



ELSEVIER

Contents lists available at ScienceDirect

## Comptes Rendus Palevol

www.sciencedirect.com



Human palaeontology and prehistory

## Talonid crests expression at the enamel–dentine junction of hominin lower permanent and deciduous molars



*Expression des crêtes du talonide à la limite émail–dentine de molaires inférieures permanentes et caduques chez les Homininés*

María Martinón-Torres<sup>a,\*</sup>, Marina Martínez de Pinillos<sup>a</sup>,  
Matthew M. Skinner<sup>b,c</sup>, Laura Martín-Francés<sup>a</sup>, Ana Gracia-Téllez<sup>d,e</sup>,  
Ignacio Martínez<sup>d,e</sup>, Juan Luis Arsuaga<sup>e</sup>, José María Bermúdez de Castro<sup>a</sup>

<sup>a</sup> National Research Center on Human Evolution (CENIEH), Paseo Sierra de Atapuerca s/n, 09002, Burgos, Spain

<sup>b</sup> Department of Anthropology, University College London, 14, Taviston Street, London, WC1H 0BW, United Kingdom

<sup>c</sup> Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103, Germany

<sup>d</sup> Centro Mixto UCM-ISCIII de Evolución y Comportamiento Humanos, Avd. Monforte de Lemos 5, Pabellón 14, 28029, Madrid, Spain

<sup>e</sup> Área de Paleontología, Departamento de Geología, Universidad de Alcalá de Henares, 28871, Alcalá de Henares, Spain

## ARTICLE INFO

## Article history:

Received 7 October 2013

Accepted after revision 11 December 2013

Available online 22 February 2014

## Keywords:

Microcomputed tomography

Enamel–dentine junction

Sima de los Huesos

Atapuerca

Spain

## Mots clés :

Microtomographie informatisée

Jonction émail–dentine

Sima de los Huesos

Atapuerca

Espagne

## ABSTRACT

The application of microtomography (mCT) to dental morphological studies has unveiled a new source of palaeobiological information, particularly in the analysis of the internal structures of teeth. In this study, we assess the expression of talonid crests at the enamel and dentine surfaces in lower permanent and second deciduous molars ( $M_2$  and  $dm_2$ ) of *H. sapiens*, *H. neanderthalensis* and Atapuerca-Sima de los Huesos (SH) hominins. In modern humans, talonid crests are described exclusively in the deciduous teeth (Korenhof, 1982) and interpreted as a primitive mammalian remnant of the talonid attachment to the trigonid. Here we report for the first time the expression of talonid crests of deciduous and permanent molars in *H. sapiens*, *H. neanderthalensis* and Middle Pleistocene hominins. We discuss possible evolutionary interpretations and suggest the importance of recording this feature in future studies.

© 2014 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

## R É S U M É

L'application de la microtomographie (mCT) aux études de morphologie dentaire a dévoilé une nouvelle source d'information paléobiologique, particulièrement dans l'analyse des structures internes des dents. Dans cette étude, nous évaluons l'expression des crêtes du talonide à la surface de l'émail et de la dentine de molaires inférieures et caduques ( $M_2$  et  $dm_2$ ) de *H. sapiens*, *H. neanderthalensis* et d'Homininés d'Atapuerca-Sima de los Huesos (SH). Chez les humains modernes, les crêtes du talonide sont exclusivement décrites dans le cas des dents caduques (Korenhof, 1982) et interprétées comme un vestige mammalien primitif de l'attache du talonide au trigonide. Ici, nous présentons pour la première fois l'expression de crêtes du talonide de molaires temporaires et permanentes chez *H. sapiens*, *H. neanderthalensis* et chez des Homininés du Pléistocène moyen. Nous discutons les interprétations évolutionnistes possibles et proposons de prendre en compte cet élément dans les futures études.

© 2014 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

\* Corresponding author.

E-mail address: [maria.martinon.torres@gmail.com](mailto:maria.martinon.torres@gmail.com) (M. Martinón-Torres).

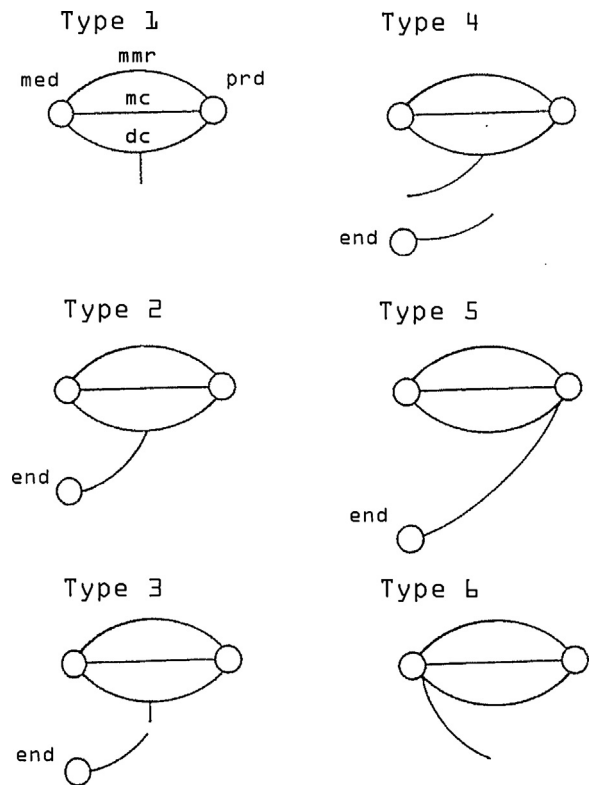
## 1. Introduction

The frequency and degree of expression of many dental discrete traits expressed on the outer enamel surface (OES) is strongly heritable. Thus, these features have become a valuable source of information to infer evolutionary relatedness among modern humans (e.g. Pilbrow, 2006; Scott and Turner, 1997), fossil hominins (e.g. Bailey, 2002a, 2004; Bermúdez de Castro et al., 2003; Irish and Guatelli-Steinberg, 2003; Gómez-Robles et al., 2008, 2012; Guatelli-Steinberg and Irish, 2005; Irish and Guatelli-Steinberg, 2003; Martín-Torres et al., 2006, 2007b, 2012; Wood and Abbott, 1983), and other hominoids (e.g. Pilbrow, 2006), as well as to investigate the evolutionary scenario in which these species evolved (e.g. Bermúdez de Castro and Martín-Torres, 2013; Martín-Torres et al., 2007b, 2011).

The morphology of the enamel–dentine junction (EDJ) has been also studied in the past in an attempt to relate the dentine core topography with OES features (e.g. Corruccini, 1987a, 1987b; Korenhof, 1960, 1961, 1978, 1982; Nager, 1960; Saki et al., 1969). It is now widely accepted that the EDJ is predominantly responsible for the external morphology of a tooth, although the precise level of concordance between both surfaces is still under study (Bailey et al., 2011; Macchiarelli et al., 2006; Martínez de Pinillos et al., 2014; Nager, 1960; Schwartz et al., 1998; Skinner et al., 2008a, 2009a, 2009b). In the past, in order to access the EDJ surface, it was necessary to apply destructive techniques or that the teeth were broken or incomplete (Korenhof, 1982; Nager, 1960; Saki et al., 1969). Using microtomography (mCT) it is now possible to virtually “segment” or separate the different tissues, and produce a 3D reconstruction of each surface in a non-destructive manner (e.g. Macchiarelli et al., 2006; Olejniczak et al., 2007).

Dental mCT studies have provided a new source of palaeobiological information, revealing a number of crests, ridges and tubercles that seem to be of evolutionary significance, but were inaccessible or did not receive systematic attention (Bailey et al., 2011; Skinner et al., 2008a). In this context, the trigonid crest pattern of variation in human species has been extensively analyzed at the OES (e.g. Bailey, 2002b; Bailey et al., 2011; Irish, 1998; Martín-Torres et al., 2007a, 2012; Scott and Turner, 1997; Turner et al., 1991). Following the pioneer work of Korenhof during the last century (Korenhof, 1978, 1982), trigonid crests have been recently studied at the EDJ by means of mCT (Bailey et al., 2011; Martínez de Pinillos et al., 2014; Skinner et al., 2008a, Zanolli and Mazurier, 2013). These studies have added new and interesting observations about the morphological variability and origin of the trigonid crests.

In contrast, the expression of a distinct crest extending from the distal trigonid crest to the talonid, also referred as “talonid crest” (Korenhof, 1982) (Fig. 1) has not been systematically studied in human populations. One reason for this lack of assessment may be the difficulty in accessing the EDJ surface non-destructively (prior to the use of mCT). Furthermore, this crest was defined as an anatomical feature only present in human deciduous lower molars and, historically, the deciduous dentition has received significantly less attention than the permanent dentition.



