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COMPARATIVE ANALYSIS OF THE GRAN DOLINA-TD6 (SPAIN) AND TIGHENNIF (ALGERIA) HOMININ MANDIBLES

ANALYSE COMPARÉE DES MANDIBULES D'HOMINIDÉS DE TIGHENNIF (ALGÉRIE) ET DE GRAN-DOLINA-TD6 (ESPAGNE)

José María Bermúdez de Castro [1], María Martinón-Torres [1], Aida Gómez-Robles [1], Leyre Prado [1], Susana Sarmiento [1]

Abstract

We present a comparative study of the Tighennif (Algeria) and Gran Dolina-TD6 (Spain) hominin mandibles, which represent two geographically near and contemporaneous populations separated by the Mediterranean sea, in order to test the hypothesis that these populations belong to the same evolutionary lineage, as it has been suggested by some authors. The Tighennif mandibles show a clear primitive structural pattern, derived in some features with regard to the oldest *Homo* specimens from *H. habilis*, as well as from the Javanese *H. erectus*. In addition, the Tighennif specimens share all these derived features with *H. ergaster* and, some of them, with *H. antecessor*. However, the Gran Dolina-TD6 specimens are remarkably smaller than those of Tighennif, and lack the robustness which characterizes the African Pleistocene mandibles. The main difference between both groups in terms of mandibular dimensions can be related to the higher corpus height characteristic of Tighennif specimens. The dental evidence reveals that North African Middle Pleistocene populations are morphologically closer to African Early Pleistocene populations than to TD6 fossils. We conclude that the Spanish and Algerian hominins belong to different hominin lineages. The Tighennif hominins, together with other contemporaneous (Thomas Quarry and Oulad Hamida 1), and perhaps later North African specimens (Sidi Abderrahaman, Salé, and Rabat [Kebitat]) should be considered as a subspecies of the *H. ergaster* species*, i.e. H. ergaster mauritanicus*, and may be the result of an evolution in isolation in this African area. In agreement with the mandibular and dental evidences, the Gran Dolina-TD6 hominins could belong to an exclusive Eurasian lineage.

Keywords: Early Pleistocene, North Africa, Europe, hominins, mandibles.

Résumé

Nous présentons une analyse comparée des mandibules des hominidés de Tighennif (Algérie) et de la Gran Dolina-TD6 (Espagne), qui représentent deux populations proches dans l'espace et le temps mais séparées par la mer Méditerranée, afin de vérifier l'hypothèse que les deux échantillons appartiennent au même lignage évolutif, comme certains auteurs l'ont

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suggéré. Les mandibules de Tighennif ont un pattern *morphologique structurel primitif, avec certains caractères dérivés par rapport à ceux des spécimens de* H. habilis *et de* H. erectus *de Java. Les mandibules de Tighennif partagent tous ces caractères dérivés avec* H. ergaster *et quelques uns avec* H. antecessor. *Néanmoins, les spécimens de la Gran Dolina-TD6 sont remarquablement plus petits que ceux de Tighennif, et sont moins robustes que les mandibules du Pléistocène d'Afrique. La principale différence entre les deux échantillons, en ce qui concerne les dimensions mandibulaires, est la grande hauteur du corps de la mandibule des spécimens de Tighennif. Les caractères dentaires révèlent que les populations du Pléistocène moyen du Nord de l'Afrique sont, du point de vue morphologique, plus proches des hominidés du Pléistocène inférieur de l'Afrique que de ceux de la Gran Dolina-TD6. Nous concluons donc que les hominidés de Tighennif et de la Gran Dolina-TD6 appartiennent à deux lignées différentes. Les hominidés de Tighennif pourraient être réunis avec les spécimens contemporains de Thomas Quarry et de Oulad Hamida 1, et peut-être avec d'autres plus tardifs comme ceux de Sidi Abderrahaman, Salé, et Rabat [Kebitat] du Nord de l'Afrique dans une même sous-espèce de* H. ergaster, i.e. H. ergaster mauritanicus*, qui serait le résultat d'une évolution locale en isolement relatif dans cette région de l'Afrique. Les hominidés de la Gran Dolina-TD6 appartiennent à une lignée exclusive de l'Eurasie, conformément aux données dentaires et mandibulaires.*

Mots-clés : *Pléistocene inférieur, Nord de l'Afrique, Europe, hominidés, mandibules*.

Version abrégée

Dans ce travail, nous présentons une comparaison métrique et morphologique entre deux échantillons de mandibules fossiles : Tighennif (Algérie) et Gran Dolina-TD6 (Espagne), qui sont proches dans l'espace et le temps, mais séparées par la mer Méditerranée. Le gisement de Tighennif est bien connu par la découverte de trois mandibules complètes, ainsi que par un os pariétal et quelques dents isolées. Tous ces fossiles humains, associés à plusieurs centaines de fossiles de mammifères et à des outillages lithiques inclus dans l'Oldowayen et l'Acheuléen (Arambourg 1954a, b), représentent les hominidés les plus anciens du Nord de l'Afrique, avec une chronologie de ca. 700 000 ans (Geraads *et al*. 1986).

Le niveau TD6 du gisement de la grotte de la Gran Dolina, située dans la Sierra d'Atapuerca, a livré plus d'une centaine de fossiles humains associés avec des mammifères fossiles et des outils lithiques de tradition oldowayenne (Carbonell *et al.* 1995). Cet ensemble, localisé sous l'inversion Matuyama/Bruhnes, est daté de ca. 800 000 ans B.P. (Parés, Pérez-González 1995, 1999 ; Falguères *et al.* 1999). L'échantillon de fossiles humains inclut trois fragments de mandibule bien conservés.

Originellement, les hominidés de Tighennif furent inclus dans l'espèce *Atlanthropus mauritanicus* par Arambourg (1954a) et postérieurement attribués à l'espèce *Homo erectus* par Le Gros Clark (1964). Les hominidés de la Gran Dolina-TD6 ont été inclus dans l'espèce *H. antecessor* (Bermúdez de Castro *et al.* 1997). Certains auteurs ont considéré la possibilité de rassembler les deux échantillons dans la même espèce : *H. mauritanicus* (Hublin 2001 ; Stringer 2003). Cependant, ces auteurs n'ont pas présenté une étude formelle pour défendre leur alternative. Par conséquent, l'objectif de ce travail est de tester l'hypothèse que les hominidés de Tighennif et de la Gran Dolina-TD6 représentent une même lignée évolutive sur les deux bords de la mer Méditerranée.

Nos résultats indiquent que les mandibules de Tighennif ont un *pattern* morphologique structurel primitif, dont certains caractères sont dérivés par rapport à ceux de *H. habilis* et des spécimens de *H. erectus* de Java. Les mandibules de Tighennif partagent tous ces caractères avec *H. ergaster* et quelques-uns avec *H. antecessor*. Néanmoins, les spécimens de la Gran Dolina-TD6 sont remarquablement plus petits que ceux de Tighennif, et sont moins robustes que les mandibules du Pléistocène d'Afrique. La principale différence entre les deux échantillons, en ce qui concerne les dimensions mandibulaires, est la grande hauteur du corps de la mandibule des spécimens de Tighennif. Les caractères dentaires révèlent que les populations du Pléistocène moyen du Nord de l'Afrique sont, du point de vue morphologique, plus proches des hominidés du Pléistocène inférieur de l'Afrique que de ceux de la Gran Dolina-TD6 (Martinón-Torres *et al*. 2007).

