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Trigonid crests expression in Atapuerca-Sima de los Huesos lower molars: Internal and external morphological expression and evolutionary inferences

Expression des crêtes du trigonide de molaires inférieures à Atapuerca-Sima de los Huesos : expression morphologique interne et externe et inférences évolutionnistes

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ABSTRACT

Trigonid crest patterning in lower molars is distinctive among Late Pleistocene hominins such as *Homo neanderthalensis*, fossil *Homo sapiens* and modern humans. In this paper, we present an examination of trigonid crest patterning in the Middle Pleistocene permanent lower molar sample ($n = 62$) of *Homo heidelbergensis* from Sima de los Huesos (SH). Crest expression was assessed from 3D models of the enamel and the dentine surfaces that were produced using micro-computed tomography (microCT). The aims of our analysis are to: 1) characterize the pattern of trigonid crest expression at the outer enamel and enamel-dentine junction surfaces (OES and EDJ) of the SH sample, 2) evaluate the concordance of expression between both surfaces, and 3) place trigonid crest variation in the SH sample into a phylogenetic context. Our results reveal a greater variability in the expression of trigonid crests at the EDJ (14 types) compared to the OES (4 types). Despite this variability, in almost all cases the expression of a continuous mid-trigonid or distal crest at the OES corresponds with the expression of a continuous mesial/mid-trigonid or distal trigonid crest, respectively, at the EDJ. Thus, it is possible to predict the type of trigonid crest pattern that would be at the OES in the case of partially worn teeth. Our study points to increased variability in trigonid crest expression in M_3s compared to M_1s and M_2s. Moreover, our analysis reveals that the SH sample matches broadly the trigonid crest patterns displayed by *H. neanderthalensis* and differs from those exhibited by *H. sapiens*, particularly in the almost constant expression of a continuous middle trigonid crest at the EDJ. However, SH hominins also exhibit patterns that have not been reported in *H. neanderthalensis* and

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H. sapiens samples. Other aspects of the variability of the trigonid crest expression at the dentine are presented and discussed.

Mots clés :
Molaires inférieures permanentes
Homo heidelbergensis
Sima de los Huesos
Homo neenderthalensis
Homo sapiens
Microtomographie
Configuration des crêtes du trigonide

RÉSUMÉ

La configuration de la crête du trigonide des molaires inférieures est caractéristique chez les homininés du Pléistocène supérieur, *Homo neanderthalensis* et *Homo sapiens* fossile, et aussi chez les humains actuels. Dans cet article, nous présentons l'examen de la configuration de la crête du trigonide d'un échantillon de molaires inférieures permanentes ($n = 62$) attribuées à *Homo heidelbergensis*, du site Pléistocène moyen de Sima de los Huesos (SH), en Espagne. L'expression de la crête est établie en modélisant les surfaces de l'émail et de la dentine à l'aide de rendus virtuels 3D basés sur un registre microtomographique (microCT). Le but de notre analyse est : 1) de caractériser le degré d'expression et la configuration de la crête du trigonide à la surface externe de l'émail (OES) et au niveau de la jonction émail–dentine (EDJ) de l'échantillon SH, 2) d'évaluer la concordance d'expression entre les deux surfaces et 3) de replacer le degré de variation de la crête du trigonide observé au sein de l'échantillon SH dans un contexte phylogénétique. En comparaison de celle observée sur l'OES (quatre types), nos résultats révèlent une grande variabilité dans l'expression de la crête du trigonide au niveau de l'EDJ (14 types). Malgré cette variabilité, dans presque tous les cas, l'expression d'une crête du trigonide intermédiaire ou distale continue sur l'OES correspond respectivement à l'expression d'une crête du trigonide mésiale/intermédiaire ou distale continue au niveau de l'EDJ. Ainsi, à partir de l'analyse de la morphologie interne, il est possible de prévoir le type de configuration de la crête du trigonide ayant existé sur l'OES dans le cas de dents partiellement usées. Notre étude souligne une variabilité croissante dans l'expression de ce trait sur les M_3s par rapport aux M_1s et M_2s. En outre, notre étude révèle que le degré de variation des configurations de la crête du trigonide dans l'échantillon de SH s'accorde avec celui observé chez *H. neanderthalensis*, mais qu'il diffère de celui de *H. sapiens*, en particulier dans l'expression presque constante d'une crête du trigonide intermédiaire continue au niveau de l'EDJ. Cependant, les homininés de SH révèlent aussi des configurations qui n'ont pas été observées chez *H. neanderthalensis* et *H. sapiens*. D'autres aspects de la variabilité dans l'expression de la crête du trigonide au niveau de la dentine sont présentés et discutés.

1. Introduction

Variation in dental form, as well as the frequency and degree of expression of many dental traits are highly heritable, making teeth more useful than other skeletal elements to assess phylogenetic relationships among fossil hominins and modern humans (Hrdlička, 1923; Kaifu et al., 2005; Martinón-Torres et al., 2007, 2012). The expression of morphological traits has been traditionally recorded in the outer enamel surface (OES), but other researchers, particularly during the last decade, have attempted to characterize the expression of these features at the enamel-dentine junction (EDJ) (Bailey et al., 2011; Macchiarelli et al., 2006; Skinner et al., 2008a,b). It is assumed that the morphology of the EDJ is largely responsible of the external morphology of a tooth (e.g., Guy et al., 2003; Nager, 1960; Schwartz et al., 1998). According to Korenhof (Korenhof, 1982; Scott and Turner, 1997) the EDJ morphology is more evolutionarily conservative than the OES morphology because "the enamel-dentine partition is much more a genetic blueprint of the occlusal anatomy of the teeth" (page 350 from Korenhof, 1982). However, the precise level of concordance between both surfaces is still under study (e.g., Bailey et al., 2011; Skinner et al., 2008b, 2009, 2010).

In the past, in order to analyze the EDJ surface it was necessary to employ destructive techniques to remove the enamel cap, or that the teeth were broken or incomplete (e.g., Corruccini, 1998; Korenhof, 1982; Nager, 1960; Suzuki and Sakai, 1973). More recently, the increasing availability of high-resolution micro-computed tomography (microCT) allows the virtual separation of the different tissues that compose a tooth, a process that is also called *segmentation*. From this segmentation, it is possible to obtain accurate three-dimensional (3D) reconstructions of detailed morphological features on both the OES and EDJ in a non-destructive manner. In this sense, dental microCT studies are expanding traditional analyses of discrete morphological traits to include their initial development on the inner enamel epithelium prior to enamel deposition; a methodology which has been shown to greatly improve our understanding of their ontogeny and variability within and among species (e.g., Ortiz et al., 2012; Skinner et al., 2008a,b).

The expression of trigonid crests on the enamel surface of human molars has revealed certain patterns of variation that seem to be taxonomically and phylogenetically informative (e.g., Bailey, 2002a; Irish, 1998; Scott and Turner, 1997; Turner et al., 1991; Zubov, 1992a). From an evolutionary point of view, the primitive mammalian cusp pattern in molars was a triangle (Vandebroek, 1967; Zubov, 1992b) (see Fig. 1.3 and Fig. 1.25 from Hillson, 2005). In humans, as in most primates, the mesial or anterior part of the lower molars is called the trigonid (trigon in upper molars), and the distal or posterior part of the lower molars

Table 1
Study sample of lower molars.
Tableau 1
Liste des molaires inférieures étudiées dans ce travail.

Species	Origin	*N* total	M_1 (*n*)	M_2 (*n*)	M_3 (*n*)
H. heidelbergensis	Sima de los Huesos[a]	62	22	18	22
H. neanderthalensis	Engis[b]	1	1	–	–
	Gibraltar[b]	3	2	1	–
	Ehringsdorf[c]	1	1	–	–
	Abri Bourgeois-Delaunay[c]	1	1	–	–
	Regourdou[c]	6	2	2	2
	Abri Suard[c]	4	3	–	1
	Krapina[c]	20	7	6	7
	Hunas[c]	1	–	–	1
	Roc de Marsal[c]	2	2	–	–
H. sapiens	Equus Cave[b]	2	2	–	–
	Qafzeh[b]	8	4	4	–
	Lagar Velho[c]	1	1	–	–
	El Mirador[a]	9	3	3	3
	CENIEH[a]	12	4	7	1

[a] CENIEH micro-computed tomography data base.
[b] ESRF© data base.
[c] NESPOS© data base.

is the talonid (talon in upper molars) (White and Folkens, 2005). Trigonid crest refers to the expression of a crest that connect the first (protoconid) with the second (metaconid) main cusps in lower molars (Scott and Turner, 1997; Turner et al., 1991) and it can arise from any lobe segment or from the marginal ridge complex as well (Bailey et al., 2011; see also below).

