The dimensions of the ATD6-113 M_2 fall within the variation of the TD6 sample, with diameters that are intermediate between the largest and the smallest values of the sample (Hominid 1 and 7, respectively). However, the M_3 is the largest of the TD6 sample. Like other TD6 individuals, ATD6-113 shows a $M_2 > M_3$ size sequence.

Age and sex

The M_3 of ATD6-113 is fully erupted and exhibits slight occlusal wear at the level of the protoconid and metaconid that only affects the enamel. Thus, this mandible probably corresponds to a young adult. The sex estimation of ATD6-113 can be made in the context of the current TD6 mandibular sample. Although there is no growth model for the TD6 hominins, and in particular for the TD6 mandibles, Rosas and Bermúdez de Castro (1999) estimated the adult

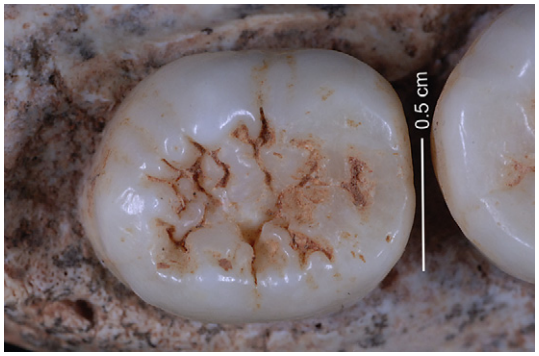

Fig. 5. Detail of the occlusal face of the M_3 of ATD6-113.

Table 4
Dental dimensions (mm) of the Gran Dolina-TD6 hominins. Hominins: H1 (ATD6-5 mandible and isolated teeth), H7 (ATD6-96 mandible), and H10 (ATD6-113 mandible). MD: mesiodistal; BL: buccolingual

	R/L	I2	R/L	C	R/L	P3	R/L	P4	R/L	M1	R/L	M2	R/L	M3
	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
H1	7.0	7.8	8.1	10.0	8.8	10.6	8.2	10.2	12.2	11.8	13.5	12.0		
H7					8.0	9.9	7.6	9.4	10.5	11.0	12.3	11.0	9.2	8.8
H10											13.0	11.6	12.1	10.4

height and thickness of the mandibular body of the ATD6-5 juvenile specimen using an ontogenetic series of African apes and modern humans. This estimate suggests that ATD6-5 would have reached similar dimensions as ATD6-113, and the two have similarly large teeth. Judging by the large size difference between the teeth of ATD6-5 (Hominin 1) and ATD6-113 (Hominin 10) on one hand, and ATD6-96 (Hominin 7) on the other hand (Table 4), we can assume that the Hominins 1 and 10 are probably males, whereas Hominin 7 may be a female. The dimensions of the upper canine of Hominid 1 are at the upper limit of the range of variation for the genus *Homo* (Bermúdez de Castro et al., 1999), which supports the sex estimate of this immature individual.

Comparative metric analysis

The thickness and height of the corpus at M_1 of ATD6-113 are low in comparison with the specimens attributed to *H. rudolfensis* (Table 3). Furthermore, specimens like those from Tighennif (1, 2, and 3), 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 M_1 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 M_3 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 M_2, no retromolar space, but a wide extramolar sulcus, and a M_3 totally covert by the ramus (see Chamberlain and Wood, 1985; Tobias, 1991; Wood, 1991; Rosas and Bermúdez de Castro, 1998, 1999; Bräuer 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 M_2 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 M_1 or M_1–M_2 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 M_3 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 M_3 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 M_2/M_3 level and the M_3 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 sagital 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 region is thick, and the alveolar planum is strongly inclined (KNM-ER 992, KGA10-1, OH 22).

It is noteworthy that none of the mandibular features considered apomorphic in the European middle and early upper Pleistocene hominins (the Neanderthal lineage) are present in the TD6 mandibles. For instance, in the Neandertal lineage the mental foramen and the lateral prominence occupy a posterior position, and there is a conspicuous retromolar space between the anterior border of the ramus and the distal end of M_3. 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; Martinón-Torres et al., 2006, 2007) and this matter will be the subject of future studies.

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