À partir de ce travail, nous concluons donc que les hominidés de Tighennif et de la Gran Dolina-TD6 appartiennent à deux lignées différentes. Les hominidés de Tighennif pourraient être réunis avec les spécimens contemporains de Thomas Quarry et de Oulad Hamida 1 et peut-être avec d'autres plus tardifs comme ceux de Sidi Abderrahaman, Salé, et Rabat [Kebitat] du Nord de l'Afrique dans une même sous-espèce de *H. ergaster*, *i.e. H. ergaster mauritanicus*, qui serait le résultat d'une évolution locale en isolement relatif dans cette région de l'Afrique. Les hominidés de la Gran Dolina-TD6 appartiennent à un groupe exclusif de l'Eurasie, d'après la morphologie mandibulaire et dentaire.

INTRODUCTION

The sand pit of Tighennif (formerly Ternifine) is located in the village of Palikao, 22 km east from Mascara in Algeria. Excavations during the 1950s in the Middle Pleistocene sandy sediments of an ancient small lake basin yielded thousands of mammal fossils, as well as Oldowan and Acheulean stone tools (Arambourg 1954a, b). The Tighennif site is particularly known by the finding of three well preserved mandibles, some isolated teeth and one parietal bone, which represent the oldest fossil hominins recovered so far from northwest Africa. The lithic assemblage can be included in the Acheulean technological complex and consists of choppers, chopping tools, polyhedrical spheroids, trihedrons, cores, retouched pieces, large and small flakes, hand axes and cleavers. The artefacts are made of quartzite, sandstone, limestone, and flint (Sahnouni, Derradji in press)

According to the paleontological and paleomagnetic data, the age of Tighennif has been estimated to be ca. 700 kyrs at the early Middle Pleistocene (Geraads *et al*. 1986). Paleomagnetic studies made on the lower deposits indicated normal polarity, and thus they may be correlated with the Brunnhes Chron. However, Sahnouni and Derradji (in press) do not rule out the correlation with the Jaramillo Subchron. These authors have pointed out the similarities between the Tighennif and Thomas Quarry 1 (level L) sites concerning the macro-mammals and lithic assemblage. The age of the last site has been recently estimated to be ca. 989 kyrs (Rhodes *et al*. 2006).

The Tighennif human fossil remains were originally classified as *Atlanthropus mauritanicus* by Arambourg (1954b) together with other remains such as those from Rabat (Thomas, Vallois 1977). These hominins were also later included into *Homo erectus* (Le Gros Clark 1964), a denomination that is nowadays preferred by some authors *to* include *other* North African human fossils such as those from Thomas Quarry and Sidi Abderrahaman (Rightmire 1990). Alternatively, other researchers have preferred to use the denomination *H. mauritanicus* (Hublin 2001; Stringer 2003). Furthermore, Hublin (2001) and Stringer (2003) have considered that the human fossils recovered from Aurora Stratum of the level TD6 in the Gran Dolina site of the Sierra de Atapuerca (Carbonell *et al.* 1995) could be also included in *H. mauritanicus* (considering the priority of the name assigned by Arambourg). However, these authors have not presented a formal study to test their hypothesis.

The cave of Gran Dolina (TD) in the Railway Trench of the Sierra de Atapuerca (northern Spain) contains an 18 meters high section formed by a succession of eleven levels, probably deposited from the late Early Pleistocene to the end of the Middle Pleistocene (Parés and Perez-González 1999). The lowermost stratigraphic levels, TD1 and TD2, contain sediments of interior facies typical of a closed cave. The paleontological record (pollen and faunal remains) is continuous from TD3 to TD11 (except TD9), and some levels (TD4, 5, 6, 7, 10, and 11) contain abundant stone tools. During the 1994-96 field seasons, near one hundred human fossils were found together with more than one thousand macrovertebrate fossil remains, as well as 268 lithic artefacts included in the Mode 1 Technology (= Oldowan tradition) (Carbonell *et al*. 1995). The human remains were later included in a new *Homo* species, *H. antecessor,* considered as possible last common ancestor to Neanderthals and modern humans lineages (Bermúdez de Castro *et al*. 1997). These fossils have been firmly dated to the late Early Pleistocene (Parés, Pérez González 1995, 1999; Falguères *et al*. 1999). During the 2003 to 2006 field seasons new findings have significantly enlarged the hominin fossil hypodigm of *H. antecessor* (Carbonell *et al*. 2005). The TD6 human assemblage now includes three mandibular remains and a large dental sample**.**

Although the information is obviously limited, we have the possibility of comparing dental and mandibular evidence from two near and almost contemporaneous Pleistocene populations separated by the Gibraltar Strait. The aim of this report is therefore to make a comparative study of the mandibles and teeth recovered from the two sites in order to make possible inferences about the phylogenetic story of the hominins represented in the Tighennif and Gran Dolina-TD human fossil samples.

THE TD6 AND TIGHENNIF SPECIMENS

Figures 1 and 2 show the three Tighennif mandibles. In Tighennif 1 both the left and right ramus are damaged and some features of this region are not available. Both the right and left P3-P4 and M1-M3 series are *in situ*, as well as the root and a part of the crown of the lateral incisors. Tighennif 2 consists of the left half of a well preserved mandible (including the symphysis) that preserves the P3-P4 and M1-M3 series *in situ*. The most complete mandible is Tighennif 3, which preserves the right I2, C, P3, P4, M1, M2, and M3, and the left P4, M1, M2, and M3 *in situ*. The three specimens belong to adult individuals.

The TD6 human assemblage includes three mandibular specimens: ATD6-5 is a fragment of the right side of the mandibular body of a juvenile specimen, with M1, M2, and M3 *in situ*, the latter still enclosed in its alveolus (figure in Rosas, Bermúdez de Castro 1999).

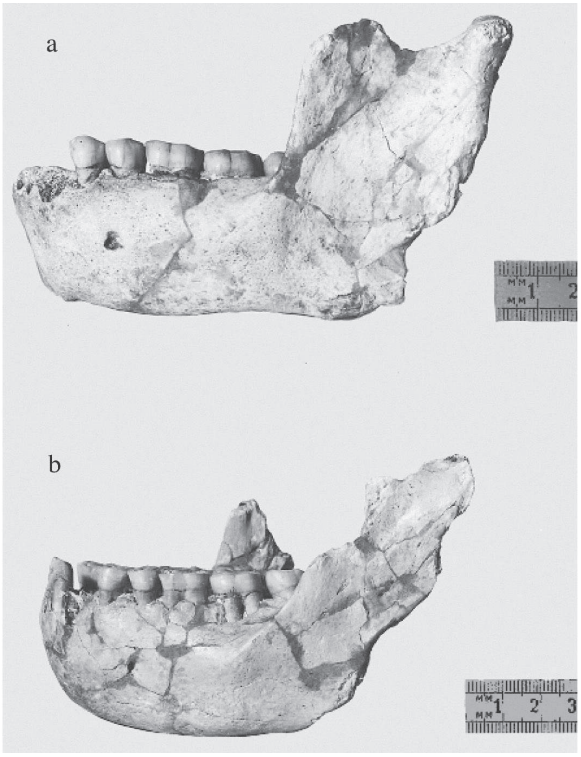

Fig. 1a—Tighennif 1; b—Tighennif 2. The photographs on the originals of Tighennif mandibles were obtained by Marcel Bovis in 1954 and donated to Emiliano Aguirre by Camille Arambourg.