**Fig. 1.** Korenhof's types of talonid crest (modified from Korenhof, 1982; Fig. 24.8). Type 1. From the middle of the distal trigonid crest a small crest runs for some length in distal direction, but is not connected to any other distinct landmark. Type 2. From the middle of the distal trigonid crest an uninterrupted crest runs to the tip of the entoconid. Type 3. From the middle of the distal trigonid crest an interrupted crest runs to the tip of the entoconid. Type 4. From the middle of the distal trigonid crest a small crest runs to the lingual side, which is reached slightly mesially from the tip of the entoconid. Type 5. From the tip of the protoconid a crest runs to the tip of the entoconid. Type 6. From the tip of the metaconid a crest runs for some distance in a distobuccal direction. Prd: protoconid, med: metaconid, end: entoconid, mmr: mesial marginal ridge, mc: middle trigonid crest, dc: distal trigonid crest.

**Fig. 1.** Types de crête du talonide de Korenhof (modifié d'après Korenhof, 1982, Fig. 24.8). Type 1. À partir du milieu de la crête du trigonide distale, une petite crête se développe sur une certaine longueur dans la direction distale, mais n'est pas connectée à quelque point que ce soit. Type 2. À partir du milieu de la crête du trigonide distale, une crête ininterrompue se développe jusqu'à l'extrémité de l'entoconide. Type 3. À partir du milieu de la crête du trigonide distale, une crête interrompue se développe jusqu'à l'extrémité de l'entoconide. Type 4. À partir du milieu de la crête du trigonide distale, une petite crête se développe du côté lingual qui est atteint à peu près mésialement par rapport à l'extrémité de l'entoconide. Type 5. À partir de l'extrémité du protoconide, une crête se développe jusqu'à l'extrémité de l'entoconide. Type 6. À partir de l'extrémité du métaconide, une crête se développe sur une certaine distance, dans une direction disto-buccale. Prd : protoconide ; med : métaconide ; end : entoconide ; mmr : arête marginale mésiale ; mc : crête du trigonide moyenne ; dc : crête du trigonide distale.

Korenhof (1982) suggested that the talonid crest resembled the original attachment of the primitive talonid to the more derived trigonid in mammals, and that its expression in human deciduous molars (but not in permanent teeth) was a proof that temporary dentitions were morphologically more conservative.

In this study, we investigate the expression of talonid crests in the deciduous and permanent lower molars from Atapuerca-Sima de los Huesos, *H. neanderthalensis* and *H. sapiens* by means of mCT. Sima de los Huesos (SH) (Atapuerca, Spain) has provided the largest Middle Pleistocene human sample coming from a single locality, providing an exceptional opportunity to explore intrapopulation variability in a fossil population (Arsuaga et al., 1991, 1993, 1997; Martínón-Torres 2012). The aims of our study are to explore the possibility that talonid crests can be expressed by other human species than *H. sapiens*, to test whether its manifestation is restricted to deciduous dentitions, and to explore its evolutionary significance.

## 2. Material and methods

Table 1 lists the samples included in this study. Following Korenhof (1982), apart from analyzing permanent lower molars, we also assessed the presence of talonid crests in the deciduous second molar ( $dm_2$ ), because of their resemblance to the morphology of permanent molars. We have only included teeth with dental wear  $\leq 5$  (Molnar, 1971). Thus, the SH subsample consists of 63 out of 123 permanent molars and 1 out of 4  $dm_2$ s. The *H. sapiens* group includes specimens from the early Late Pleistocene (Qafzeh, Israel and Equus Cave, South Africa), late Late Pleistocene (Lagar Velho, Portugal and La Madeleine 4, France), Calcolithic and Bronze Age (Mirador Cave, Sierra de Atapuerca) and a modern human collection (CENIEH's dental sample) composed of clinically extracted teeth from patients of known age and sex, representing a modern Spanish population.

Each molar of the SH sample, as well as those from El Mirador and the CENIEH's dental collections, were scanned with a mCT 80 (Scanco Medical, Switzerland) held at the CENIEH installations. Teeth were scanned with the following parameters: 70Kv, 114  $\mu$ A and  $512 \times 512$  to  $4096 \times 4096$  image matrix. The resulting isometric voxel

size ranged from  $18 \mu m^3$  to  $74 \mu m^3$ . The obtained image stack was imported into Amira 5.3.3 (Visage Imaging, Inc.) and the segmentation of the tissues was done semi-automatically with manual corrections. No filters were applied. For the rest of the comparative dental sample, we have obtained the microCT scans from the NESPOS and ESRF databases (see Table 1).

Talonid crests were scored at the EDJ according to Korenhof's classifications. He described six types as follows (Korenhof, 1982: 357–358; see Fig. 1).

Type 1. From the middle of the distal trigonid crest a small crest runs for some length in distal direction, but is not connected to any other distinct landmark.

Type 2. From the middle of the distal trigonid crest an uninterrupted crest runs to the tip of the entoconid.

Type 3. From the middle of the distal trigonid crest an interrupted crest runs to the tip of the entoconid.

Type 4. From the middle of the distal trigonid crest a small crest runs to the lingual side, which is reached slightly mesially from the tip of the entoconid.

Type 5. From the tip of the protoconid a crest runs to the tip of the entoconid.

Type 6. From the tip of the metaconid a crest runs for some distance in a distobuccal direction.

In his definition of the talonid crest, Korenhof (1982:357) states that it “extends from some part of the distal trigonid crest”. However, from Table 24.3 (Korenhof, 1982), we can see that the author correlated the expression of some talonid crests with some trigonid crest types where the distal trigonid crest was absent or it was discontinuous (e.g. trigonid crest types 3, 4, 5 and 6). Thus, following his work, we suggest it would be more appropriate to define talonid crests as starting from “some part of the distal trigonid” (removing the term *crest*).

We calculated the absolute and relative frequencies of expression of talonid crests for SH, *H. neanderthalensis* and *H. sapiens*. We also recorded the expression of an entoconid ridge that we interpreted as a “trace” of Korenhof's type

**Table 1**

Study sample composition. Numbers in brackets refer to the sample size, counting only one antimer per individual.

**Tableau 1**

Composition de l'échantillonnage étudié. Les nombres entre parenthèses renvoient à la taille de l'échantillon, en comptant seulement un antimère par individu.

Species	Origin	Total n permanent molars	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>	dm <sub>2</sub>	
<i>H. heidelbergensis</i>	Sima de los Huesos <sup>a</sup>	63 (43)	22 (14)	19 (11)	22 (18)	1	
<i>H. neanderthalensis</i>	Abri Bourgeois-Delaunay <sup>c</sup>	1	1	–	–	–	
	Abri Suard <sup>c</sup>	4 (4)	3 (3)	–	1 (1)	1	
	Ehringsdorf <sup>c</sup>	1	1	–	–	–	
	Engis <sup>b</sup>	1	1	–	–	–	
	Gibraltar <sup>b</sup>	3 (2)	2 (1)	1 (1)	–	1	
	Hunas <sup>c</sup>	1	–	–	1	–	
	Krapina <sup>c</sup>	21 (21)	7 (7)	7 (7)	7 (7)	6	
	Regordou <sup>c</sup>	6 (3)	2 (1)	2 (1)	2 (1)	–	
	Roc de Marsal <sup>c</sup>	2 (1)	2 (1)	–	–	–	
	<i>H. sapiens</i>	CENIEH <sup>a</sup>	12 (12)	4 (4)	7 (7)	1	–
		El Mirador <sup>a</sup>	9 (9)	3 (3)	3 (3)	3(3)	1
Equus Cave <sup>b</sup>		2 (2)	2 (2)	–	–	–	
La Madeleine 4 <sup>c</sup>		–	–	–	–	2	
Lagar Velho <sup>c</sup>		1	1	–	–	1	
Qafzeh <sup>b</sup>		8 (4)	4 (2)	4 (2)	–	2	

<sup>a</sup> CENIEH microCT database.

<sup>b</sup> ESRF<sup>®</sup> database.

<sup>c</sup> NESPOS<sup>®</sup> database.

**Table 2**

Frequency of occurrence of talonid crests in lower permanent molars.

**Tableau 2**

Fréquence d'occurrence des crêtes du talonide dans les molaires inférieures permanentes.

Talonid crest	SH		<i>H. neanderthalensis</i>		<i>H. sapiens</i>	
	Total sample	Only one antimeres	Total sample	Only one antimeres	Total sample	Only one antimeres
<b>Present</b>						
<b>n</b>	4	3	5	5	0	0
<b>%</b>	6.3	7	12.5	14.2	0	0
<b>Absent</b>						
<b>n</b>	59	40	35	30	32	28
<b>%</b>	93.7	93	87.5	85.7	100	100
<b>Total</b>	63	43	40	35	32	28

4 (see Results). We performed a non-parametric Chi<sup>2</sup> test (PAST, Hammer et al., 2001) to determine if the frequencies of expression of the talonid crests and the mesial entoconid ridge in each dental class, as well as the total molar sample, were significantly different ( $P < 0.05$ ) among groups. Due to the small sample size, the statistical analyses were only applied to permanent molars. We provide the results of the Chi<sup>2</sup> test with both antimeres included (to maximize the N) and with only one antimeres [following the individual count method of Turner et al. (1991)].