Following the pioneer work of Korenhof (Korenhof, 1982; Scott and Turner, 1997), trigonid crests have recently been studied at the EDJ by means of microCT (Bailey et al., 2011; Skinner et al., 2008b). These studies have confirmed that the distinctive trigonid crest expression at the OES in Neanderthals is matched at the EDJ, both in terms of frequency and morphology (Bailey et al., 2011). In particular, the expression of conspicuous and continuous middle trigonid crests in lower molars has been interpreted as typical of *Homo neanderthalensis* (Bailey, 2002b; Martinón-Torres, 2006). We now know that this species is not only characterized by the high frequency of expression of middle trigonid crests, but also that the structures underlining this crest in the dentine may be different to the ones that contribute to the middle trigonid crest expression in other hominin species (Bailey et al., 2011). However, evolutionary origin and timing of this distinctive Neanderthal pattern remain unclear, as the EDJ expression of the trait has not been examined in geochronologically older hominin species.

In this study, we aim to investigate the expression of trigonid crests at EDJ of the Atapuerca-Sima de los Huesos lower molar sample by means of microCT. Sima de los Huesos site is a small cavity of approximately $8\,m^2 \times 4\,m^2$ that belongs to the Cueva Mayor-Cueva del Silo karst system (Atapuerca, Spain). This site has provided the largest Middle Pleistocene *Homo* fossil record coming from the same place and, to date, the human fossils recovered sum up more than 6500 remains, about the 80% of the worldwide human fossil record for the Middle Pleistocene (Bermúdez de Castro et al., 2004a,b). This extraordinary accumulation gives us the opportunity to study intrapopulation variability in a fossil population (Arsuaga et al., 1991, 1993, 1997; Bermúdez de Castro et al., 2004; Martinón-Torres et al., 2012). Sima de los Huesos hominins have been assigned to *Homo heidelbergensis*, a species that has been interpreted as ancestral to *H. neanderthalensis*, although the exact relationship between both taxa is still matter of debate (Arsuaga et al., 1997; Hublin, 2009; Martinón-Torres et al., 2012; Mounier et al., 2009). Our objectives are to:

- characterize the pattern of trigonid crest expression at the OES and EDJ of the SH sample;
- evaluate the concordance of expression between both surfaces;
- place trigonid crest variation in the SH sample into a phylogenetic context and in particular in relation to *H. neanderthalensis*.

2. Materials

2.1. The Sima de los Huesos dental sample

Although the SH dental sample consists of 213 permanent molars, of which 123 are lower molars, we have only included in this study those that were isolated or included in a mandibular fragment small enough to fit in the microCT scanner. In addition, and following Bailey et al. (2011), we excluded those with wear degree higher than category 5 (Molnar, 1971).

2.2. Comparative sample

We compare the SH molars to a sample of *H. neanderthalensis* specimens and to a sample of early and contemporary *H. sapiens*, since the latter is considered the sister lineage of *H. neanderthalensis* (Table 1). The Neanderthal and *H. sapiens* samples were taken from NESPOS© and ESRF© data bases, from El Mirador Cave – an archaeological site located at the southern side of the

Sierra de Atapuerca with human remains from Calcolitic and Bronze Ages (Cáceres et al., 2007) – and from CENIEH's dental collection, composed of clinically extracted teeth from patients of known age and sex, representing a modern Spanish population.

3. Methods

Each molar of the SH sample and the contemporary *H. sapiens* sample, as well as those from El Mirador, was scanned with a Scanco Medical AG Micro-Computed Tomography 80, housed at the CENIEH. The Scanco Medical Micro-CT80 system is characterized by a maximum scan size diameter of 75.8 mm and a maximum scan length of 140 mm, with image matrix from 512 × 512 to 4096 × 4096 pixels. Scans of the *H. heidelbergensis* teeth from Sima de los Huesos used a peak energy of 70 kV and intensity of scanning of 114 μA. The sample time of one projection is 800 000 μs, and the microCT takes nearly 500 parallel projections for each 180°. The resultant slice thickness ranged from 18 to 36 micrometers (μm). Segmentation of the microCT volume was done semi-automatically with manual corrections using AMIRA 5.3.3 (Visage Imaging, Inc.) and no filters were applied. For the rest of the comparative dental sample, we have obtained the microCT scans from the NESPOS© and ESRF© databases.

3.1. Terminological considerations and scoring procedures

Dental literature has been employing different terminologies to refer to the same anatomical parts (e.g., Bailey et al., 2011; Carlsen, 1987; Korenhof, 1982; Martinón-Torres et al., 2012; Scott and Turner, 1997; Turner et al., 1991; Wu and Turner, 1993). In order to avoid confusion and to allow the reproducibility of our method among researchers, we specify below the terms and the terminology sources we have used in this manuscript (Fig. 1). These terms and terminology are based on morphology of the OES. We consider a **cusp** an occlusal projection from the crown (White and Folkens, 2005) that is typically made up of three different **segments** (also called accessory lobes by Scott and Turner, 1997): mesial, middle or essential, and distal. The middle or essential segment is the lobe bearing the cusp (Carlsen, 1987; Scott and Turner, 1997), and the free apex on top of the essential segment will be called **cusp tip** (note that Carlsen, 1987, called it essential cusp, but Scott and Turner, 1997, simply call it cusp).

Arising from these concepts about the basic components of a molar, we can now discuss the different terminologies published so far to refer to the trigonid crests. In 1982, Korenhof analyzed deciduous molars and defined a *mesial* (*sic*) trigonid crest – although Wu and Turner (1993) and Bailey et al. (2011) assumed that Korenhof also called it *middle* trigonid crest – and a distal trigonid crest. These crests were joining the mesial and the distal parts, respectively, of the two main mesial cusps of a lower molar. Wu and Turner (1993) defined a *middle* and a *distal* trigonid crest, but they did not find individuals expressing both crests at the same time. According to them, when a complete crest connects the middle portions of the mesial cusps

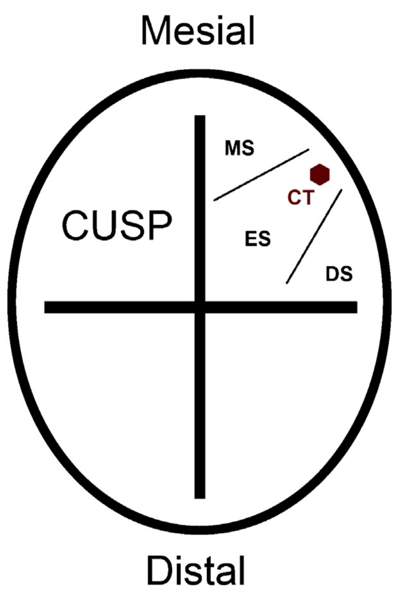

Fig. 1. Scheme of some of the molar crown structures used in this study. MS: mesial segment; ES: essential segment; DS: distal segment; CT: cusp tip.

Fig. 1. Schéma de quelques structures de couronne de molaires utilisées dans cette étude. MS : segment mésial ; ES : segment essentiel ; DS : segment distal ; CT : pointe de la cuspide.

and it lies mesialward, but not on the marginal border, it should be called a middle trigonid crest; otherwise it would be a distal trigonid crest. Scott and Turner (1997) only described a distal trigonid crest, defining it as a crest or ridge that courses buccolingually along the distal aspect of the primitive trigonid, now represented by the protoconid and metaconid.

Finally, in recent studies, Skinner et al. (2008b) and Bailey et al. (2011), scored crests at the EDJ based on their origin and the relative position of one to another, defining a mesial, a middle and a distal trigonid crest. According to them, a mesial trigonid crest could occur between the mesial marginal ridge and the middle trigonid crest or even between cusp tips as far as its position is substantially mesialward within the tooth contour [although according to Carlsen's terminology (Carlsen, 1987) that would be a middle-middle crest]. Although we acknowledge the atypical mesial position of some middle trigonid crests (Fig. 9b from Bailey et al., 2011), in order to standardize terms to discuss anatomy in such a detail, we have preferred to subscribe to the notion the middle or essential segment is the one bearing the cusp tip (Carlsen, 1987; Scott and Turner, 1997). Within this framework, we propose that the three types of crests should be scored independently of the presence/absence of the other, in a similar way as they are scored at the OES (e.g., Guatelli-Steinberg and Irish, 2005; Martinón-Torres et al., 2012).