Fig. 1a - Tighennif 1 ; b - Tighennif 2. Les photographies des originaux des mandibules de Tighennif ont été obtenues par Marcel Bovis en 1954 et offertes à Emiliano Aguirre par Camille Arambourg.

Fig. 2—Left lateral view of Tighennif 3.

Fig. 2 - Vue latérale gauche de Tighennif 3.

Fig. 3a—Lateral view of ATD6-96; b—medial view of ATD6-96.

Fig. 3a - Vue latérale de ATD6-96 ; b - vue médiale de ATD6-96.

This specimen, as well as some isolated maxillary and mandibular teeth, belongs to Hominid 1 (the holotype of *H. antecessor*). ATD6-96 (Hominid 7) is the left half of a small and gracile mandible of an adult individual with the premolars and molars in place (*fig. 3*) (Carbonell *et al.* 2005). The third specimen, ATD6-113 (Hominid 10) is a

fragment of the left side of the mandibular body with a part of the ramus, which preserves the M2 and M3 *in situ* and it was found in the 2006 excavation season. The third molar is fully erupted and exhibits slight occlusal wear at the level of the protoconid and metaconid that only affects the enamel. Thus, this mandible may correspond to a young adult. The increased TD6 human hypodigm allow us now to do a proper comparison with the Tighennif specimens.

METHODS

For comparative purposes, a large number of fossil *Homo* mandibles and teeth were included in our study (*tables I, II, III*). Observations and data were recorded on the following original fossil samples: Atapuerca-Sima de los Huesos, Arago, Atapuerca-TD6, Tighennif, Sangiran, and Dmanisi, as well as on some high-quality casts. We have grouped the specimens into different species in accordance with the criteria of different authors (*e.g.* Wood 1992; Schwartz, Tattersall 1999 ; Tattersall 2000). Thus, we have differentiated taxonomically the Early Pleistocene East African hominins (*H. ergaster*) from the Asian Pleistocene hominins (*H. erectus*). Furthermore, we have distinguished between the Chinese and Javanese *H. erectus* because, according to different authors, they show some regional and temporal variations (Rightmire 1990; Grimaud-Hervé *et al.* 2000; Antón 2002; Babá *et al.* 2003). The species *H. heidelbergensis* includes the European Middle Pleistocene hominins, according to the criteria expressed by Arsuaga *et al.* (1999) (but see also an alternative opinion in Rightmire 1996). The Dmanisi mandibles were not included in a particular species because their taxonomic status are a current disputed matter among the specialists (*e.g.* Gabunia,Vekua 1995; Rosas, Bermúdez de Castro 1998; Gabunia *et al.* 2002; Rightmire *et al.* 2005).

Features and data of several mandibular specimens were confirmed or obtained from tables 5, 6, and 7 of Rosas (2001) and table 2 of Rosas and Bermúdez de Castro (1999). Our methodological approach is cladistic and the description, definition and evaluation of the status (primitive or derived) of the mandibular features (*table IV*) are taken from Rosas (2001). Thickness of the mandibular body was measured at the M1 and at lateral prominence location (*tables II, III*). In both cases, the measurement was taken between the external side of the mandibular body and the most prominent point of the internal side. Height of the mandibular body was taken between the basal and the alveolar borders, keeping the callipers parallel to the external side of the mandibular body**.** A scatter biplot is provided in order to illustrate the variability of the mandibular corpus robustness (the corpus width at M1 level divided by the corpus height at the same level) against the corpus height. In the D211 Dmanisi mandible we had to do an estimation of the corpus height since the corpus base is broken at the M1 level. The slope of the regression line, the correlation coefficient and the p-value of the regression was calculated for those groups with a sample size large enough to obtain the parameters: *H. ergaster*, *H. erectus*, *H. heidelbergensis* and *H. neanderthalensis*.

The mesiodistal (MD) and buccolingual (BL) dimensions were obtained in the TD6 and Tighennif teeth, according to the technique quoted in Bermúdez de Castro (1993).

COMPARATIVE ANALYSIS

The mandibles

As it has been previously pointed out, the Tighennif mandibles are extremely massive and robust (Howell 1960; Arambourg, Hoffstetter 1963), whereas the TD6 specimens are particularly gracile. Nevertheless, before comparing the dimensions of the TD6 mandibles with those of Tighennif it is necessary to consider the possible effect of sexual dimorphism in the specimens size. Judging by the remarkable size difference between the teeth of Hominid 1 (ATD6-5) and Hominid 10 (ATD6-113) from TD6 on one hand, and Hominid 7 (ATD6-96) on the other hand (*table I*), we can assume that the Hominid 1 and 10 are probably males, whereas Hominid 7 would be female. The dimensions of the upper canine of Hominid 1 are at the upper limit of the variation range of the genus *Homo*, which supports the sex status of this immature individual. Thus, we think that males and females are present at least in the TD6 sample. Interestingly, the thickness and height of the ATD6-113 mandible (the largest of the Gran Dolina-TD6 sample) are similar to those of Tighennif 2 (the smallest of the North African sample) (*table II*).

The thickness and height of the mandibular body of the Tighennif mandibles are similar to those of *H. erectus* from Java, whereas the same variables of the TD6 specimens are similar to those of the *H. erectus* from China (*table III)*. The ramus breadth of the ATD6-96 mandible (40.6 mm) is lower than those of Tighennif 2 (45.8 mm)

and Tighennif 3 (47.3 mm). The height of the ramus in ATD6-96 is 60 mm, whereas in Tighennif 2 and 3 this measurement is 78.5 and 85.6, respectively. According to Howell (1960), the total length and bicondylar dimensions of Tighennif 3 exceed those of the Mauer mandible.

								Gran Dolina-TD6					
		Tighennif 1		Tighennif 2		Tighennif 3		H 1		H 7		H 10	
Side	Tooth	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
R	12					(5.6)	7.3						
L	12							7.0	7.8				
R	C					7.8	10.3						
L	C							8.1	10.0				
R	P3	8.5	10.2			8.8	10.2	8.8	10.6				
L	P3	8.4	10.1	8.7	11.2					8.0	9.9		
R	P4	8.4	10.2			8.2	10.2	8.2	10.2				
L	P4	8.4	10.0	9.2	11.4	7.7	10.2			7.6	9.4		
R	M1	13.2	12.6			12.4	12.0	12.2	11.8				
L	M1	12.9	12.3	14.0	13.0	12.4	12.2			10.5	11.0		
R	M2	13.00	13.2			12.6	12.0	13.5	12.0				
L	M2	13.2	13.2	14.0	13.6	12.6	12.2			12.3	11.0	13.1	11.4
R	M3	12.4	12.2			12.3	11.5						
L	M3	12.4	12.2	13.2	12.7	12.0	11.0			9.2	8.8	12.5	10.6

Isolated teeth from Tighennif			
R	Lower I1	-	6.7
R	Lower I2	7.1	7.0
L	Lower C	9.0	10.0
L	Upper dm1	8.3	9.8
L	Upper dm2	10.3	11.7
R	Upper M1-M2	12.0	14.5

Table I—Dental dimensions (mm) of the Tighennif and Gran Dolina-TD6 mandibles and isolated teeth. H: Hominids 1 (ATD6-5 mandible and isolated teeth), 7 (ATD6-96 mandible) and 10 (ATD6-113 mandible) from TD6. MD: mesiodistal; BL: buccolingual.