### 3. Results

#### 3.1. Permanent molars

Table 2 presents the frequencies of expression of talonid crests in each of the studied groups. Table 3 lists the specimens that present this feature. For SH permanent molars, the crest was absent in M<sub>1</sub>s and M<sub>2</sub>s, but it was present in four M<sub>3</sub>s, representing the 6.3% of the SH permanent lower molars sample (4 out of 63) and the 18.2% of the SH M<sub>3</sub>s sample (4 out of 22). If we choose only one antimeres per individual, following the individual count method (Turner et al., 1991) the frequency of expression of talonid crests is 3 out of 43 SH lower permanent molars (7%) and 3 out of 18 (16.7%) of SH M<sub>3</sub>s.

For the *H. neanderthalensis* sample we found two M<sub>1</sub> s and three M<sub>3</sub>s with a talonid crest, all of them from the Krapina collection. These represent 12.5% of the total Neanderthal sample (5 out of 40), the 10.5% of the Neanderthal

M<sub>1</sub>s (2 out of 19) and 27.3% of the Neanderthal M<sub>3</sub>s (3 out of 11). If we choose only one antimeres (Turner et al., 1991) per individual, the frequencies are 14.2% (5 out of 35) for the total lower molar Neanderthal sample, 12.5% (2 out of 16) of the Neanderthal M<sub>1</sub>s, and 30% (3 out of 10) of the Neanderthal M<sub>3</sub>s. We did not find any talonid crests in our *H. sapiens* permanent molar sample.

There are no significant differences between SH and *H. neanderthalensis* for any of the categories studied (Table 4). If both antimeres are included, the differences are significant between SH and *H. sapiens* and between *H. neanderthalensis* and *H. sapiens* for the M<sub>3</sub>s and the total molar sample. If only one antimeres is included, only the differences between *H. neanderthalensis* and *H. sapiens* for the total molar sample remain significant.

Table 5 specifies the frequency of occurrence of each of the six types of talonid crest patterns described by Korenhof (1982) at the EDJ of the SH, *H. neanderthalensis* and *H. sapiens* samples. In order to compare our values for the deciduous sample with those obtained by Korenhof (1982) we included both antimeres.

The most common pattern in SH is Type 2, present in 3 out of 4 cases and representing a 4.8% of the total SH lower molar sample and a 13.6% of the SH M<sub>3</sub>s sample. Only one individual presents a type 1 (1.6% of the total SH molar sample and 4.5% of the SH M<sub>3</sub> sample).

The four SH teeth with a talonid crest present a relatively complex occlusal morphology, due to the expression of accessory cusps and the rotation of the main cusps. The expression of a talonid crest contributes to the atypical conformation of these teeth (Fig. 2). AT-2277 (Fig. 2A) presents a clear type 2 pattern, also evident at the OES, with a distinct crest that runs from the mid-point of the distal trigonid crest to the tip of the entoconid. The same type is found in AT-1959 (Fig. 2B), although the talonid is strongly reduced in its lingual side and the crests are mesially rotated. In AT-2273 (Fig. 2C) the talonid crest is particularly evident at the OES. At the EDJ we can distinguish a short crest running from a low distal trigonid crest to the tip of the entoconid. The strong lingual deviation of the central groove results in an atrophied metaconid and thus, the talonid crest is also lingually deviated and less symmetrical than in Korenhof's prototype 2. Finally, AT-2271 (Fig. 2D) has been scored as Korenhof's type 1, since it displays a small crest running from the distal trigonid crest in a distal direction, that it is not connected to the any distinct landmark.

**Table 3**

Summary of the specimens with a talonid crest in this study.

**Tableau 3**

Présentation des spécimens à crête talonide étudiés.

Species	Tooth type	Specimen	Talonid crest type
<i>H. heidelbergensis</i>	AT-2277	RM <sub>3</sub>	Type 2
	AT-1959	RM <sub>3</sub>	Type 2
	AT-2273	LM <sub>3</sub>	Type 2
	AT-2271	LM <sub>3</sub>	Type 1
<i>H. neanderthalensis</i>	D106	LM <sub>3</sub>	Type 5
	D81	LM <sub>1</sub>	Type 6
	D5	LM <sub>3</sub>	Type 1
	D7	RM <sub>3</sub>	Type 4
	D105	RM <sub>1</sub>	Type 4
	D65	Ldm <sub>2</sub>	Type 6
<i>H. sapiens</i>	La Madeleine 4	Rdm <sub>2</sub>	Type 1
	Lagar Velho	Rdm <sub>2</sub>	Type 3

**Table 4**

Chi<sup>2</sup> comparison of the frequencies of expression of talonid crests and mesial entoconid ridge (see text for explanation) between each pair of groups.

**Tableau 4**

Comparaison « Chi<sup>2</sup> » des fréquences d'expression des crêtes du talonide et d'une arête mésiale à l'entoconide (voir texte pour plus d'explications) entre chaque paire de groupes.

	M1		M2		M3		Total molar sample	
	Talonid	Mesial End ridge	Talonid	Mesial End ridge	Talonid	Mesial End ridge	Talonid crest	Mesial End ridge
SH vs. NEA	<i>P</i> : 0.12	<i>P</i> : 0.76	–	<i>P</i> : 0.89	<i>P</i> : 0.54	<i>P</i> : 0.57	<i>P</i> : 0.28	<i>P</i> : 0.55
SH vs. SAP	–	<b><i>P</i>: 0.02<sup>†</sup></b>	–	<i>P</i> : 0.89	<b><i>P</i>: 0.00<sup>†</sup></b>	<i>P</i> : 0.92	<b><i>P</i>: &lt;0.001<sup>†</sup></b>	<i>P</i> : 0.55
NEA vs. SAP	<i>P</i> : 0.21	<b><i>P</i>: 0.01<sup>†</sup></b>	–	<i>P</i> : 0.06	<b><i>P</i>: 0.01<sup>†</sup></b>	0.77	<b><i>P</i>: &lt;0.001<sup>†</sup></b>	<b><i>P</i>: 0.02<sup>†</sup></b>

<sup>†</sup> Denotes statistical significance (*P* < 0.05). In this chart, both antimeres were included (see text for Chi<sup>2</sup> results when following the individual count method).

**Table 5**

Frequency of occurrence of the six types of talonid crest pattern in the SH lower permanent molars. In order to compare with Korenhof's sample (Korenhof, 1982), frequencies are calculated including both antimeres.

**Tableau 5**

Fréquence d'occurrence des six types de patron de crêtes du talonide dans les molaires inférieures permanentes de SH. Pour une comparaison avec l'échantillon de Korenhof (Korenhof, 1982), les fréquences sont calculées incluant les deux antimères.

Talonid crest	SH				Neanderthal				<i>H. sapiens</i>			
	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>	% total	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>	% total	M1	M2	M3	% total
<b>0</b>												
N	22	19	18	59	17	10	8	35	14	14	4	32
%	100	100	81.8	95.1	89.4	100	72.7	87.5	100	100	100	100
<b>Type 1</b>												
N	–	–	1	1	–	–	1	1	–	–	–	–
%	–	–	4.5	1.6	–	–	9.1	2.5	–	–	–	–
<b>Type 2</b>												
N	–	–	3	3	–	–	–	–	–	–	–	–
%	–	–	13.6	4.8	–	–	–	–	–	–	–	–
<b>Type 3</b>												
N	–	–	–	–	–	–	–	–	–	–	–	–
%	–	–	–	–	–	–	–	–	–	–	–	–
<b>Type 4</b>												
N	–	–	–	–	1	–	1	2	–	–	–	–
%	–	–	–	–	5.3	–	9.1	5	–	–	–	–
<b>Type 5</b>												
N	–	–	–	–	–	–	1	1	–	–	–	–
%	–	–	–	–	–	–	9.1	2.6	–	–	–	–
<b>Type 6</b>												
N	–	–	–	–	1	–	–	1	–	–	–	–
%	–	–	–	–	5.3	–	–	2.5	–	–	–	–
<b>Total</b>	22	19	22	63	19	10	11	40	14	14	4	32