Methodologically, to score the trigonid crests we draw a straight line from the protoconid to the metaconid tip. Any trigonid crest lying *distal* to this line is classified as a **distal trigonid crest (DTC)**, and over or mesial to this line as a **middle (MdTC)** or **mesial trigonid crest (MeTC)** (Fig. 2). If one of the ends of the crest that runs along the mesial

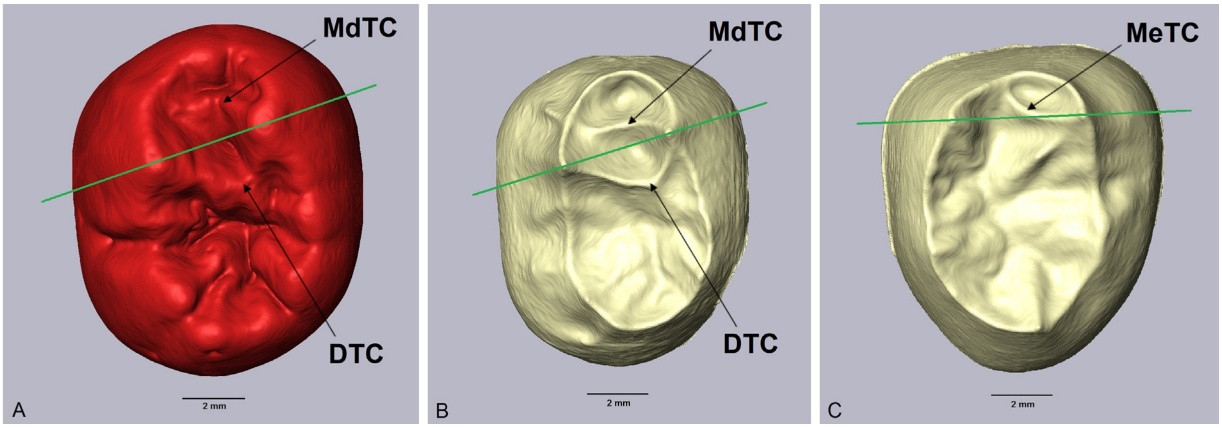

Fig. 2. (Color online.) A. Occlusal enamel surface of AT-2271 (M_3) from Sima de los Huesos (SH) illustrating a middle trigonid crest (MdTC) and a distal trigonid crest (DTC). B. Occlusal dentine surface from AT-2271 illustrating a corresponding middle trigonid crest (MdTC) and a distal trigonid crest (DTC). C. Dentine from AT-143 (M_3) of the SH site where we can see a mesial trigonid crest (MeTC). The green line from protoconid tip to metaconid tip defines the position and classification of the crests.

Fig. 2. (Couleur en ligne.) A. Surface occlusale d'émail d'AT-2271 (M_3) de SH illustrant une crête du trigonide intermédiaire (MdTC) et une crête du trigonide distale (DTC). B. Surface occlusale de dentine d'AT-143 (M_3) du site SH où l'on observe une crête du trigonide médiale (MeTC). C. La ligne verte depuis la pointe du protoconide jusqu'à la pointe du métaconide définit la position et la classification des crêtes.

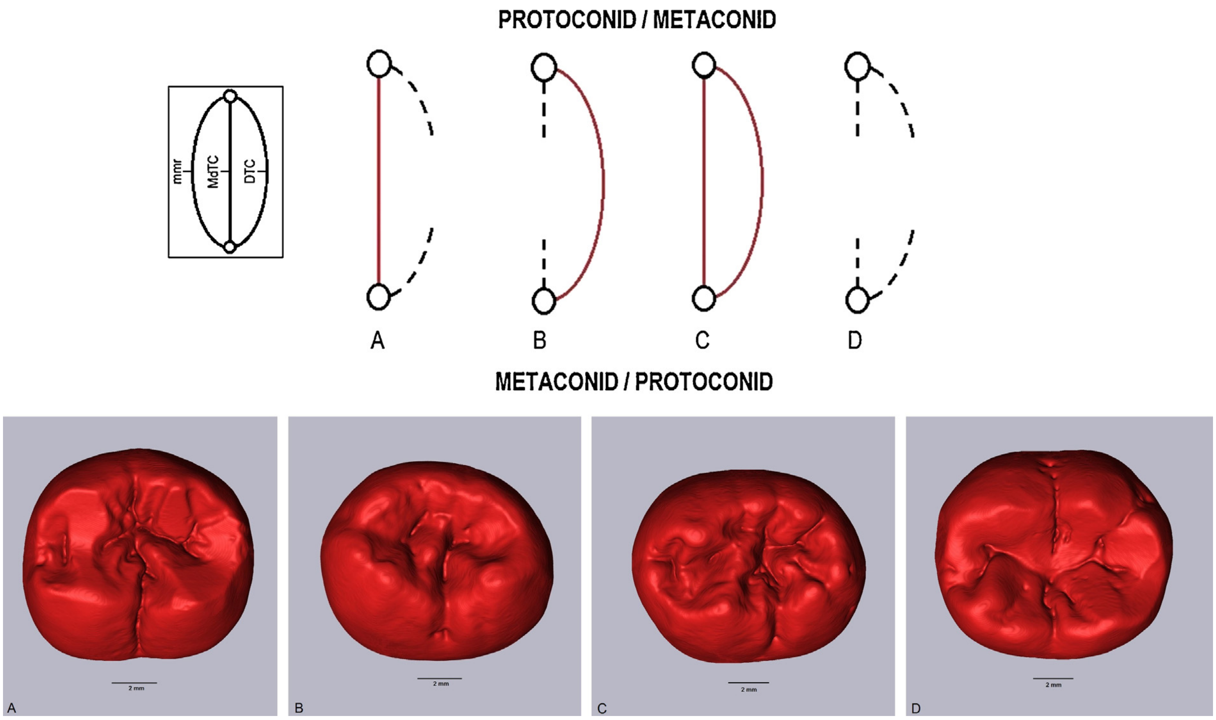

Fig. 3. (Color online.) Top: scheme of the four basic types of trigonid crests on enamel surface identified in our study. Scheme represents the occlusal surface at the outer enamel surface (OES) including the tips of the cusps (represented by the open circles) of the protoconid and metaconid (mmr: mesial marginal ridge). Explanation in the text. Bottom: examples of different types of trigonid crests on the enamel surface: type A (AT-946); type B (AT-2385); type C (AT-2271); type D (AT-943).

Fig. 3. (Couleur en ligne.) En haut : schéma des quatre types de base des crêtes du trigonide sur la surface de l'émail identifié dans notre étude. Le schéma représente la surface occlusale au niveau de l'OES incluant les pointes des cuspides (représentées par les cercles ouverts) des protoconide et métaconide (mmr : arête marginale mésiale). Explication dans le texte. En bas : exemples de différents types de crêtes du trigonide sur la surface de l'émail : type A (AT-946) ; type B (AT-2835) ; type C (AT-2271) ; type D (AT-943).

Based on Korenhof, 1982.

Table 2
Percentages and frequencies of the continuous middle (MdTC) and distal trigonid crest (DTC) at the OES (only one antimere included). We consider the trait is "present" when the crest is continuous. Otherwise we consider that the trait is "absent".
Tableau 2
Pourcentages et fréquences des crêtes du trigonide intermédiaires (MdTC) et distales (DTC) au niveau de l'OES (un seul antimère inclus). Le trait est considéré comme « présent » lorsque la crête est continue. Sinon, le caractère est considéré comme « absent ».

	Total molar sample	M_1	M_2	M_3
Middle trigonid crest at OES				
SH	93.0% (40/43)	100.0% (14/14)	100.0% (11/11)	83.3% (15/18)
H. neanderthalensis	97.0% (33/34)	100.0% (16/16)	100.0% (8/8)	90.0% (9/10)
H. sapiens	39.2% (11/28)	50.0% (6/12)	25.0% (3/12)	50.0% (2/4)
Distal trigonid crest at OES				
SH	25.5% (11/43)	0.0%	0.0%	61.1% (11/18)
H. neanderthalensis	20.5% (7/34)	6.2% (1/16)	12.5% (1/8)	50.0% (5/10)
H. sapiens	0.0%	0.0%	0.0%	0.0%

OES: outer enamel surface; SH: Sima de los Huesos; *H. neanderthalensis*: *Homo neanderthalensis*; *H. sapiens*: *Homo sapiens*.

aspect of the protoconid and metaconid goes to the mesial marginal ridge we define it as a MeTC. If not, we define it as a MdTC [what Korenhof (1982) calls mesial trigonid crest, in our study is considered as a middle trigonid crest]. We are aware that this method may imply some problems in the case of teeth with more atypical shapes and where the cusp tips are displaced. However, it relies in the anatomical components of a tooth and thus, we believe it is more consistent in the identification of the components. The recognition of the crests depending on the co-expression of other crests and the relative position of one respect to another (Bailey et al., 2011) would be indeed more problematic in the case of displaced cusps or atypical shapes. Based on observations of the study sample it is not possible at the OES to reliably differentiate a mesial (i.e., one in which a part of the crest meets the marginal ridge) from a middle trigonid crest. Therefore, at the OES we only score a middle trigonid crest and a distal trigonid crest, following traditional scoring systems (Korenhof, 1982; Scott and Turner, 1997). Furthermore, in those cases where an accessory cusp 7 (or metaconulid) is present and spatially belongs to the trigonid, we consider it as part of the distal segment of the metaconid. Summarizing, and taking into account all the anatomical considerations above, at the OES we recognize four basic types of trigonid crest expression (Fig. 3):

- type A: a continuous MdTC and an absent or discontinuous DTC;
- type B: continuous DTC and absent or discontinuous MdTC;
- type C: continuous MdTC and DTC;
- type D: absent or discontinuous MdTC and DTC.