Tabl. I - Dimensions (mm) des dents isolées et des dents en place des mandibules de Tighennif et Gran Dolina-TD6. H: Hominidés 1 (mandibule ATD6-5 et dents isolées), 7 (mandibule ATD6-96), et 10 (mandibule ATD6-113) de la Gran Dolina-TD6. MD: mésio-distal ; BL : bucco-lingual.

	Tighennif 1		Tighennif 2		Tighennif 3		ATD6-5		ATD6-96		ATD6-113	
	T	H	T	H	T	H	T	H	T	H	T	H
Corpus at M1	19.8	36.2	16.6	33.4	19.5	37.0	16.3	26.7	16.6	28.5	19.0*	31.0*
Corpus at LP	23.2	37.5	22.2	31.2	23.7	36.0	–	–	18.6	27.5	20.0	32.0
Ramus breadth	–		45.8		47.3		–		40.6		–	
Ramus height	–		78.5		85.6		–		60.0		–	
Symphysis height	36.0		33.3		37.5		–		–		–	

Table II—Measurements (mm) of the Tighennif and Gran Dolina-TD6 mandibles. T: thickness; H: height.

Tabl. II - Mesures (mm) des mandibules de Tighennif et de la Gran Dolina-TD6. T : épaisseur ; H : hauteur.

Species	Thickness, mm (n)	Height, mm (n)	Robustness (n)
Homo habilis	19.7 ± 2.3 (5)	29.3 ± 2.2 (4)	64.5 ± 5.3 (4)
H. ergaster#	19.8 ± 1.4 (8)	31.2 ± 2.8 (8)	63.8 ± 5.0 (8)
H. erectus (Java)*	21.3 ± 3.9 (5)	38.8 ± 5.3 (5)	54.9 ± 5.8 (5)
H. erectus (China)**	16.5 ± 1.8 (7)	28.6 ± 3.3 (7)	58.0 ± 5.6 (7)
Tighennif	18.6 (3)	35.5 (3)	52.4 (3)
Sidi Abderraman	17.0	35.8	47.5
H. antecessor	17.3 (3)	28.7 (3)	60.2 (3)
H. heidelbergensis+	16.4 ± 1.7 (16)	30.8 ± 3.4 (16)	53.4 ± 5.1 (16)
H. neanderthalensis++	15.3 ± 1.7 (21)	32.1 ± 3.3 (21)	47.9 ± 5.1 (21)

Data are given as means ± SD

This sample 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.

* This sample includes the Sangiran mandibles 1B, 5, 8, and 9.

** This sample includes the mandibles from Zhoukoudian, Lantian, Hexian, and PA86.

+ This sample includes the Arago, Atapuerca-Sima de los Huesos, Mauer and Montmaurin specimens (see Rosas, Bermúdez de Castro 1999).

++ See Rosas and Bermúdez de Castro (1999) for the composition of this sample.

Table III—Measurements of the mandibular body at the level of M1 in some Homo *species and specimens.*

Tabl. III - Mesures du corps mandibulaire (épaisseur, hauteur et robustesse) au niveau de la première molaire (M1) chez quelques espèces et spécimens du genre Homo.

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)	Coverted	Partially coverted	Uncovered
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	Flat	–
10 - Gonion profile	Expanded	Regular	Truncated
11 - Position of condyle in relation to mandibular notch	Lateral	Medial	–
12 - Posterior subalveolar fossa	Shallow	Moderately hollowed	Deep
13 - Alveolar prominence	Present	Absent	–

Table IV—State of the mandibular features analyzed in table V [partially modified (features and scores) from Rosas (2001)].

Tabl. IV - État des caractéristiques mandibulaires analysées dans le tableau V [modifié partiellement (caractéristiques et état) d'après Rosas (2001)].

Figure 4 shows a clear relationship between increasing robusticity and decreasing corpus height in Pleistocene hominin mandibles. The plot shows two pairs of regression lines clearly differentiated. The lowest two lines correspond to *H. neanderthalensis* and *H. heidelbergensis*, although they do not show especially high correlation coefficients (0.264 and 0.318, respectively). These lines are almost superimposed, with a slope of -0.744 (p-value = 0.020) and a constant of 71.87 for *H. neanderthalensis* and a slope of -0.835 (p-value = 0.023) and a constant of 79.15 for *H. heidelbergensis*. The upper lines correspond to *H. erectus* and *H. ergaster* but, although they are superimposed, the line corresponding to *H. erectus* is not significant (p-value = 0.301) due to the presence of outliers such as Sangiran 6. However, *H. ergaster* line presents a significant regression model (p-value = 0.003), with a correlation coefficient of 0.735.

The slopes of the regression lines are almost the same for all the groups analyzed, but the lines corresponding to the more primitive groups are above the ones corresponding to later species, such as *H. heidelbergensis* and *H. neanderthalensis*. This could imply that in more recent groups, a given corpus width tends to be related to a lower corpus height, whereas the same corpus width would correspond to a higher height in more primitive groups.

Regarding to the species analyzed in this study, we can observe that Tighennif and Sidi Abderraman specimens are located nearby the *H. ergaster* regression line (they