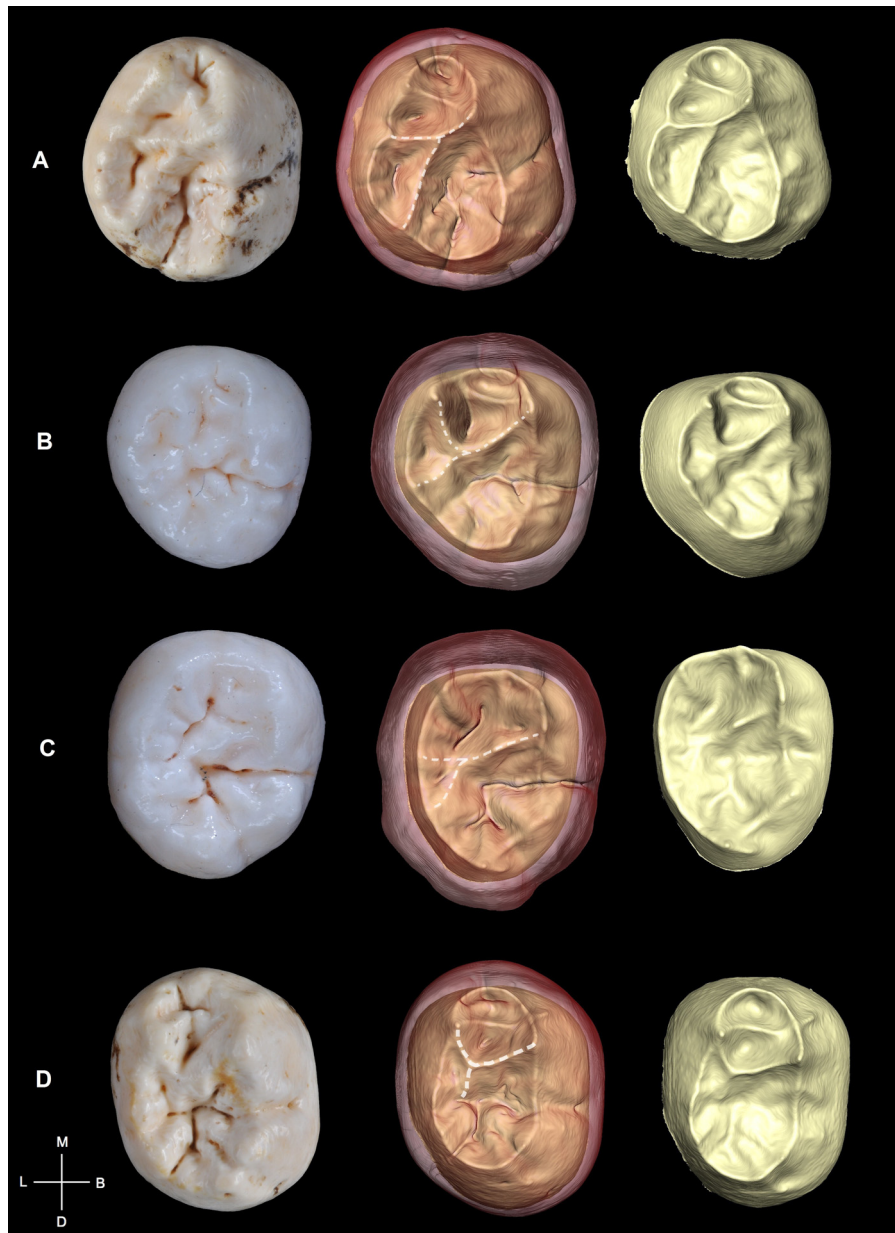
Of the four cases we scored a talonid crest in SH, two belong to the same individual (Individual XVIII) but the left molar expresses type 1 (AT-2271) whereas the right molar (AT-2277) expresses type 2. We think that AT-2271 (Fig. 2D) could be a case of a “truncated” type 2, where the strong reduction of the lingual cusps (metaconid and the entoconid) together with the concomitant expression of a C7 has interrupted the connection of the talonid crest with the entoconid. For AT-2273 (Fig. 2C) there is no corresponding antimeres, and in AT-1959 (Fig. 2B) the talonid crest is absent in its antimeres (AT-1945).

For the Neanderthal M<sub>1</sub> sample (Fig. 3), D105 presents type 4 and D81 (Fig. 3B) presents type 6. Although in his definition Korenhof (1982) stated that in type 6 the talonid crest runs from the tip of the metaconid for some distance in distobuccal direction, in D81 the crest would run as far as the tip of the hypoconid. For the Neanderthal M<sub>3</sub>s we scored type 1 (in D5, Fig. 3C), type 4 (in D7, Fig. 3D) and type 5 (in D106, Fig. 3A).

### 3.2. Deciduous molars

Regarding the dm<sub>2</sub> (Fig. 4), we only identified three cases with a talonid crest as defined by Korenhof (1982): 2 out of 6 *H. sapiens* specimens (33.3%) and 1 out of 8 *H. neanderthalensis* specimens (12.5%) (Table 3). The dm<sub>2</sub> from La Madeleine 4 (Fig. 4B) expresses type 1, the commonest pattern in Korenhof's sample. In the dm<sub>2</sub> from Lagar Velho (Fig. 4C) we scored type 3, which is the third most frequent in Korenhof's sample. Finally, D65 (Fig. 4A) displays a type 6 crest that runs from the metaconid tip to the entoconid tip. This crest was the second most frequent in Korenhof's sample after type 1.

The percentages of talonid crests in our deciduous samples are remarkably lower than those recorded by Korenhof in his medieval Japanese human sample (Table 6). However, it is interesting to note that in 8 out of 8 (100%) dm<sub>2</sub>s from the *H. neanderthalensis* sample, 2 out of 6 (33%) dm<sub>2</sub>s of the *H. sapiens* sample, and in the single dm<sub>2</sub> from SH, we identified a small ridge, mesial to the entoconid essential ridge



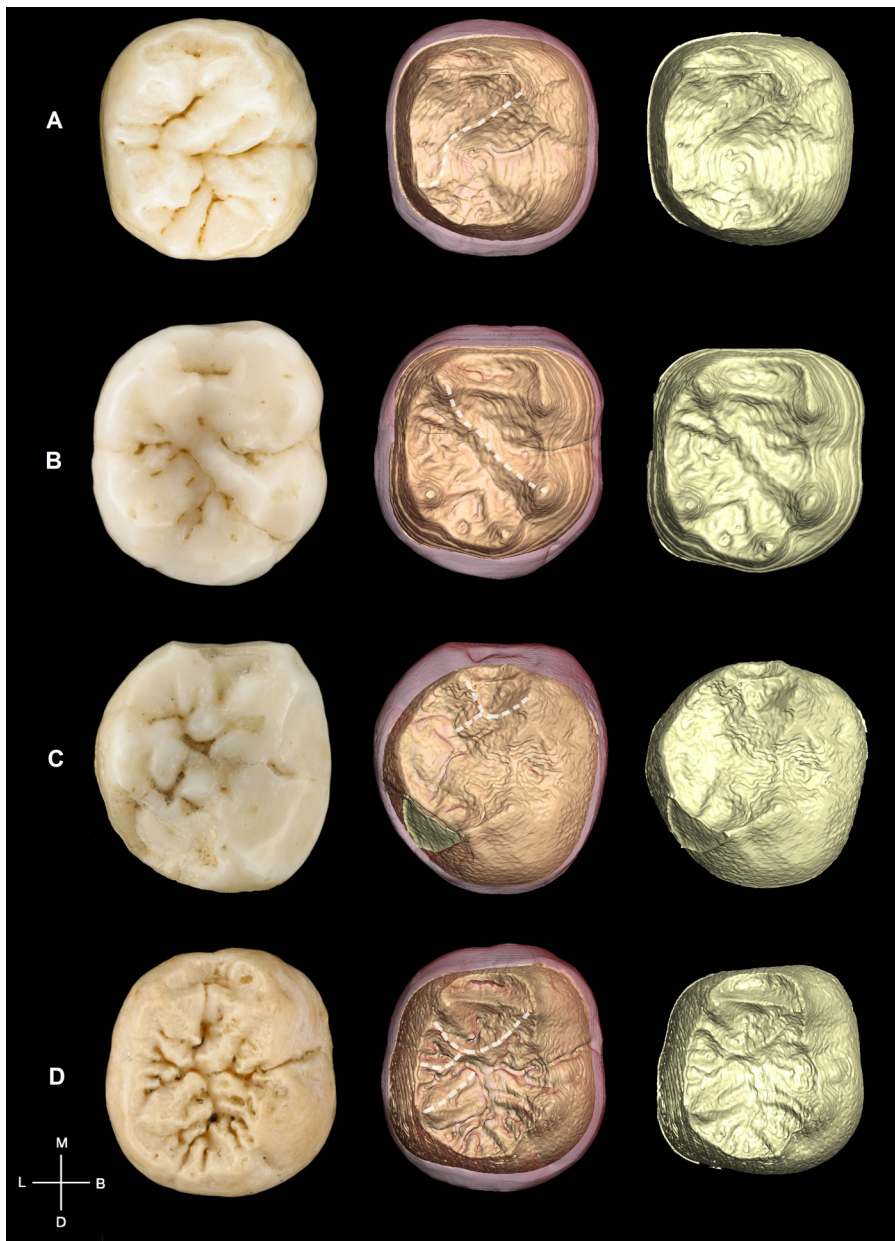
**Fig. 2.** (Color online) Talonid crest types of the SH permanent lower molar sample. (A) AT-2277 (right M<sub>3</sub>, type 2); (B) AT-1959 (right M<sub>3</sub>, type 2); (C) AT-2273 (left M<sub>3</sub>, type 2); (D) AT-2271 (left M<sub>3</sub>, type 1). C and D have been mirrored. Teeth not to scale.