Although both antimeres were analyzed, we employed the unilateral count method (Turner, 1987), and in case of asymmetry we have chosen the tooth with the highest degree of expression for the trait because we consider that it has more strongly expressed the genetic signal. Since the analyzed dental features are minimally affected by sexual dimorphism (Turner et al., 1991) both sexes have been pooled together. We report the inventory of the trigonid crest patterns of variation found at the EDJ in the SH molar sample, as well as the frequencies and percentages of the trigonid crests pattern at both the OES and EDJ per molar class. To test for significant correspondence of the TC patterns between the OES and the EDJ among SH, *H. neanderthalensis* and *H. sapiens*, a non-parametric Chi-square (PAST, Hammer et al., 2001) test is used. For the statistical analysis of the OES, the data were dichotomized into "presence" and "absence" (we considered that the trait is "present" when the crest is continuous, otherwise we consider that the trait is absent). For the statistical comparison of the EDJ, we compare the frequencies of "continuous", "discontinuous", and "absence". Results were considered statistically significant with a P-value < 0.05.

4. Results

4.1. Trigonid crest types at the OES

Table 2 presents the frequency of expression of a continuous MdTC and DTC at the OES. We observe that the totality of the SH and Neanderthal M_1 and M_2 samples present a continuous MdTC. For the M_3s, this type of crest is present in the 83.3% of the SH sample and the 90% of the *H. neanderthalensis*. Concerning to *H. sapiens*, almost half of the sample analyzed presents this expression of a MdTC, with the highest value for M_1s (50%) and M_3s (50%), followed by M_2s (25%). Regarding a **continuous DTC** at the OES, we observe that for the SH sample, these are only present in the M_3s. Meanwhile, the Neanderthal sample is the only one that exhibits continuous DTC in all molar types, with an increase from M_1 to M_3. In the sample of *H. sapiens*, there are no examples with continuous DTC.

The results of analyses of trait frequencies at the OES between species are provided in Table 3. If we dichotomize the expression into present (continuous crest) and absent (discontinuous or absent crest) we observe that SH and Neanderthals possess significantly higher frequencies of MdTC presence than *H. sapiens* for the M_1, M_2 and total molar sample. For the M_3s, the frequency of a MdTC in *H. sapiens* is lower but they are not significant. Regarding the frequency of DTC presence, once again SH and Neanderthals present higher frequencies for the M_3 and for the whole molar sample. In summary, *H. sapiens* shows significant differences (P < 0.05) when compared with SH and

Table 3
Chi-square test among SH, *Homo neanderthalensis* (NEA) and *Homo sapiens* (SAP) for each tooth position in order to analyze the differences in the trait frequencies (presence/absence) of MdTC and DTC at the OES.
Tableau 3
Test du Chi^2 parmi les spécimens de SH, *Homo neanderthalensis* (NEA) et *Homo sapiens* (SAP) pour chaque type de dent, afin d'analyser les différences entre les fréquences de trait (présence/absence) des MdTC et DTC au niveau de l'OES.

OES (presence/absence)				
	MdTC		DTC	
	NEA	SAP	NEA	SAP
SH				
M_1	–	0.00[a]	0.34	–
M_2	–	0.00[a]	0.22	–
M_3	0.62	0.15	0.56	0.02[a]
Total	0.42	0.00[a]	0.60	0.00[a]
NEA				
M_1		0.00[a]		0.37
M_2		0.00[a]		0.20
M_3		0.09		0.07
Total		0.00[a]		0.01[a]

OES: outer enamel surface; SH: Sima de los Huesos; DTC: distal trigonid crest; MdTC: middle and distal trigonid crest.
[a] Data correspond to *P*-values ($P < 0.05$).

Neanderthal samples; the former possessing a lower frequency of trigonid crest presence than the two latter.

4.2. Trigonid crest types at the EDJ

The variety and combinations of trigonid crests on the dentine surface of the SH sample is much greater than that expressed at the enamel surface. Table 4 presents comprehensive typology and description of all types, which are also illustrated in a schematic form (Fig. 4) and on actual SH specimens (Fig. 5). Table 5 shows that the expression of the **continuous MeTC** usually increases from the M_1 to the M_3. *H. sapiens* are the only group with a discontinuous MeTC. For the SH sample we did not record any M_1 with a continuous MeTC. In general terms, the **continuous MdTC** decreases its expression from the M_1s to the M_3s. Overall, M_1s from the SH sample present this expression of a MdTC. As it was the case for the MeTC, only *H. sapiens* exhibits a discontinuous MdTC. In relation to the **continuous DTC** on the dentine, we can observe that this expression is only present in SH and Neanderthals. The *H. sapiens* sample only presents a discontinuous DTC and only in M_1s and M_2s. In particular, all the M_2s from SH and 7 of 8 Neanderthal M_2s present a discontinuous DTC.

Table 6 displays the results of analyses of trait expression (continuous/discontinuous/absent) at the EDJ among species. Concerning the MeTC, it is relevant to note that there are no significant differences among the three groups whereas for the MdTC and the DTC, *H. sapiens* exhibits significant differences with the other two. SH sample possesses significantly higher frequencies of MdTC expression than *H. sapiens* for the M_1, M_2 and total molar sample. Regarding the DTC, SH shows higher frequencies of expression than *H. sapiens* for the M_2, M_3 and the total molar sample. Thus, the frequencies of MdTC for the M_3s and DTC for M_1s in *H. sapiens* are lower, but not significant. Meanwhile, Neanderthals shows significantly higher frequencies of MdTC and DTC expression than *H. sapiens* but only for the total molar sample. For the M_1s, M_2s and M_3s

Table 4
Typology and description of trigonid crest forms identified at the dentine surface of the SH sample.
Tableau 4
Typologie et description des formes de crêtes du trigonide identifiées à la surface de la dentine de l'échantillon SH.

Type 1	Continuous MdTC with an absent or discontinuous DTC
Type 2	Continuous MeTC with an absent or discontinuous DTC
Type 3	Continuous DTC when at least one of the origins is the distal segment, with an absent or discontinuous MeTC or MdTC
Type 4	Absent or discontinuous DTC when at least one of the origins is the distal segment, with an absent or discontinuous MeTC or MdTC. The number of distal ridges can be variable
Type 5	Continuous MdTC and a continuous DTC arising from the middle segments
Type 6	Continuous MdTC and a continuous DTC when at least one of the origins is the distal segment
Type 7	Continuous MdTC and a discontinuous DTC when at least one of the origins is the distal segment
Type 8	Continuous MdTC and a discontinuous DTC arising from the distal segments
Type 9	Continuous MeTC and continuous DTC when at least one of the origins is the distal segment
Type 10	Continuous MdTC, a discontinuous DTC when at least one of the origins is the distal segment, and a pronounced distal ridge on one side
Type 11	Continuous MeTC or MdTC, a discontinuous DTC when at least one of the origins is the distal segment, and a discontinuous DTC originated from the distal segments
Type 12	Continuous MdTC, a discontinuous DTC arising from the middle segments and discontinuous DTC arising from the distal segments
Type 13	Continuous MeTC, a discontinuous DTC arising from the middle segments and discontinuous DTC arising from the distal segments
Type 14	Continuous MeTC, a discontinuous DTC when at least one of the origins is the distal segment, and a pronounced distal ridge on one side

DTC: distal trigonid crest; MdTC: middle and distal trigonid crest; MeTC: mesial trigonid crest.

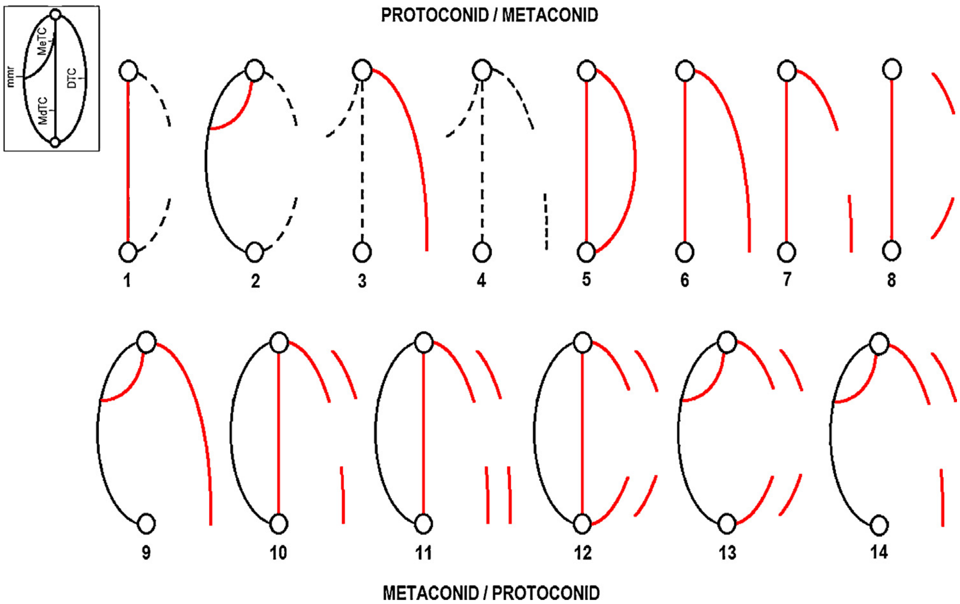

Fig. 4. (Color online.) Scheme of all types of trigonid crests on dentine surface identified in our study from the Sima de los Huesos (SH) molar sample. Explanation in Table 4. View is towards the occlusal surface of the enamel-dentine junction (EDJ) including the tips of the dentine horn (represented by circles) of the protoconid and metaconid and the mesial marginal ridge (represented by the continuous black line). Dashed lines mean that the crest is absent or discontinuous.