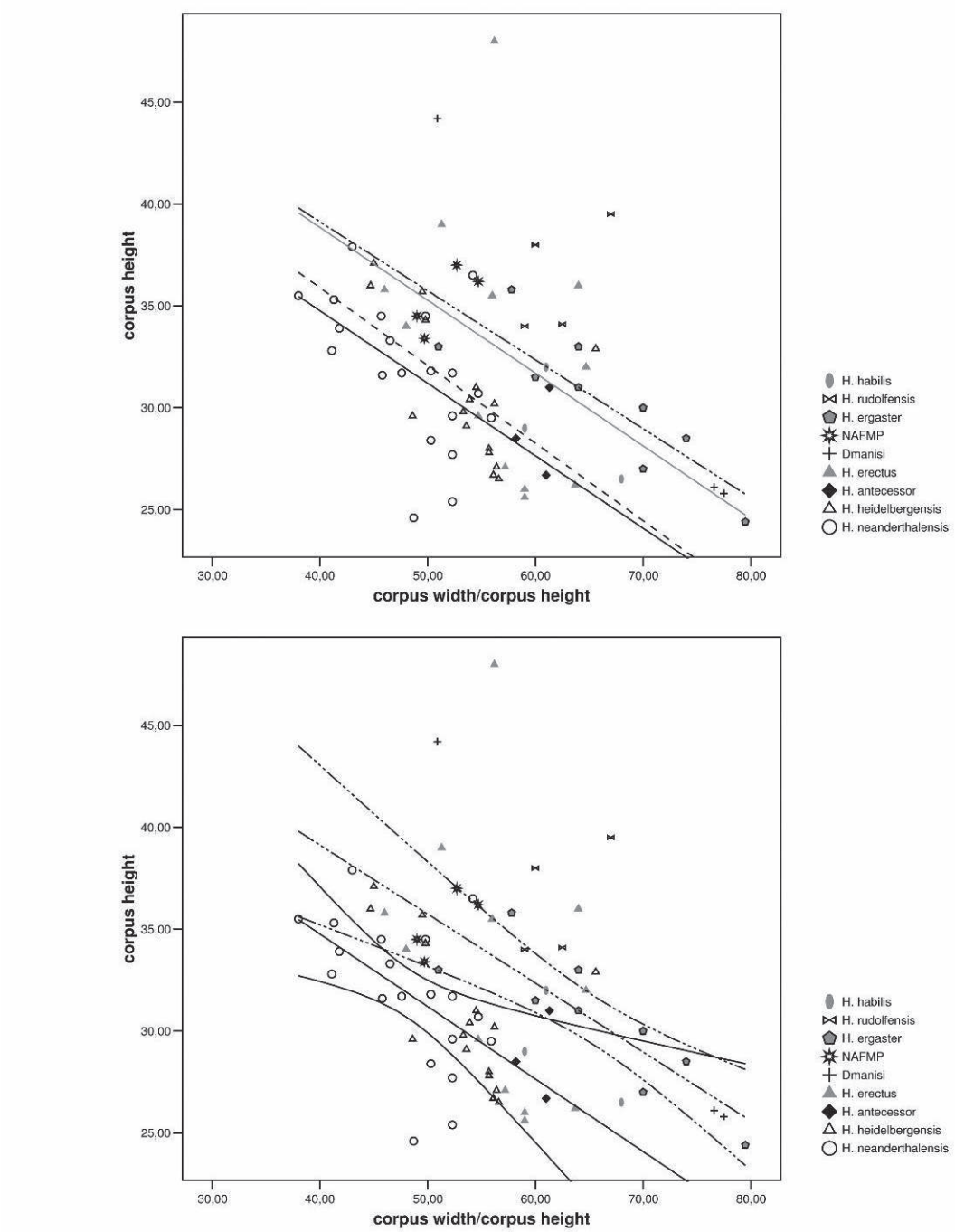

Fig. 4—Robusticity index versus *mandibular height. A. Regression line for* H. ergaster, H. erectus, H. heidelbergensis *and* H. neanderthalensis*. B. Confidence intervals at 95% for* H. ergaster *and* H. neanderthalensis. *It is important to note the position of Tighennif and Gran Dolina-TD6 in the plot (see text for explanation), as well as the big difference in the corpus index/corpus height ratio between D 2600 and both D 211 and D 2735 Dmanisi mandibles, as it was previously noticed (Skinner* et al. *2006; Bermúdez de Castro* et al. *submitted). D 2735 is located over* H. ergaster *line, whereas D 211 is located on the* H. neanderthalensis *line. Both individuals, however, display low corpus height compared with their corpus width, whereas D 2600 is out of the main point cloud due to its elevated corpus height. NAFMP: North Africa Middle Pleistocene fossils (Tighennif and Thomas Quarry).*

Fig. 4 - Graphique qui met en rapport l'indice de robustesse et la hauteur du corps mandibulaire. A. Ligne de régression pour H. ergaster, H. erectus*,* H. heidelbergensis *et* H. neanderthalensis*. B. Intervalles de confiance à 95 % pour* H. ergaster *et* H. neanderthalensis*. Notez la position des spécimens de Tighennif et de la Gran Dolina-TD6 dans le graphique (voir le texte pour une explication détaillée) ainsi que la grande différence entre D 2600, d'une part, et D 211 et D 2735 d'autre part, comme l'ont signalé d'autres auteurs (Skinner* et al. *2006 ; Bermúdez de Castro* et al. *soumis). D 2735 est placé au-dessus de la ligne de* H. ergaster*, tandis que D 211 est placé sur la ligne de* H. neanderthalensis*. Ces deux spécimens de Dmanisi présentent cependant une grande épaisseur du corps mandibulaire par rapport à la hauteur, tandis que D 2600 se situe à l'écart, du fait de la grande hauteur de son corps mandibulaire. NAFMP : fossiles du Pléistocène moyen du Nord de l'Afrique (Tighennif et Thomas Quarry).*

all are included in the mean confidence interval at the 95% for this regression model, as it is showed in *fig. 4*). Nevertheless, Gran Dolina individuals are mainly located close to the *H. neanderthalensis* line with the exception of the ATD6-78 specimen that lies closer to the *H. ergaster* line but still close to the limit of the *H. neanderthalensis* interval of confidence (*fig. 4*).

Concerning morphological features, the main mental foramen is placed at the P3-P4 level in the three Tighennif specimens, a primitive feature shared with *H. habilis, H. ergaster, H. erectus, H. antecessor*, and the Dmanisi mandibles (D 211, D 2735, and D 2600) (*table V*). In Tighennif 3 the right side exhibits two additional foramina at the P4-M1 level, whereas in the left side three secondary foramina at the P4 and P4-M1 level are also present. Multiple foramina are common in early specimens like Mauer, ATD6-96 or in the totality of the Zhoukoudian sample (Tobias 1991). The anterior marginal tubercle is well marked (especially in the right side) and placed at the P3-P4 level in Tighennif 1. It is also marked in Tighennif 2 and placed at the P4 level, just behind the main foramen. In Tighennif 3, this tubercle is not well differentiated from the prominent marginal torus, which starts at the P3 level and ends up at the lateral prominence level. The Tighennif specimens are also plesiomorphic for this feature, if we consider that the first appearance of this trait (anterior marginal tubercle at the C-P3 level) occurs in some early *Homo* specimens, such as OH 37, KNM-ER 1802, or D 211 (Rosas, Bermúdez de Castro 1998). A minor difference between these specimens and the Tighennif mandibles is that the anterior marginal tubercle is placed in a slightly backward position in the North Africa specimens. Interestingly, the specimen ATD6-96 from Gran Dolina lacks anterior marginal tubercle and thus, it differs from the Tighennif mandibles. The lateral prominence is marked in Tighennif 1 and 2, and rather less

	Homo							
Mandibular features	*habilis*	*ergaster*	*erectus (Java)*	*erectus (China)*	*Tighennif*	*antecessor*	*heidel-bergensis*	*neander-thalensis*
1	A	A, B	A	A, B	A	A	B, C	C
2	A, O	A, O	A	A, O	A	O	A, B, C	A, B, C
3	A	C	A	B	A, B	A	C	C
4	A	A, B	A, B	B, C	B	B	B, C	C
5	A	A, B	A, B	A, B	B	B	B, C	C
6	A, B	A, B	A, B	A	A	A	A	A, B, C
7	A	A, B	A	A	A, B	A	A, B, C	B, C
8	A	A, B, C	A	A	A, B	B	A, B, C	B, C
9	-	A	A	A	A	A	A, B	B
10	-	A, B	-	A, B	A, B	B	B, C	B, C
11	-	A	-	A	A	A	A, B	B
12	A	A	A	C	B	B	B, C	C
13	A	A	A	A, B	A	B	A, B	B

Table V—State of the mandibular features listed in table IV in different Homo *species and groups.*

Tabl. V - État des caractéristiques mandibulaires numérotées dans le tableau IV chez différentes espèces et groupes du genre Homo.

pronounced in Tighennif 3. In Tighennif 1 it is advanced and located at the M2 level, like in the TD6 specimens. In Tighennif 2 and Tighennif 3 the lateral prominence is placed at the M2 and M2-M3 level, respectively. Again, this feature is primitive in this mandibular sample and shared with the Early Pleistocene European and African *Homo* species as well as with Asian *H. erectus* (*table V*). In the Dmanisi specimens, D 211 and D 2735, the lateral prominence is advanced and placed at the M1-M2 level, whereas in D 2600 it is located at the M2-M3 level.