**Fig. 2.** (Couleur en ligne) Types de crête du talonide d'un échantillonnage de molaires inférieures permanentes de SH. (A) AT-2277 (M<sub>3</sub> droite, type 2); (B) AT-1959 (M<sub>3</sub>, type 2); (C) AT-2273 (M<sub>3</sub>, type 2); (D) AT-2271 M<sub>3</sub> gauche, type 1). C et D sont présentées en miroir. Les dents ne sont pas à l'échelle.

(Table 7). This ridge could resemble a talonid crest of type 4, where a small crest runs from the distal trigonid crest to the lingual side, ending at a point that is mesial to the tip of the entoconid. However, this ridge is too short and does not connect with the trigonid, so we consider that it does not fulfill Korenhof's standards to be termed a "talonid crest". In a few cases, the mesial entoconid ridge can be identified also at the OES (see Fig. 5), but its expression is less clear than at the EDJ.

A similar ridge can be found in a large number of permanent lower molars (Table 7). For the M<sub>1</sub>s, this

mesial entoconid ridge was present in 86.4% of SH, 89.5% of Neanderthals and only a 50% of the *H. sapiens* sample. For the M<sub>2</sub>s, the mesial ridge of the entoconid was present in 47.4% of SH, 40% of *H. neanderthalensis* and 14.3% of *H. sapiens*. Finally, for the M<sub>3</sub>s, the mesial ridge was expressed in 27.3% of SH, 18.2% of *H. neanderthalensis* and 25% of *H. sapiens* sample. If we include both antimeres, *H. sapiens* is significantly different to SH for the M<sub>1</sub>, and to *H. neanderthalensis* for the M<sub>1</sub> and the total molar sample (Table 4). If only one antimeres is included, the differences between SH and *H. sapiens*



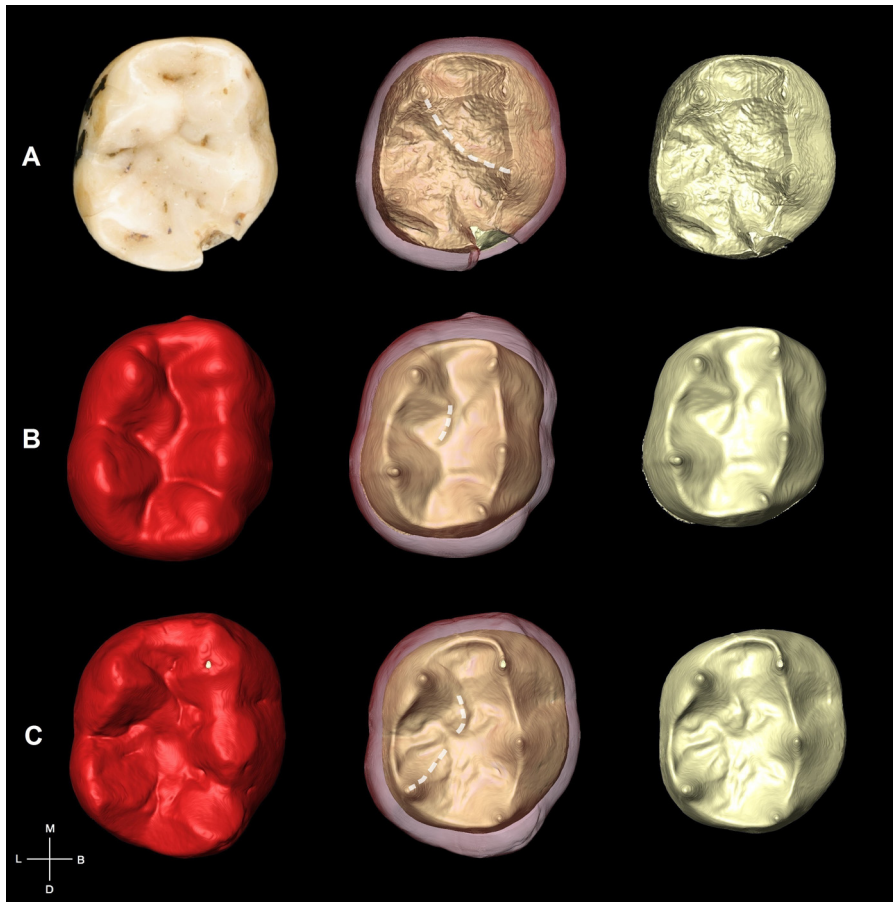
**Fig. 3.** (Color online) Examples of talonid crest types of the Neanderthal permanent lower molar sample. (A) D106 from Krapina (left M<sub>3</sub>, type 5); (B) D81 from Krapina (left M<sub>1</sub>, type 6); (C) D5 (left M<sub>3</sub>, type 1) and D7 (right M<sub>3</sub>, type 4). A, B and C specimens have been mirrored. Teeth not to scale.

**Fig. 3.** (Couleur en ligne) Exemples de types de crête du talonide d'un échantillonnage de molaires inférieures permanentes de Néandertal. (A) D106 de Krapina (M<sub>3</sub> gauche, type 5); (B) D81 de Krapina (M<sub>1</sub> gauche, type 6); (C) D5 (M<sub>3</sub> gauche, type 1) et D7 (M<sub>3</sub> droite, type 4); Les spécimens A, B et C ont été présentés en miroir. Les dents ne sont pas à l'échelle.

become significant for the M<sub>2</sub> and for the total molar sample.

As stated above, and until the morphological variability of the entoconid cusp is better known, we have preferred not to include this mesial entoconid ridge in the talonid crest scoring. As an example, the Equus Cave molar (Fig. 5E) presents a ridge in the area of interest, but not only does this ridge not reach the trigonid, it is too small to be considered a crest. Thus, we have preferred to be conservative regarding this feature. However, if we were to include this

mesial entoconid ridge in the talonid crest scoring, the percentages would clearly change (Table 8). For permanent molars, the prevalence in M<sub>1</sub> would change from 0% to 86.4% in SH, from 10.5% to 100% in *H. neanderthalensis*, and from 0% to 56% in *H. sapiens*. For M<sub>2</sub>s, frequencies would shift from 0% to 47.4% in SH, from 0% to 50% in Neanderthals, and from 0% to 14.3% in modern humans. If we include the mesial entoconid ridge within talonid crest types, in M<sub>3</sub>s frequencies would change from 6.3% to 45.4% in SH, from 27.3% to 45.4% in *H. neanderthalensis*, and from 0% to 25%.



**Fig. 4.** (Color online) Examples of talonid crest types in the  $dm_2$  sample. (A) D65 from Krapina (type 6); (B) Madeleine 4 (type 1); (C) Lagar Velho (type 3). A has been mirrored. Teeth not to scale.

**Fig. 4.** (Couleur en ligne) Exemples de types de crête du talonide d'un échantillonnage de  $dm_2$ . (A) D65 de Krapina (Type 6); (B) Madeleine 4 (type 1); (C) Lagar Velho (type 3); A est présenté en miroir. Les dents ne sont pas à l'échelle.

For the total molar sample, the frequency of expression of talonid crests in SH would change from 6.3% to 60.3%, from 12.5% to 72.5% in *H. neanderthalensis*, and from 0% to 31.2% in modern humans. However, with clearer proportions in all cases, SH and *H. neanderthalensis* would still show higher frequencies for this feature than *H. sapiens*. For the  $dm_2$ , frequencies would change from 12.5% to 100% in *H. neanderthalensis*, and from 33.3% to 66.6% in *H. sapiens*, and it would be also present in the only  $dm_2$  from SH.