Fig. 4. (Couleur en ligne.) Schéma de tous les types de crêtes du trigonide sur la surface de dentine identifiées dans notre étude sur l'échantillon de molaire SH. Explication dans le Tableau 4. La vue est vers la surface occlusale de l'EDJ, incluant les pointes de la corne de dentine (représentées par des cercles) des protoconide et métaconide et de l'arête marginale mésiale (représentée par une ligne continue noire). Les lignes tiretées signifient que la crête est absente ou discontinue.

the frequencies in *H. sapiens* once again are lower, but not significant.

4.3. Variability of the trigonid crest types at the EDJ

The four basic types of trigonid expression at the OES contrast with a wider spectrum of crests types and combinations at the EDJ. As seen in Table 7, type A at the OES is associated with higher variability at the EDJ (10 types), followed by type C (6 types at the EDJ), type D (4 types) and type B (1 type). However, and despite this variability, all teeth generally present a strong correlation between the enamel and dentine surface in the sense that a continuous MdTC at the OES corresponds with a continuous MeTC or MdTC at the EDJ, and vice versa. Similarly, a continuous DTC at the OES tends to correspond with a continuous DTC at the EDJ.

Type A at the OES (continuous MdTC with absent or discontinuous DTC) can be represented at the dentine surface by a continuous MeTC or MdTC in combination with a

Table 5
Frequencies and percentages of the continuous mesial (MeTC), middle (MdTC) and distal trigonid crest (DTC) at the EDJ (only one antimere included). We consider the trait is "present" when the crest is continuous. Otherwise we consider that the trait is "absent".
Tableau 5
Pourcentages et fréquences des crêtes du trigonide mésiales (MeTC), intermédiaires (MdTC) et distales (DTC) au niveau de la jonction émail–dentine (EDJ) (un seul antimère inclus).

	Total molar sample	M_1	M_2	M_3
Mesial trigonid crest at EDJ				
SH	20.9% (9/43)	0.0%	27.2% (3/11)	33.3% (6/18)
H. neanderthalensis	20.5% (7/34)	12.5% (2/16)	25.0% (2/8)	30.0% (3/10)
H. sapiens	7.14% (2/28)	8.3% (1/12)	0.0%	25.0% (1/4)
Middle trigonid crest at EDJ				
SH	72.0% (31/43)	100.0% (14/14)	72.7% (8/11)	50.0% (9/18)
H. neanderthalensis	76.4% (26/34)	87.5% (14/16)	75.0% (6/8)	60.0% (6/10)
H. sapiens	39.2% (11/28)	58.3% (7/12)	25.0% (3/12)	25.0% (1/4)
Distal trigonid crest at EDJ				
SH	23.2% (10/43)	0.0%	0.0%	55.5% (10/18)
H. neanderthalensis	14.7% (5/34)	6.2% (1/16)	12.5% (1/8)	30.0% (3/10)
H. sapiens	0.0%	0.0%	0.0%	0.0%

DTC: distal trigonid crest; MdTC: middle and distal trigonid crest; MeTC: mesial trigonid crest; EDJ: enamel-dentine junction; SH: Sima de los Huesos.

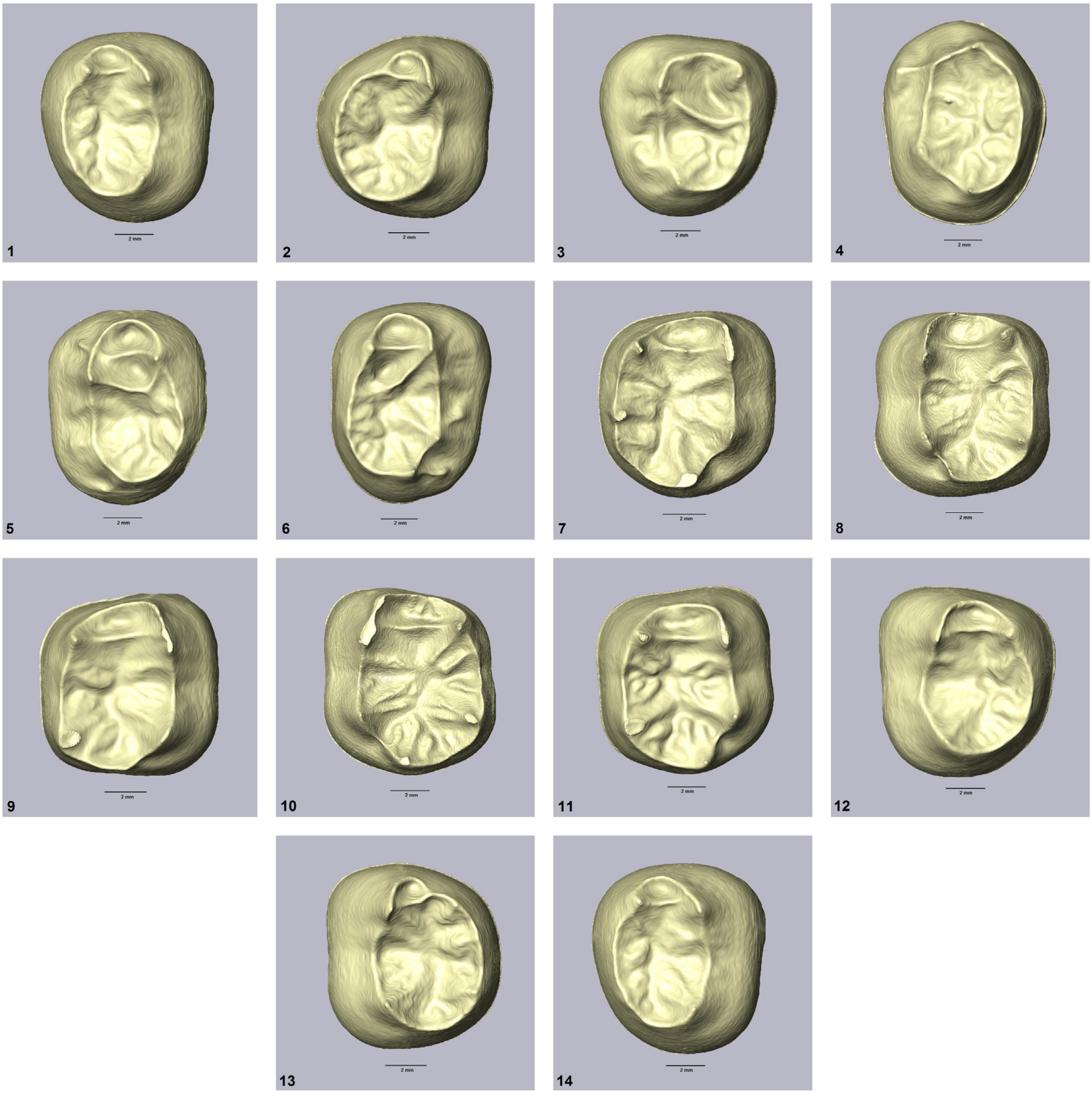

Fig. 5. (Color online.) Examples of different types of trigonid crests on the dentine: type 1 (AT-169); type 2 (AT-1761); type 3 (AT-1945); type 4 (AT-1473); type 5 (AT-2271); type 6 (AT-942); type 7 (AT-141); type 8 (AT-829); type 9 (AT-2438); type 10 (AT-3934); type 11 (AT-2276); type 12 (AT-2270); type 13 (AT-557); type 14 (AT-811). Right molar images (type 2, 5, 6, 7, 9 and 11) have been mirrored to facilitate the comparisons.