As it is seen in norma lateralis, the M3 is partially covered by the ramus in Tighennif 1, Tighennif 2, and the left side of Tighennif 3. In the last specimen, the M3 is almost visible in norma lateralis. The primitive status in *Homo* for this feature is a M3 totally covered by the ascending ramus, as it happens in KNM-ER 1501, OH 13, OH 37, OH 7, KNM-WT 15000, KNM-BK 8518, or in D 2735. Thus, the Tighennif mandibles exhibit a first derived state that also appears in *H. ergaster* and the Eurasian Early and Middle Pleistocene specimens, including the TD6 specimens (*table V*), although in these cases no retromolar space is present. The trigonum postmolare is oblique in the three Tighennif mandibles, although in Tighennif 1 this area tends to be more horizontal. However, we cannot affirm that this specimen shares this trait with the Neanderthals and Atapuerca-Sima de los Huesos mandibular sample, where a broad and horizontal retromolar space is well developed as a true apomorphic feature. The length of the trigonum postmolare is about 7.0 mm in Tighennif 1, less than 5.0 mm in Tighennif 2 and between 8.0 and 9.0 mm in Tighennif 3. In ATD6-96 the trigonum postmolare measures 7.0 mm, whereas in ATD6-113 the value is 7.2. According to Rosas (2001) this would be the primitive condition observed in *Homo*.

The medial aspect of the Tighennif mandibles approaches that of *H. ergaster* (KNM-ER 992, KNM-WT 15000, KNM-ER 730), and *H. erectus* from Java. At the M3 level, the mylohyoid line is 14.4, 11.4, and 16.0 mm below the alveolar margin in Tighennif 1, 2, and 3, respectively. Furthermore, the mylohyoid line is subparallel (Tighennif 1 and 2) and almost parallel to the alveolar border in Tighennif 3. In both the mylohyoid orientation and position, the Tighennif specimens preserve the primitive status, shared with most *Homo* species, except *H. neanderthalensis*, the Atapuerca-Sima de los Huesos hominins (*table V)* and surprisingly, the D 2600 mandible from Dmanisi. The subalveolar fossa in both the Tighennif and TD6 mandibles is moderately hollowed, thus deviating from the primitive condition (shallow or practically absent subalveolar fossa) observed in *H. habilis, H. ergaster,* and *H. erectus* from Java (*table V*). The alveolar prominence is well developed in the Tighennif mandibles as in other African Early and Middle Pleistocene specimens and thus, it diverges from the derived condition (no sign of alveolar prominence) observed for instance in *H. antecessor* and the Eurasian Pleistocene specimens. In the TD6 mandibles, the mylohyoid groove forms a small angle with the alveolar margin: 35º in ATD6-5, 42º in ATD6-96 and 37º in ATD6-113. The mylohyoid groove is more vertical and the angle substantially higher in the Tighennif specimens: 67º in Tighennif 2, and 60º in Tighennif 3. It is noteworthy to mention that in this trait, TD6 fossils show the lowest values recorded for the genus *Homo* (Rosas, Bermúdez de Castro 1999), with the exception of KNM-ER 820 and KNM-WT 15000 that, however, are juveniles. Thus, with regard to this feature, the Gran Dolina specimens are clearly dissimilar to the African Middle Pleistocene mandibles.

In early *Homo* specimens, the posterior symphyseal surface is characterized by a strong superior transverse torus and an extremely inclined alveolar planum. This is the case for *H. habilis* (OH 13, OH 37), and KNM-ER 1805, or the Dmanisi specimens, but also for some *H. ergaster* mandibles (KNM-BK 8518, and OH 22). This shelf-like structure is less pronounced in African and Asian Middle Pleistocene hominins, as well as in Javanese *H. erectus* (Sangiran 1, 5, 8, and 22: Kaifu *et al*. 2005). Tobias (1991: p. 329) estimated the angle between the alveolar planum and the dental alveolar plane to quantify this feature. According to Tobias estimations, the value of this angle is 22º in OH 13, 25º in OH 37, whereas in Tighennif 1, 2, and 3 the values are 43º, 36º, and 48º, respectively. In ATD6-96, the only TD6 specimen in which it is possible to measure this angle, the value is 60º and thus, in this trait, the Gran Dolina-TD6 specimens would be more derived than those from Tighennif.

In the Tighennif mandibles the relief of the masseteric fossa is relatively excavated as in most Pleistocene hominins, whereas the relief of the pterigoyd fossa is shallow. In both features, the Tighennif specimens do not deviate from the primitive condition observed in the genus *Homo*. Likewise, the Tighennif specimens retain the primitive condition for the position of the condyle in relation to mandibular notch. In fact, the crest defining the mandibular notch meets the condyloid process in the lateral part of the articular surface instead in the medial part, which is the derived condition observed in

Neanderthals. The gonion profile is expanded or regular in the Tighennif mandibles and regular in ATD6-96.

The shape of the alveolar arcade of the Tighennif 1 and 3 tends to be parabolic, whereas the Plio-Pleistocene East African specimens (*e.g.* OH 13, OH 37, or KNM-ER 1802), as well as the Dmanisi mandibles show a more narrow U-shaped arcade, with the canines located at the corners (Rosas, Bermúdez de Castro 1998; Kaifu *et al.* 2005). The length/width index of the alveolar arcade (infradental ID-M3 distance/bi-molar M3-M3 distance), which gives an objective measure of this shape, is lower than 100 in the Tighennif specimens and greater than 100 in OH 13, KNM-ER 1805, KNM-ER 992, KNM-BK 8518, and in the three Dmanisi mandibles. According to Kaifu *et al.* (2005), the KNM-BK 67 is considerably distorted and the alveolar arcade of this specimen may be wider than we have previously estimated (Rosas, Bermúdez de Castro 1998). In the Javanese *H. erectus* Kaifu *et al.* (2005) obtain an index of 110 for Sangiran 9, and 108 for Sangiran 22, whereas in Chinese *H. erectus*, the values are lower: 92-83 in Lantian, and 88 in Zhoukoudian H1. A photographic restoration of the ATD6-96 mandible (see Carbonell *et al.* 2005) provides an index value of the alveolar arcade of about 100. Despite it is an estimation, it is clear that shape of the alveolar arcade in the Gran Dolina specimen is gently pointed, and the P3 is not aligned with the anterior dentition, as it is characteristic of Neanderthals.

The shape of the ramus in Tighennif 2 resembles that of ATD6-96. However, Tighennif 3 shows a particular ramus shape, with an extremely pronounced height, a prominent and massive coronoid process that exceeds the condyle in height, and with the deepest point of the notch being close to the condylar process. In ATD6-96 the coronoid process and condyle show a symmetrical appearance, and the deepest point of the mandibular notch is approximately equidistant to both processes.