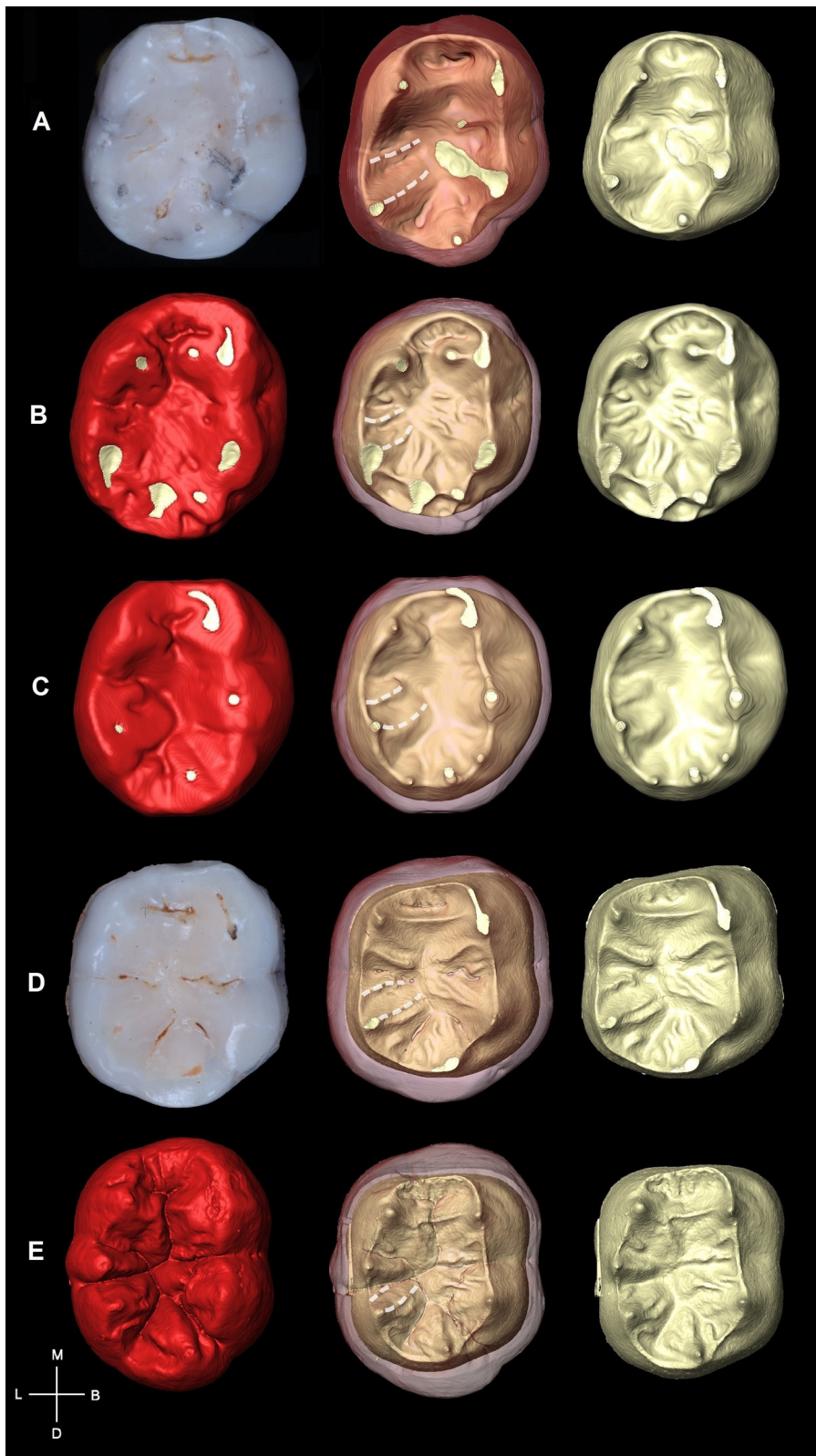
#### 4. Discussion

In 1982, Korenhof published a “new landmark” on modern human dentitions, based on his study of the  $dm_2$  endocasts of a Sangiran medieval population, and called it a “talonid crest”. He considered it “a new and constant feature not observed in permanent molars”, and interpreted it as a primitive feature because of its resemblance to the primitive attachment of the trigonid to the talonid (Korenhof, 1982: 357).

In our study, we have identified the expression of a talonid crest in some permanent molars at both the EDJ and the OES of a hominin Middle Pleistocene population

and Neanderthals, but this crest is absent in our *H. sapiens* sample. According to Korenhof (1982) this trait was only present in deciduous teeth and was proof of a more conservative morphology in these teeth than in permanent ones. However, this statement would not be supported by our data because we have also scored it in permanent teeth, and its frequencies of expression in the  $dm_2$  of SH and *H. neanderthalensis* are lower than in permanent molars. However, it could be that our results are conditioned by our small sample sizes, particularly for temporary dentitions.

Furthermore, the frequency of expression of talonid crests in Korenhof's *H. sapiens*  $dm_2$  sample is remarkably higher (88.5%) than that obtained in our study for this species (33.3%). This is particularly surprising because Korenhof described this feature as almost ubiquitous in deciduous dentitions. It could be that the high frequencies of talonid crests in Korenhof's modern sample is a peculiarity of the medieval Javanese population and cannot be extrapolated to the *H. sapiens* species. It could also be that we are underestimating the frequencies of expression of talonid crests in our sample. Indeed, we have identified in our study the frequent expression of a mesial ridge in



**Fig. 5.** (Color online) Examples of the expression of a mesial ridge at the entoconid in (A) AT-2398 (right  $dm_2$ ), (B) Gibraltar HA 40,26 (right  $dm_2$ ), (C) Qafzeh 15 (right  $dm_2$ ), (D) AT-3933 (right  $M_1$ ) and (E) Equus Cave (right  $M_1$ ) that could resemble Korenhof's type 4. Teeth not to scale.

**Fig. 5.** (Couleur en ligne) Exemples d'expression d'une arête mésiale à l'entoconide pour (A) AT-2398 ( $dm_2$  droite), (B) Gibraltar HA 40,26 ( $dm_2$  droite), (C) Qafzeh 15 ( $dm_2$  droite), (D) AT-3933 ( $M_1$  droite) et (E) grotte Equus ( $M_1$  droite) qui pourraient ressembler au type 4 de Korenhof. Les dents ne sont pas à l'échelle.

**Table 6**

Frequency of occurrence of the six types of talonid crest pattern in the lower deciduous second molars. In order to compare with Korenhof's sample (Korenhof, 1982), frequencies are calculated including both antimeres.

**Tableau 6**

Fréquence d'occurrence des six types de patron de crêtes du talonide dans les molaires inférieures temporaires secondes. Pour une comparaison avec l'échantillon de Korenhof (Korenhof, 1982), les fréquences sont calculées en incluant les deux antimères.

Talonid crest	Korenhof's <i>H. sapiens</i> sample <sup>a</sup>	SH	<i>H. neanderthalensis</i>	<i>H. sapiens</i>
<b>Type 1</b>				
N	22	–	–	1
%	42.3			16.7
<b>Type 2</b>				
N	2	–	–	–
%	3.8			
<b>Type 3</b>				
N	6	–	–	1
%	11.5			16.7
<b>Type 4</b>				
N	1	–	–	–
%	1.9			
<b>Type 5</b>				
N	2	–	–	–
%	3.8			
<b>Type 6</b>				
N	13	–	1	–
%	25		12.5	
<b>Total</b>				
N	46	0	1	2
%	88.5	0	12.5	33.3

<sup>a</sup> Although it is not clear from his manuscript, we assume that 46 out of 52 of the dm<sub>2</sub>s studied by Korenhof have talonid crest, that is, 6 teeth do not present a talonid crest

the entoconid of the dm<sub>2</sub> and some permanent molars that could be interpreted as a “trace” or vestige of Korenhof's type 4. This mesial ridge is more frequent in SH and *H. neanderthalensis* et permanent and deciduous molars than in *H. sapiens* (except for the M<sub>3</sub>). This ridge is too short and does not attach to the trigonid, so from a conservative perspective we have not included its expression within Korenhof's type 4. Future studies may shed light on whether this ridge should be understood as a feature related to the morphological variability of the entoconid cusp or is indeed a component of a talonid crest. Currently, beyond hominoids (Skinner et al., 2008b) or the trigonid cusps (e.g. Bailey et al., 2011; Martínez de Pinillos et al.,

2014), little is known about the crests and ridges that consistently form at the EDJ on other molar cusps such as the entoconid. Interestingly, a similar ridge seems to be present in PCG.2, a dm<sub>2</sub> from the Sangiran Dome (see Fig. 5C from Zanolli et al., 2012) and in Tighenif 2, possibly confirming the presence of a talonid crest type 4 in the latter (Zanolli and Mazurier, 2013; Zanoll, pers. comm.). If demonstrated that this mesial entoconid ridge is related to Korenhof's Type 4, the number of talonid crests for permanent and deciduous molars would be substantially higher in all groups, and would remain higher for SH and *H. neanderthalensis* than for *H. sapiens*. Frequencies would be also higher in temporary dentitions,

**Table 7**

Frequency of occurrence of the mesial entoconid ridge in our sample (see text for explanation). Both antimeres are included.