Fig. 5. (Couleur en ligne.) Exemples de différents types de crêtes du trigonide sur la dentine : type 1 (AT-169) ; type 2 (AT-1761) ; type 3 (AT-1945) ; type 4 (AT-1943) ; type 5 (AT-2271) ; type 6 (AT-942) ; type 7 (AT-141) ; type 8 (AT-829) ; type 9 (AT-2438) ; type 10 (AT-3934) ; type 11 (AT-2276) ; type 12 (AT-2270) ; type 13 (AT-557) ; type 14 (AT-811). Les images de molaires droites (des types 2, 5, 6, 7, 9 et 11) ont été réfléchies par un miroir pour faciliter la comparaison.

discontinuous DTC, except in Qafzeh 10 (left M_2) where a MeTC or MdTC at the EDJ is absent (type 4). **Type B** (continuous DTC with absent or discontinuous MdTC) at the OES corresponds with an absent or discontinuous MeTC or MdTC and a continuous DTC in all cases. **Type C** at the OES (continuous MdTC and DTC) corresponds to the co-expression of two continuous crests also at the EDJ, except in AT-100 (left M_3) where the MeTC or MdTC at the EDJ is absent -type 3-, AT-811 (right M_3) where the DTC at the EDJ is discontinuous -type 14- and in Regourdou 1, Krapina D4 and Krapina D106 that show at the EDJ a type 2 (MeTC continuous with an absent or discontinuous DTC) crest. **Type D** (absent or discontinuous MdTC and DTC) is also related on the dentine with an absent or discontinuous MeTC or MdTC and a discontinuous DTC in all cases except EQ-H5 (right M_1) where the MdTC is continuous at the EDJ -type 11- and MIR4 P22 205 (left M_1) where there is a continuous MeTC or type 2 at the EDJ.

Table 6
Chi-square test among SH, *Homo neanderthalensis* (NEA) and *Homo sapiens* (SAP) for each tooth position in order to analyze the differences in the trait presence (continuous/discontinuous/absence) of MeTC, MdTC and DTC at the EDJ.
Tableau 6
Test du Chi^2 parmi les spécimens de SH, *Homo neanderthalensis* (NEA) et *Homo sapiens* (SAP) pour chaque type de dent afin d'analyser les différences dans la présence de trait (continu/discontinu/absence) des MeTC, MdTC et DTC au niveau de l'EDJ.

EDJ (continuous/discontinuous/absence)	MeTC		MdTC		DTC	
	NEA	SAP	NEA	SAP	NEA	SAP
SH						
M_1	0.17	0.27	0.17	0.00[a]	0.38	0.09
M_2	0.91	0.10	0.91	0.03[a]	0.22	0.01[a]
M_3	0.85	0.74	0.61	0.08	0.07	0.00[a]
Total	0.97	0.14	0.66	0.00[a]	0.08	0.00[a]
NEA						
M_1		0.72		0.07		0.49
M_2		0.14		0.05		0.06
M_3		0.85		0.19		0.12
Total		0.19		0.00[a]		0.02[a]

DTC: distal trigonid crest; MdTC: middle and distal trigonid crest; MeTC: mesial trigonid crest; EDJ: enamel-dentine junction.
[a] Data correspond to *P*-values ($P < 0.05$).

4.4. Frequencies of expression for the types at the OES and EDJ by tooth class

We have detailed the frequency of the different types of trigonid crest expression on both enamel and dentine surfaces for the M_1 (Table 8), M_2 (Table 9) and M_3 (Table 10) samples using the individual count method. In the M_1s, the highest frequency of expression at the OES for the SH and Neanderthals samples corresponds to **type A**, with a 100% for the former and all but one specimen for the latter. In contrast, in *H. sapiens* **type A** is expressed by half of the sample whereas the other half expresses **type D**. Interestingly, **type D** is absent in SH and *H. neanderthalensis*. At the EDJ, and taking into account that this surface shows more variability than the enamel, we can observe that the most representative trigonid crest types for the SH, Neanderthal and *H. sapiens* samples are **type 8**, **type 10** and **type 4**, respectively.

Concerning the M_2s (Table 9) and at OES, we can observe the same pattern for the SH and Neanderthal samples, with **type A** being displayed by the totality of the sample in the former and all but one in the latter. However, for *H. sapiens* the maximum value at the OES is represented by **type D** (which in turn is absent in SH and Neanderthal M_2s) and the lowest by **type A** (which in turn was the most frequent type in SH and *H. neanderthalensis* M_2s). At the EDJ, the highest frequencies are for **types 11** and **13** for the SH M_2s; **types 7**, **10** and **14** for Neanderthals; and **type 4** for *H. sapiens*, which is present by a little more than half of the sample.

With regard to the M_3 samples, there is a greater variability between the trigonid crest types on enamel and dentine than in M_1s and M_2s (Table 10). For the SH sample, the four types are represented, with **type C** being the most frequent and **type D** the least. Neanderthals exhibit the same pattern as the SH sample with the exception that they do not display **type B**. In *H. sapiens*, half of the sample presents **type A** and the other half displays **type D**. At the EDJ, the highest frequency for the SH M_3s corresponds to **types 5** and **6** in Neanderthals corresponds to **type 2**, and in *H. sapiens* to **type 4**.

Table 7
Variability of the TC types found at the EDJ and their correspondence to the OES from all the studied groups.
Tableau 7
Variabilité des types TC trouvés à la EDJ et leur correspondance au niveau de l'OES de tous les groupes étudiés.

Enamel (OES)	Dentine (EDJ)
Type A	1 - 2 - 4 - 7 - 8 - 10 - 11 - 12 - 13 - 14
Type B	3
Type C	2 - 3 - 5 - 6 - 9 - 14
Type D	2 - 4 - 7 - 11

OES: outer enamel surface; EDJ: enamel-dentine junction; TC: trigonid crest.

5. Discussion

5.1. Variability and frequency of expression at the EDJ

Despite a greater variability in the expression of trigonid crests at the EDJ (14 types) compared to the OES (4 types), in almost all cases there is concordance between the presence of a continuous mid-trigonid and/or distal trigonid crest at the OES and the presence of a continuous mesial/mid-trigonid and/or distal trigonid crest at the EDJ. As an example, and with only a few exceptions presented below, a type A at the OES (continuous MdTC) always corresponds at the EDJ with types where the MeTC or the MdTC is continuous (types 1, 2, 7, 8, 10, 11, 12, 13, 14). Similarly, a type C at the OES (continuous DTC) always corresponds at the EDJ with types where the DTC – regardless the origin – is continuous. This is particularly useful in the case of worn teeth, because it allows estimation of the type of trigonid crest pattern that would have been present at the unworn OES.

Regarding the distal trigonid crest at the EDJ, Wu and Turner (1993) did not find individuals expressing both a MdTC and DTC, and Bailey et al. (2011) did not observe molars with a distal-distal configuration ("true" distal trigonid crest sensu Bailey et al., 2011). Conversely, our study identified several cases of co-expression of MdTC and DTC, and we have also found cases of "true" distal trigonid crest in SH sample; although they are not very common (2 molars or 4.7%) and only M_3s display it (Fig. 6). Concerning a crest that connects middle and distal segments, Bailey et al. (2011) found only a small number of cases (and only in *Homo sapiens*) whereas in our analysis we have found five M_3s from SH sample (11.6%) and four molars from Krapina – one M_1, one M_2 and two M_3s – from *H. neanderthalensis* (11.8%). However, there are no examples in our *H. sapiens* sample that present this type of trigonid crest pattern. These discrepancies may be related to the limitations of trying to characterize the variability of a species with small sample sizes and possibly to some differences in the scoring system employed in Bailey et al. (2011) and our study (see Terminological considerations and Scoring procedures section).

Table 8
Frequency of expression of trigonid crests and their percentages on both enamel and dentine for the M_1 permanent molars analyzed of *Homo heidelbergensis*, *Homo neanderthalensis* and *Homo sapiens.*
Tableau 8
Fréquence d'expression des crêtes du trigonide et pourcentages associés sur l'émail et la dentine pour les molaires permanentes M_1 analysées issues de *Homo heidelbergensis*, *Homo neanderthalensis* et *Homo sapiens*.

SH				Homo neanderthalensis				Homo sapiens			
OES types	n/%	EDJ types	n/%	OES types	n/%	EDJ types	n/%	OES types	n/%	EDJ types	n/%
A	14 (100%)	1	1 (7.14%)	A	15 (93.75%)	1	0	A	6 (50%)	1	1 (8.33%)
B	0	2	0	B	0	2	0	B	0	2	1 (8.33%)
C	0	3	0	C	1 (6.25%)	3	0	C	0	3	0
D	0	4	0	D	0	4	0	D	6 (50%)	4	4 (33.33%)
Total	14	5	0	Total	16	5	0	Total	12	5	0
		6	0			6	1 (6.25%)			6	0
		7	2 (14.28%)			7	1 (6.25%)			7	1 (8.33%)
		8	4 (28.57%)			8	1 (6.25%)			8	2 (16.66%)
		9	0			9	0			9	0
		10	3 (21.42%)			10	5 (31.25%)			10	1 (8.33%)
		11	3 (21.42%)			11	3 (18.75%)			11	1 (8.33%)
		12	1 (7.14%)			12	3 (18.75%)			12	1 (8.33%)
		13	0			13	0			13	0
		14	0			14	2 (12.50%)			14	0
		Total	14			Total	16			Total	12

OES: outer enamel surface; EDJ: enamel-dentine junction; SH: Sima de los Huesos.