Teeth

In a previous paper (Bermúdez de Castro *et al.* 1999) we observed some similarities between the teeth of the Hominid 1 from TD6 and the teeth of the Tighennif 3 specimen. With an enlarged sample, we can now see that the teeth of the TD6 Hominids 1 and 10 are large and comparable in size to those of Tighennif 1 and 3, although somewhat smaller than that of Tighennif 2 (*table I*). However, and taking into account that the sexual dimorphism factor can be reasonably discounted for size differences between samples, we see that the teeth of Hominid 7 are small and out of the variability of the Tighennif sample.

In addition, in a multivariate study of the dental measurements of I2-M2 using a shape distance and a principal component analysis of some *Homo* specimens, we observed certain proximity between the TD6 Hominid 1 and Tighennif 3 (Bermúdez de Castro *et al.* 1999). In general, dental proportions of these specimens are comparable (*table I*) and these observations have been precisely used by some authors to conclude that the two hominin samples may belong to a same species (Hublin 2001; Stringer 2003).

Recent and detailed dental studies have shed light to this matter concluding that the similarities between TD6 and Tighennif hominins are primitive for the genus *Homo* and that the fossils from Gran Dolina are more derived in some traits than the fossils from North African Middle Pleistocene (Martinón-Torres 2006; Martinón-Torres *et al.* 2006). In particular, North African Middle Pleistocene hominins show the same dental plesiomorphies and apomorphies as *H. ergaster* species (Martinón-Torres *et al.* 2007). Table VI summarizes some of the dental morphological traits that are relevant for comparison. Tighennif and Gran Dolina-TD6 fossils share some primitive dental traits like the expression of a buccal cingulum in lower canines and premolars and the shape of their lower P3s. In these groups, lower P3s are strongly assymetrical with an oblique maximum bucco-lingual diameter with regard to the mesio-distal diameter. These specimens display a wide talonid that comprises a distolingual and a distobuccal component. Preliminary geometric morphometric exploration of lower P3s shape (Martinón-Torres 2006) reveals that Tighennif and TD6 P3s share the same morphospace than the African Pliocene hominins. However, this conformation would be primitive for the genus *Homo* and, therefore, of restricted utility for taxonomical and phylogenetic assessment. In contrast, TD6 lower P4s show a transformation with respect to earlier hominins like *H. habilis, H. ergaster, H. erectus*, and the Dmanisi and Thigennif specimens. In contrast to a large and expanded occlusal polygon typical of primitive specimens, the occlusal polygon of TD6-Gran Dolina lower P4s undergoes a reduction and occupies a peripheral position with regard to the external outline (Martinón-Torres *et al.* 2006). Although this tooth class keeps some primitive traits such as the assymetrical contour and the development of accessory lingual cusps,

Feature	NAFMP	TD6
Shovel shape I2mx 0: classic shovel shape 1: triangular shovel shape	0	1
Form of Cmx 0: flared, "talonid"-like marginal ridges, 1: incisor-like	0	0
Cingulum in Mx C and Pm 0: present 1: absent	0	0
Form of M1mx 0: squared outline, distance between lingual cusps < or = than between buccal cusps 1: rhomboidal outline with protruding hypocone and distance between lingual cusps > than between buccal	0	1
M1mx/M2mx 0: M1 < M2, 1: M1 > M2	0	0
Form of P3md 0: strongly assymetrical and conspicuous talonid 1: symmetrical or moderately symmetrical	0	0
Form of P4md 0: assymetrical with expanded occlusal polygon 1: assymetrical with reduced occlusal polygon	0	1
Transverse crest in P4md 0: commonly absent 1: frequently present	0	0 and 1
Buccal talonid in P4md 0: present, 1: absent	0	1
Mid-trigonid crest in M1 and/orM2 0: frequently absent, 1: present	0	1
M1md/M2md sequence 0: M1 < M2,1: M1 ≥ M2	0*	0
M2md/M3md sequence 0: M2 < M3, 1: M2 ≥ M3	1	1

NAFMP: North African Middle Pleistocene populations

For the size sequence of molar series we calculated crown computed area (CCA). We consider that Xi = Xj if CCA Xi/CCA Xj is > 0.96 and < 1.04.

*Rabat is M1 > M2

Table VI—Comparative summary of some dental morphological traits in North African Middle Pleistocene and Gran Dolina-TD6 hominins.

Tabl. VI - Résumé comparatif de quelques traits morphologiques dentaires chez les hominidés du Pléistocène moyen d'Afrique du Nord et de la Gran Dolina-TD6.

TD6 hominins, Middle Pleistocene populations from Europe and *H. neanderthalensis* have lost the buccal component of the talonid that characterizes the hominin species from the Pliocene and the Early Pleistocene from Africa and Asia. This buccal component of the talonid is so conspicuous in Tighennif specimens that is delimitated in the occlusal contour of the teeth by a characteristic buccal indentation (*fig. 5*). This conformation suggests that, despite belonging to the early Middle Pleistocene, Tighennif fossils would have kept the primitive state whereas the Early Pleistocene TD6 fossils would have started a different evolutionary path.

Fig. 5—P3 to M3 occlusal view of ATD6-96 (a) and Tighennif 2 (b). Note the primitive aspect of P3s in both specimens and the differences between P4s morphology. In Tighennif, the arrow head points the buccal delimitation of the buccal component of the talonid that TD6 fossils have lost (see text for explanation). Note also the size difference between the two mandibles.

Fig. 5 - Vue occlusale de ATD6-96 (P3-M3) (a) et Tighennif 3 (P3-M3) (b). Notez l'aspect primitif des P3 chez les deux spécimens et la différence morphologique entre les P4. Chez Tighennif, la flèche montre la délimitation buccale du talonide, qui est absente sur les fossiles de la Gran Dolina-TD6. Notez aussi la différence de taille entre les deux mandibules.

Although no upper dental remains were recovered from the Tighennif site, we can make some inferences by comparing TD6 fossils with the Rabat specimen, since it has been also assigned to the same group as the Thigennif mandibles (Thomas, Vallois 1977). Rabat specimen shows a classic shovel shape that despite being pronounced does not display the incipient *triangular shovel shape* described in *H. antecessor* and *H. erectus* (Martinón-Torres 2006; Martinón-Torres *et al.* 2007). In these groups, the enlarged marginal ridges define a deep and narrow longitudinal lingual fossa that gives to the occlusal view a characteristic triangular shape (Martinón-Torres *et al.* in press). This conformation will be more pronounced in the European Middle Pleistocene populations and *H. neanderthalensis*, becoming the typical condition in these groups (Martinón-Torres 2006; Martinón-Torres *et al.* 2007). Similarly, Rabat upper first molars keeps the primitive shape for the genus *Homo* with a quadrangular outline and expanded occlusal polygon whereas TD6 fossils present a rhomboidal contour with relative distal displacement of the lingual cusps and the protrusion in the external outline of a bulging hypocone (Gómez-Robles *et al.* in press).

DISCUSSION AND CONCLUDING REMARKS

The earliest evidence of hominins in the Maghreb is the Ain Hanech site in Algeria, which could date back to the Olduvai subchron (1.770-1.950 kyrs), according to the faunal remains and the paleomagnetic data (Sahnouni 1998; Sahnouni, Heinzelin (de) 1998; Sahnouni *et al.* 2002; Sahnouni, Derradji in press; but see also Geraads *et al.* 2004). The Ain Hanech site has yielded a lithic assemblage of Oldowan technology similar to those recovered from Olduvai Bed I and Lower Bed II and Koobi Fora (Sahnouni *et al.* 2002). In Morocco, the oldest lithic assemblage comes from the late Early Pleistocene deposits of unit L of the Thomas Quarry 1 site, dated of circa 1.0 Ma (Raynal *et al.* 2001; Rhodes *et al.* 2006). The lithic assemblage consists of Acheulean artefacts made of quartzite and flint.