**Tableau 7**

Fréquence d'occurrence de l'arête mésiale d'entoconide dans notre échantillonnage (voir le texte pour plus d'explications). Les deux antimères sont inclus.

	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>	Total permanent	dm <sub>2</sub>
SH	19/22 86.4%	9/19 47.4%	6/22 27.3%	34/63 54%	1/1 100%
NEA	17/19 89.5%	5/10 50%	2/11 18.2%	24/40 60%	8/8 100%
SAP	7/14 50%	2/14 14.3%	1/4 25%	10/32 31.2%	2/6 33.3%

**Table 8**

Frequency of occurrence of talonid crests in our sample if we include the mesial entoconid ridge. Both antimeres are included.

**Tableau 8**

Fréquence d'occurrence de crêtes du talonide dans notre échantillonnage, si l'on inclut l'arête mésiale d'entoconide. Les deux antimères sont inclus.

	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>	Total permanent	dm <sub>2</sub>
SH	19/2286.4%	9/1947.4%	10/2245.4%	38/63 60.3%	1/1 100%
NEA	19/19 100%	5/10 50%	5/11 45.4%	29/40 72.5%	8/8 100%
SAP	7/14 50%	2/14 14.3%	1/4 25%	10/32 31.2%	4/6 66.6%

although in the case of our *H. sapiens* it would still not reach the 100% that Korenhof scored in his medieval sample.

Regarding the polarity of this feature, it would be necessary to explore the pattern of talonid crest variation in other hominin groups. Indeed, attending to the expression of crests at the trigonid, we know that a continuous mid-trigonid crest is a primitive feature that can be found in early hominin groups such as *H. erectus*, *H. georgicus* and *H. antecessor* (Martín-Torres et al., 2007b, 2008; Zanolli and Mazurier, 2013). However, the particularly high frequencies of expression of this trait in SH and *H. neanderthalensis* (Bailey, 2000, 2002a; Bailey et al., 2011; Martínez de Pinillos et al., 2014; Martín-Torres et al., 2012) can be interpreted as *derived* in this group with regard to *H. sapiens*. We know now that many of the so-called “typical Neanderthal” features are not apomorphies but distinctive combinations of primitive features (e.g. Bailey, 2002b, Bermúdez de Castro et al., 2012; Franciscus and Trinkaus, 1995; Martín-Torres et al., 2006; Patte, 1962). Thus, although the talonid crest could be a primitive feature as suggested by Korenhof (1982), the higher frequencies of talonid crests in European Middle Pleistocene populations and Neanderthals could be a *derived* feature in this lineage. Interestingly, the high frequency of *distal* trigonid crests on M<sub>3s</sub> was cited as diagnostic in the differentiation of *H. neanderthalensis* and *H. sapiens* (Bailey, 2002a, 2002c; Bailey et al., 2011). The same pattern was also found in the SH dentitions (Martín-Torres et al., 2012) where the frequencies of *distal* trigonid crests in M<sub>3s</sub> were particularly high (Martín-Torres et al., 2012; Martínez de Pinillos et al., 2014). Our study reveals that most talonid crests in permanent molars are displayed by M<sub>3s</sub>, so it might be that talonid crests follow a similar pattern of variation as *distal* trigonid crests in SH and *H. neanderthalensis* with regard to *H. sapiens* (Bailey et al., 2011; Martín-Torres et al., 2012).

However, we should not ignore the fact that the only two populations where talonid crests were scored in permanent teeth (Krapina and SH) are the only groups with a sample large enough to assess intrapopulational variability. Future studies in more and larger hominin samples may provide more representative frequencies of expression for this trait.

Finally, we suggest that talonid crests may represent an interesting morphological variable to score in dental anthropological studies and possibly to include in the Arizona State University Dental Anthropology System (ASUDAS, Turner et al., 1991). The significant differences between groups in the pattern of expression despite the small sample sizes, merits further exploration in other hominins in order to understand its real evolutionary meaning.

## Acknowledgments

We thank all members of the Atapuerca research team, in particular those who excavated the Sima de los Huesos site, for their dedicated work. We also acknowledge several people for providing access to the studied

material and for their helpful assistance: R. Macchiarelli, P. Semal and P. Bayle from NESPOS society; E. Carbonell and M. Lozano (Institut Català de Paleoeologia Humana i Evolució Social, Tarragona, Spain). We are also grateful to G.R. Scott for his always enlightening insights on dental morphology. Special thanks are given to C. Zanolli for kindly sharing the Tighenif EDJ images and his opinion on the morphology of these specimens. We thank P. Fernández-Colón and E. Lacasa-Marquina from the Restoration and Conservation Department of the CENIEH, and M.C. Ortega from Centro de Evolución y Comportamiento Humanos (ISCIII, Madrid) for the restoration and conservation of the SH collection. We also thank R. Macchiarelli and two anonymous reviewers for their valuable comments that helped to improve the quality of the manuscript. The mCT scanner of the SH, Mirador and CENIEH dental collections were performed at CENIEH with the collaboration of CENIEH staff. This research was supported with funding from the Dirección General de Investigación of the Spanish Ministerio de Educación y Ciencia (Project N. CGL2009-12703-C03-01); Secretaría de Estado, Investigación, Desarrollo e Innovación of the Spanish Ministerio de Economía y Competitividad (Project CGL2012-38434-C03-02); Consejería de Educación de la Junta de Castilla y León (Project CEN074A12-1), and Leakey Foundation. Fieldwork at Atapuerca is supported by the Consejería de Cultura y Turismo of the Junta de Castilla y León and the Fundación Atapuerca. M.M.-P. and L. M.-F. had the benefit of a predoctoral grant from the Fundación Atapuerca and the Fundación Duques de Soria.

*Grant sponsorship:* Spanish Ministerio de Educación y Ciencia, Consejería de Educación de la Junta de Castilla y León, Spanish Ministerio de Economía y Competitividad, Leakey Foundation, Fundación Duques de Soria.

## References

- Arsuaga, J.L., Carretero, J.M., Martínez, I., Gracia, A., 1991. Cranial remains and long bones from Atapuerca/Ibeas (Spain). *J. Hum. Evol.* 20, 191–230.
- Arsuaga, J.L., Martínez, I., Gracia, A., Carretero, J.M., Carbonell, E., 1993. Three new human skulls from the Sima de los Huesos Middle Pleistocene site in Sierra de Atapuerca, Spain. *Nature* 362, 534–537.
- Arsuaga, J.L., Martínez, I., Gracia, A., Lorenzo, C., 1997. The Sima de los Huesos crania (Sierra de Atapuerca Spain). A comparative study. *J. Hum. Evol.* 33, 219–281.
- Bailey, S.E., 2000. Dental morphological affinities among Late Pleistocene and recent humans. *Dent. Anthropol.* 14, 1–8.
- Bailey, S.E., 2002a. A closer look at Neanderthal postcanine dental morphology: I. The mandibular dentition. *New Anatomist* 269, 148–156.
- Bailey, S.E., 2002b. A closer look at neanderthal postcanine dental morphology: the mandibular dentition. *Anat. Rec.* 269, 148–156.
- Bailey, S.E., 2002c. Neanderthal dental morphology: implications for modern human origins. Arizona State University (PhD dissertation).
- Bailey, S.E., 2004. A morphometric analysis of maxillary molar crowns of Middle–Late Pleistocene hominins. *J. Hum. Evol.* 47, 183–198.
- Bailey, S.E., Skinner, M.M., Hublin, J.J., 2011. What lies beneath? An evaluation of lower molar trigonid crest patterns based on both dentine and enamel expression. *Am. J. Phys. Anthropol.* 145, 505–518.
- Bermúdez de Castro, J.M., Carretero, J.M., García-González, R., Rodríguez-García, L., Martín-Torres, M., Rosell, J., Blasco, R., Martín-Francés, L., Modesto, M., Carbonell, E., 2012. Early Pleistocene human humeri from the gran dolina-TD6 site (Sierra de Atapuerca, Spain). *Am. J. Phys. Anthropol.* 147, 604–617.