Concerning the origin of the crests that conform the middle trigonid crest at the EDJ, we can observe that from the SH molars analyzed (n = 43) there are 31 specimens with MdTC, 20 of which (64.5%) present a middle-middle crest (see Fig. 7) (i.e., a "true" middle trigonid crest *sensu* Bailey et al., 2011) whereas the remaining 11 (35.5%) present a MdTC of mesial-middle origins. Moreover, in our study we have found that the majority of the molars with a MdTC show a crest that remains high between the cusps (grade 3 from Bailey et al., 2011), a type that Bailey et al., 2011 found in their Neanderthal sample, but not in their modern human sample. In accordance with Bailey et al. (2011), this type of crest was also recorded in our *H. neanderthalensis* sample (67.6%) and it was absent in *H. sapiens*. However, grade 3 (*sensu* Bailey et al., 2011) was also present in 77.4% of the SH group.

In addition, among all the molar classes, the M_3s are those with more variability and complexity. Their rather atypical morphologies (i.e., rotation of the cusps within the tooth contour or reduced main cusps in combination with accessory cusps) (see Martinón-Torres et al., 2012), prevented in some cases an easy identification of the morphological features. As an example, in AT-100 the marginal ridge is atrophied and ends at the mesial part of the molar, making it difficult to distinguish whether there is a continuous MeTC or not (Fig. 8). Indeed, most of the cases showing a "mismatch" between surfaces corresponded to atypical teeth. Despite of this inconvenience, there is a general concordance in the expression of continuous crests at the OES and the EDJ, with only some exceptions in which what seems to be a continuous MdTC on the enamel surface actually is a discontinuous MeTC at the EDJ (two for

Table 9
Frequency of expression of trigonid crests and their percentages on both enamel and dentine for the M_2 permanent molars analyzed of *Homo heidelbergensis*, *Homo neanderthalensis* and *Homo sapiens.*
Tableau 9
Fréquence d'expression et pourcentages associés des crêtes du trigonide présentes sur l'émail et la dentine pour les molaires permanentes M_2 analysées issues de *H. heidelbergensis*, *H. neanderthalensis* et *H. sapiens*.

SH				Homo neanderthalensis				Homo sapiens			
OES types	n/%	EDJ types	n/%	OES types	n/%	EDJ types	n/%	OES types	n/%	EDJ types	n/%
A	11 (100%)	1	2 (18.18%)	A	7 (87.5%)	1	0	A	3 (25%)	1	0
B	0	2	0	B	0	2	0	B	0	2	0
C	0	3	0	C	1 (12.5%)	3	0	C	0	3	0
D	0	4	0	D	0	4	0	D	9 (75%)	4	9 (75%)
Total	11	5	0	Total	8	5	0	Total	12	5	0
		6	0			6	1 (12.50%)			6	0
		7	0			7	2 (25%)			7	0
		8	0			8	1 (12.50%)			8	2 (16.66%)
		9	0			9	0			9	0
		10	1 (9.09%)			10	2 (25%)			10	1 (8.33%)
		11	3 (27.27%)			11	0			11	0
		12	2 (18.18%)			12	0			12	0
		13	3 (27.27%)			13	0			13	0
		14	0			14	2 (25%)			14	0
		Total	11			Total	8			Total	12

OES: outer enamel surface; EDJ: enamel-dentine junction; SH: Sima de los Huesos.

Table 10
Frequency of expression of trigonid crests and their percentages on both enamel and dentine for the M_3 permanent molars analyzed of *Homo heidelbergensis*, *Homo neanderthalensis* and *Homo sapiens*.
Tableau 10
Fréquence d'expression et pourcentages associés des crêtes du trigonide présentes sur l'émail et la dentine pour les molaires permanentes M_3 analysées issues de *Homo heidelbergensis*, *Homo neanderthalensis* et *Homo sapiens*.

SH				Homo neanderthalensis				Homo sapiens			
OES types	n/%	EDJ types	n/%	OES types	n/%	EDJ types	n/%	OES types	n/%	EDJ types	n/%
A	6 (33.33%)	1	0	A	4 (40%)	1	0	A	2 (50%)	1	1 (25%)
B	2 (11.11%)	2	1 (5.55%)	B	0	2	3 (30%)	B	0	2	1 (25%)
C	9 (50%)	3	2 (11.11%)	C	5 (50%)	3	0	C	0	3	0
D	1 (5.56%)	4	1 (5.55%)	D	1 (10%)	4	1 (10%)	D	2 (50%)	4	2 (50%)
Total	18	5	3 (16.66%)	Total	10	5	1 (10%)	Total	4	5	0
		6	3 (16.66%)			6	2 (20%)			6	0
		7	0			7	0			7	0
		8	1 (5.55%)			8	1 (10%)			8	0
		9	2 (11.11%)			9	0			9	0
		10	1 (5.55%)			10	1 (10%)			10	0
		11	1 (5.55%)			11	1 (10%)			11	0
		12	0			12	0			12	0
		13	2 (11.11%)			13	0			13	0
		14	1 (5.55%)			14	0			14	0
		Total	18			Total	10			Total	4

OES: outer enamel surface; EDJ: enamel-dentine junction; SH: Sima de los Huesos.

SH, three for Neanderthals and one for *H. sapiens* sample) (Fig. 9); and with three *H. sapiens* molars in which what seems to be a discontinuous MdTC on the enamel surface actually is a continuous MdTC at the EDJ (Fig. 10). As stated above, it is uncommon and when it occurs it is usually in atypical teeth and often complicated with the expression of a C7.

5.2. Taxonomical implications

In our study, we have followed some traditional criteria from the ASUDAS (Turner et al., 1991; Wu and Turner, 1993) to score the trigonid crest at the OES (for more details see Terminological Considerations above), but we have also recorded the full variability expressed at the EDJ to have a more precise knowledge morphological variation in the SH sample. According to Bailey et al. (2002a,b) and Martinón-Torres et al. (2012) the expression at the OES of a continuous MdTC is a typical Neanderthal feature, but this feature is also present in the Middle Pleistocene hominins fossils from Europe like Sima de los Huesos and Arago—but not in Mauer despite being the holotype of the species *Homo heidelbergensis*. This trait can be also present in earlier species like *H. erectus*, *H. georgicus* and *H. antecessor* but their expression is less pronounced than in Neanderthals and the frequencies tend to be lower (e.g., Martinón-Torres et al., 2007, 2008, 2012; Zanolli, 2013). The pattern of expression of this feature at the OES coincides with previous studies about the OES of SH dentitions that have shown that these fossils present the classic Neanderthal

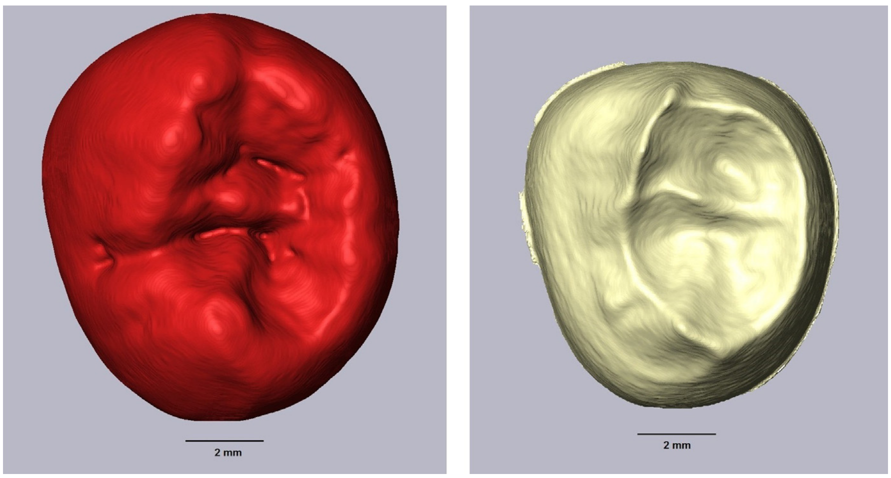

Fig. 6. (Color online.) Illustration of a "true" distal trigonid crest at enamel-dentine junction (EDJ) and outer enamel surface (OES) in an M_3 molar specimen (AT-2385). Virtual reconstruction of dentine and enamel computer models on micro-computed tomography.
Fig. 6. (Couleur en ligne.) Illustration d'une « vraie » crête du trigonide distale au niveau de l'EDJ et de l'OES dans un spécimen de molaire M_3 (AT-2385). Reconstitution virtuelle de modèles de dentine et d'émail informatisés sur un registre microtomographique.