Although it may be possible to recognize some small differences between early and late populations (Sahnouni, Derradji in press), the North African human occupation may have been continuous during the entire Early and Middle Pleistocene. During the Middle Pleistocene, hominins who were able to manufacture the Acheulean technology occupied a relatively narrow fringe between the Mediterranean coast and the Sahara desert. The later would have operated as a geographic barrier during cold and arid events (Demenocal 1995) for the genetic contact between the Maghreb and the African tropical populations. These isolation periods may have produced

local endemism and genetic drift, leading to the formation of particular paleodemes (in the sense of Howell 1999) or subspecies in this African region.

The possible genetic contact between these paleodemes and the southern European hominids across the Gibraltar Strait should not be discarded during warm and cold events, when the distance between Africa and Europe diminished to 6.5 km (Alimen 1975; Giles-Pacheco, Santiago Pérez 1987; Arribas, Palmqvist 2002; Finlayson 2002). These authors use either the archaeological or the paleontological evidence for their suggestions. However, direct paleoanthropological comparative data for the late Lower-early Middle Pleistocene was not available until now.

In the present study we have observed that the Tighennif and Gran Dolina-TD6 mandibles share some plesiomorphic traits for the genus *Homo* (features 1, 3, 6, 7, 9, and 11 in *table IV*). From the cladistic point of view, these traits are not useful for taxonomical purposes. Furthermore, certain lengthening of the mandibular corpus produces in the Tighennif mandibles the appearance of a short and inclined retromolar area and that their reduced M3s are not totally hidden by the ramus, as seen in norma lateralis (traits 4 and 5 in *table IV*). The Tighennif mandibles share this derived structural pattern with *H. erectus, H. ergaster,* and *H. antecessor*. The absence of alveolar prominence (feature 13 in *table IV*) in the Gran Dolina specimens clearly separates this hominin sample from the northwest African group. Furthermore, ATD6-96 does not exhibit the strong backwards inclination of this surface and the markedly developed alveolar plane that is present in the Tighennif specimens. Likewise, the development of the superior transverse torus (Tighennif 3) is absent in ATD6-96. The shape of the ramus in Tighennif 3 is also completely different from that of ATD6-96, especially with regard to the incisura semilunaris profiles, which is almost symmetrical in ATD6-96, whereas in Tighennif 3 it exhibits an absolutely high coronoid process compared with the condylar height.

On the other hand, the Gran Dolina specimens are remarkably smaller than those of Tighennif, and lack the robustness which characterizes the African Pleistocene mandibles. The scatter biplot of the robustness index against the corpus height shows that primitive specimens tend to possess higher corpus for a given corpus width than later groups (*fig. 4*). In this graph it can be also observed that Tighennif specimens, as well as Sidi Abderraman one, display this trend of having very high corpus height in relation to their corpus width. Two out of the three *H. antecessor* studied specimens follow the trend of more recent groups by displaying low mandibles in relation to their width. Thus, the main difference between both groups in terms of mandibular dimensions can be related to the higher corpus height characteristic of Tighennif individuals.

The dental evidence reveals that North African Middle Pleistocene populations are morphologically closer to *H. ergaster* populations than to *H. antecessor* groups (Martinón-Torres 2006; Martinón-Torres *et al.* 2007). Although some similitude can be found between Tighennif and TD6 teeth, those features are plesiomorphic for the genus *Homo* and therefore, of limited discriminative power for taxonomical and phylogenetic purposes. However, despite their primitive morphology, *H. antecessor* teeth show some dental specializations more typical of the Pleistocene Eurasian populations that would be ratifying different evolutionary stories (Martinón-Torres *et al.* 2007). These features would be in accordance with a previous work that stated a possible Asian origin for the Gran Dolina TD6 populations (Carbonell *et al.* 2005). Compared to the African Pleistocene species from *H. habilis* to North African Middle Pleistocene populations, anterior dentitions of the hominin groups found in the Eurasian continent are generally characterized by higher frequencies of the most pronounced grades of *mass additive* traits (term by Irish 1988), such as shovel shape, cingular derivates, mesial canine ridge and strong labial convexity (Martinón-Torres 2006; Martinón-Torres *et al.* 2007). This pattern could be the morphological translation of the tendency to the relative expansion of the anterior dentition ascertained in the Middle Pleistocene populations (Wolpoff 1971). This trend will reach its maximum expression with European Middle Pleistocene and *H. neanderthalensis* populations although its expression as well as incipient degrees of triangular shovel shape or the particular conformation of their upper first molars can be traced back in *H. erectus* (for the triangular shovel shape) and *H. antecessor* populations (for both traits) (Martinón-Torres *et al.* in press). Interestingly, Tighennif populations, despite belonging to the Middle Pleistocene, are out of this trend. Furthermore, posterior dentitions in the fossil populations of the Eurasian Pleistocene (*H. erectus*, *H. antecessor*, *H. heidelbergensis* and *H. neanderthalensis*) show some qualitative traits derived from dentognathic reduction processes particularly pronounced in later *Homo* populations (Kaifu *et al.* 2005; Martinón-Torres 2006;

Martinón-Torres *et al*. 2007). Among those traits we can find the lower P4s morphology which highlights different evolutionary trends between Tighennif and TD6 populations.

In this report, it has been described a mandibular and dental "gigantism" in North African Pleistocene populations with dimensions that overpass contemporaneous populations from the European Middle Pleistocene (Bermúdez de Castro *et al*. 1997; Bermúdez de Castro, Rosas 1998) and even *H. erectus* (see Kaifu *et al*. 2005). It has been also stated that Middle Pleistocene fossils from North Africa may represent a morphological divergence of this part of the continent (Hublin 1989). The persistence of a marked macrodontism in the North African series could be the result of a regional evolutionary continuity or the adaptation of some local conditions (Hublin 1989). In our opinion, this particular combination of primitive traits with a relative "gigantism" with respect to other contemporaneous populations suggest that the North African group could be the result of an evolution in isolation of an *H. ergaster* subpopulation.

From all these evidences we consider that the Tighennif hominins, together with other contemporaneous (Thomas Quarry and Oulad Hamida 1), and perhaps later North African specimens (Sidi Abderrahaman, Salé, and Rabat [Kebitat]) belong to a hominin lineage, independent from the European lineage which include the Gran Dolina-TD6 hominins. For those who are prepared to accept that the African Early Pleistocene hominins (*H. ergaster*) and the Asian Early Pleistocene hominins (*H. erectus*) should be included in different species, and considering authoritative opinions of some workers (*e.g*. Wood 1992; Klein 1999; Schwartz, Tattersall 1999; Tattersall 2000) as well as our evolutionary study of the dental hominin evidence (Martinón-Torres 2006; Martinón-Torres *et al*. 2007), we suggest that *H. ergaster mauritanicus* is a reasonably taxonomical option for this Maghrebian group.

Finally, since the Italian Ceprano calvaria belongs to the same chronological age range than the TD6 hominins (see Manzi 2004), it would be also interesting to make a comparative study between this specimen and the cranial remains from Tighennif.

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