- Bermúdez de Castro, J.M., Martín-Torres, M., Sarmiento, S., Lozano, M., 2003. Gran Dolina-TD6 versus Sima de los Huesos dental samples from Atapuerca: evidence of discontinuity in the European Pleistocene population? *J. Archaeol. Sci.* 30, 1421–1428.
- Bermúdez de Castro, J.M., Martín-Torres, M., 2013. A new model for the evolution of the human Pleistocene populations of Europe. *Quatern. Int.* 295, 102–112.
- Corruccini, R.S., 1987a. The dentinoenamel junction in primates. *Int. J. Primatol.* 8, 99–114.
- Corruccini, R.S., 1987b. Relative growth from the dentino-enamel junction in primate maxillary molars. *J. Hum. Evol.* 2, 263–269.
- Franciscus, R.G., Trinkaus, E., 1995. Determinants of retromolar space presence in Pleistocene *Homo* mandibles. *J. Hum. Evol.* 28, 577–595.
- Gómez-Robles, A., Martín-Torres, M., Bermúdez de Castro, J.M., Prado, L., Sarmiento, S., Arsuaga, J.L., 2008. Geometric morphometric analysis of the crown morphology of the lower first premolar of hominins, with special attention to Pleistocene *Homo*. *J. Hum. Evol.* 55, 627–638.
- Gómez-Robles, A., Bermúdez de Castro, J.M., Martín-Torres, M., Prado-Simón, L., Arsuaga, J.L., 2012. A geometric morphometric analysis of hominin upper second and third molars with particular emphasis on European Pleistocene populations. *J. Hum. Evol.* 63, 512–526.
- Guatelli-Steinberg, D., Irish, J.D., 2005. Brief Communication: Early Hominin Variability in First Molar Dental Trait Frequencies. *Am. J. Phys. Anthropol.* 128, 477–484.
- Hammer, O., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontol. Electron.* 4, 9.
- Irish, J.D., 1998. Dental morphological affinities of Late Pleistocene through recent sub-Saharan and North African peoples. *Bull. Mem. Soc. Anthropol. Paris* 10, 237–272.
- Irish, J.D., Guatelli-Steinberg, D., 2003. Ancient teeth and modern human origins: An expanded comparison of African Plio-Pleistocene and recent world dental samples. *J. Hum. Evol.* 45, 113–144.
- Korenhof, C.A.W., 1960. Morphogenetical aspects of the human upper molar. *Uitgeversmaatschappij, Utrecht, The Netherlands* (PhD dissertation).
- Korenhof, C.A.W., 1961. The enamel-dentine border: a new morphological factor in the study of the (human) molar pattern. *Proc. Koninklijke. Neder-lands. 64B*, 544–639.
- Korenhof, C.A.W., 1978. Remnants of the trigonid crests in medieval molars of man of Java. In: Butler, P.M., Joysey, K. (Eds.), *Development function and evolution of teeth*. Academic Press, New York, pp. 157–169.
- Korenhof, C.A.W., 1982. Evolutionary trends of the inner enamel anatomy of deciduous molars from Sangiran (Java, Indonesia). In: Kurtén, B. (Ed.), *Teeth: form function and evolution*. Columbia University Press, New York, pp. 350–365.
- Macchiarelli, R., Bondioli, L., Debenath, A., Mazurier, A., Tournepiche, J.-F., Birch, W., Dean, M.C., 2006. How Neanderthal molar teeth grew. *Nature* 444, 748–751.
- Martínez de Pinillos, M., Martín-Torres, M., Skinner, M.M., Arsuaga, J.L., Gracia-Téllez, A., Martínez, I., Martín-Francés, L., Bermúdez de Castro, J.M., 2014. Trigonid crests expression in Atapuerca-Simade los Huesos lower molars: internal and external morphological expression and evolutionary inferences. *C. R. Palevol.*, <http://dx.doi.org/10.1016/j.crpv.2013.10.008> (accepted).
- Martín-Torres, M., Bastir, M., Bermúdez de Castro, J.M., Gómez, A., Sarmiento, S., Muela, A., Arsuaga, J.L., 2006. Hominin lower second premolar morphology: evolutionary inferences through geometric morphometric analysis. *J. Hum. Evol.* 50, 523–533.
- Martín-Torres, M., Bermúdez de Castro, J., Gómez-Robles, A., Sarmiento, S., Muela, A., Arsuaga, J.L., 2007a. Gran Dolina-TD6 and Sima de los Huesos dental samples: Preliminary approach to some dental characters of interest for phylogenetic studies. In: Bailey, S.E., Hublin, J.J. (Eds.), *Dental Perspectives on Human Evolution*. Springer-Verlag, Berlin, pp. 65–79.
- Martín-Torres, M., Bermúdez de Castro, J.M., Gómez-Robles, A., Arsuaga, J.L., Carbonell, E., Lordkipanidze, D., Manzi, G., Margvelashvili, A., 2007b. Dental evidence on the hominin dispersals during the Pleistocene. *PNAS* 104, 13279–13282.
- Martín-Torres, M., Bermúdez de Castro, J.M., Gómez-Robles, A., Margvelashvili, A., Prado, L., Lordkipanidze, D., Vekua, A., 2008. Dental remains from Dmanisi (Republic of Georgia): Morphological analysis and comparative study. *J. Hum. Evol.* 55, 249–273.
- Martín-Torres, M., Dennell, R., Bermúdez de Castro, J.M., 2011. The Denisova hominin need not be an out of Africa story. *J. Hum. Evol.* 60, 51–55.
- Martín-Torres, M., Bermúdez de Castro, J.M., Gómez-Robles, A., Prado-Simón, L., Arsuaga, J.L., 2012. Morphological description and comparison of the dental remains from Atapuerca-Sima de los Huesos site (Spain). *J. Hum. Evol.* 62, 7–58.
- Molnar, S., 1971. Human Tooth Wear. Tooth Function and Cultural Variability. *Am. J. Phys. Anthropol.* 34, 175–190.
- Nager, G., 1960. Der vergleich zwischen dem räumlichen Verhalten des Dentin-kronenreliefs und dem Schmelzrelief der Zahnkrone. *Acta Anat.* 42, 226–2250.
- Olejniczak, A.J., Gilbert, C.C., Martin, L.B., Smith, T.M., Ulhaas, L., Grine, F.E., 2007. Morphology of the enamel-dentine junction in sections of anthropoid primate maxillary molars. *J. Hum. Evol.* 53, 292–301.
- Patte, E., 1962. La dentition des Néanderthaliens. *Masson Paris*.
- Pilbrow, V., 2006. Lingual Incisor Traits in Modern Hominoids and an Assessment of Their Utility for Fossil Hominoid Taxonomy. *Am. J. Phys. Anthropol.* 129, 323–338.
- Saki, T., Sasaki, I., Hanmura, H., 1969. A morphology study of enamel-dentine border on the Japanese dentition. Part IV. Mandibular premolar. *J. Anthropol. Soc. Nippon.* 77, 71–98.
- Schwartz, G.T., Thackeray, J.F., Reid, C., van Reenan, J.F., 1998. Enamel thickness and the topography of the enamel-dentine junction in South African Plio-Pleistocene hominids with special reference to the Carabelli trait. *J. Hum. Evol.* 35, 523–542.
- Scott, G.R., Turner, C.G., 1997. *The Anthropology of Modern Human Teeth: Dental Morphology and its Variation in Recent Human Populations*. Cambridge University Press, Cambridge.
- Skinner, M.M., Gunz, P., Wood, B.A., Hublin, J.-J., 2008a. Enamel-dentine junction (EDJ) morphology distinguishes the lower molars of *Australopithecus africanus* and *Paranthropus robustus*. *J. Hum. Evol.* 55, 979–988.
- Skinner, M.M., Wood, B.A., Boesch, C., Olejniczak, A.J., Rosas, A., Smith, T.M., Hublin, J.-J., 2008b. Dental trait expression at the enamel-dentine junction of lower molars in extant and fossil hominoids. *J. Hum. Evol.* 54, 173–186.
- Skinner, M.M., Gunz, P., Wood, B.A., Boesch, C., Hublin, J.-J., 2009a. Discrimination of extant *Pan* species and subspecies using the enamel-dentine junction morphology of lower molars. *Am. J. Phys. Anthropol.* 140, 234–243.
- Skinner, M.M., Wood, B.A., Hublin, J.-J., 2009b. Protostylid expression at the enamel-dentine junction and enamel surface of mandibular molars of *Paranthropus robustus* and *Australopithecus africanus*. *J. Hum. Evol.* 56, 76–85.
- Turner, C.G.I., Nichol, C.R., Scott, G.R., 1991. Scoring Procedures for Key Morphological Traits of the Permanent Dentition: The Arizona State University Dental Anthropology System. In: Kelley, M.A., Spencer Larsen, C. (Eds.), *Advances in Dental Anthropology*. Wiley-Liss, pp. 13–31.
- Wood, B., Abbott, S.A., 1983. Analysis of the dental morphology of Plio-Pleistocene hominids I. Mandibular molars: crown area measurements and morphological traits. *J. Anat.* 136, 197–219.
- Zanolli, C., Bondioli, L., Mancini, L., Mazurier, A., Widiyanto, H., Macchiarelli, R., 2012. Brief communication: two human fossil deciduous molars from the Sangiran Dome (Java Indonesia): outer and inner morphology. *Am. J. Phys. Anthropol.* 147, 472–481.
- Zanolli, C., Mazurier, A., 2013. Endostructural characterization of the *H. heidelbergensis* dental remains from the early Middle Pleistocene of Tighenit Algeria. *C. R. Palevol.* 12, 293–304.