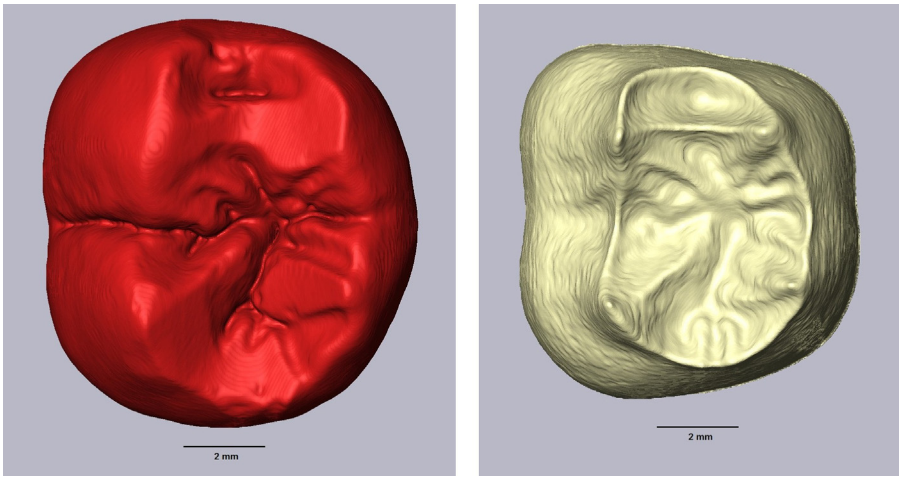

Fig. 7. (Color online.) Illustration of a "true" middle trigonid crest at enamel-dentine junction (EDJ) and outer enamel surface (OES) in an M_2 molar specimen (AT-946). Virtual reconstruction of dentine and enamel computer models based on micro-computed tomography.
Fig. 7. (Couleur en ligne.) Illustration d'une « vraie » crête du trigonide intermédiaire au niveau de l'EDJ et de l'OES d'un spécimen de molaire M_2 (AT-946). Reconstitution virtuelle de modèles de dentine et d'émail informatisés sur un registre microtomographique.

combination of traits (Bermúdez de Castro, 1986; Bermúdez de Castro et al., 1999; Martinón-Torres et al., 2007, 2012). Now, using microCT and virtual segmentations, we can ratify those resemblances at the EDJ. Our study reveals that at the EDJ there is a greater number of SH molars with a middle or mesial trigonid crest than without it, that the middle crest is more frequent than the mesial one and that there is a high proportion of lower molars with a continuous mesial (MeTC) or middle trigonid crest (MdTC) and a discontinuous distal trigonid crest (DTC), which means a clear predominance of type A at the OES. This type is also frequent in our Neanderthal sample and very rare in our *H. sapiens* sample, ratifying the results of Bailey et al. (2011). In addition to the differences in the frequency of expression, there are six trigonid crest types that are expressed in the SH and *H. neanderthalensis* that are absent in the *H. sapiens* group (i.e., types 3, 5, 6, 9, 13 and 14). If analysis of larger and geographically diverse modern human samples confirms this difference, it may be of particular utility in the taxonomic assignment of isolated teeth.

Although a direct comparison between our study and Bailey et al. (2011) analysis is not possible because of the different scoring systems employed, it was possible to make some general assessments between both (Table 11). Thus, if we focus on the percentages that show a continuous MdTC - grade 2 and 3 of Bailey et al. (2011) with a discontinuous DTC, we can assert that the almost constant expression of this pattern in our SH and Neanderthals molars in contrast with the low percentages in

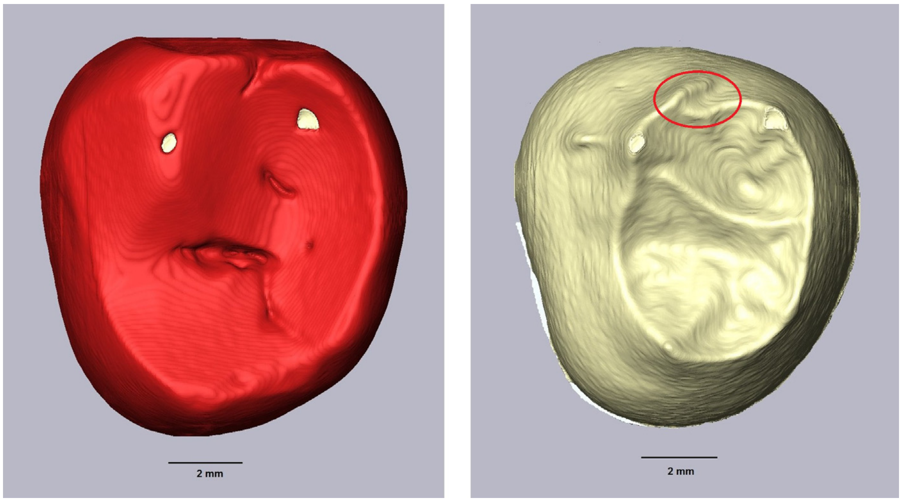

Fig. 8. (Color online.) Enamel and dentine surface of a M_3 (AT-100) with an atrophied mesial marginal ridge (MMR) (see text for specific mention). Virtual reconstruction of dentine and enamel computer models on micro-computed tomography.
Fig. 8. (Couleur en ligne.) Surface de dentine et d'émail d'une M_3 (AT-100) avec une arête marginale mésiale (MMR) atrophiée (voir texte pour mention spécifique). Reconstitution virtuelle de modèles de dentine et d'émail informatisés sur un registre microtomographique.

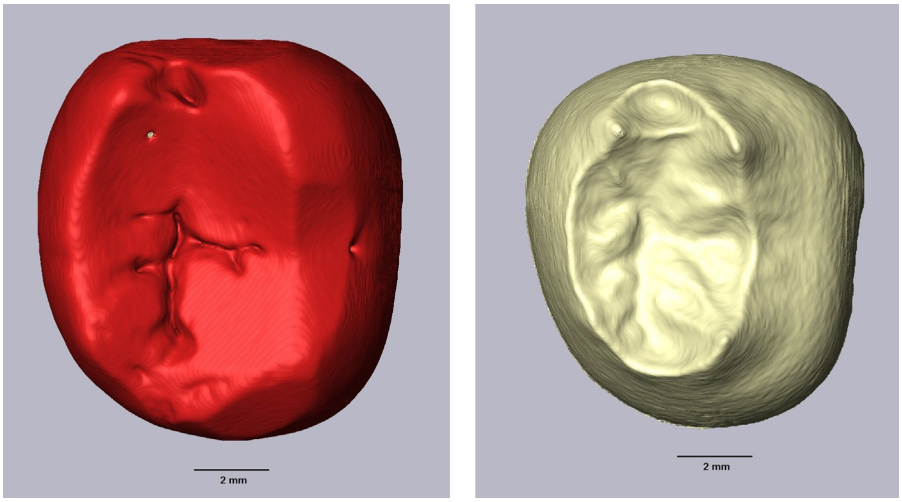

Fig. 9. (Color online.) Enamel and dentine surface of a M_3 (AT-811) with lack of correspondence (see text for specific mention). Virtual reconstruction of dentine and enamel computer models on micro-computed tomography.
Fig. 9. (Couleur en ligne.) Surface de l'émail et de la dentine d'une M_3 (AT-811) avec absence de correspondance (voir le texte pour plus de détails). Reconstruction virtuelle de modèles informatiques pour l'émail et la dentine à partir de données microtomographiques.

our *H. sapiens* sample, is in concordance with the results presented by Bailey et al. (2011) (Fig. 11). Indeed, when a continuous MdTC is present in other group rather than SH or *H. neanderthalensis*, the crests are low and dip further at the sagittal sulcus (this study; Bailey et al., 2011; Zanolli and Mazurier, 2013). As previously stated by Bailey et al., 2011, the structures underlining the MdTC in the dentine tend to be different to the ones that contribute to the middle trigonid crest in other hominin species (Bailey et al., 2011). As an example, the expression of a continuous MdTC at the EDJ in other groups such as *Pan, A. africanus, Homo sapiens* (Bailey et al., 2011) or the North African Middle Pleistocene hominins from Tighenif (Zanolli and Mazurier, 2013) is usually associated to a grade 2. In addition, the expression of a continuous MdTC in *H. sapiens* is never associated with a grade 3 (this study; Bailey et al., 2011).

We have also identified a wide spectrum of trigonid crest types at the EDJ. Importantly, there are three trigonid crests types (types 3, 9 and 13) that are only present in the SH sample and have not been found in the Neanderthal or the *H. sapiens* group. Future studies in larger samples are necessary to know whether these SH exclusive types are present in other hominin groups or if they are particular to the SH group. If they are present in earlier hominins it would mean SH retains some primitive features that are lost in classic Late Pleistocene Neanderthals, as it happens with other cranial and postcranial elements (Arsuaga et al., 1997). On the contrary, if it is confirmed

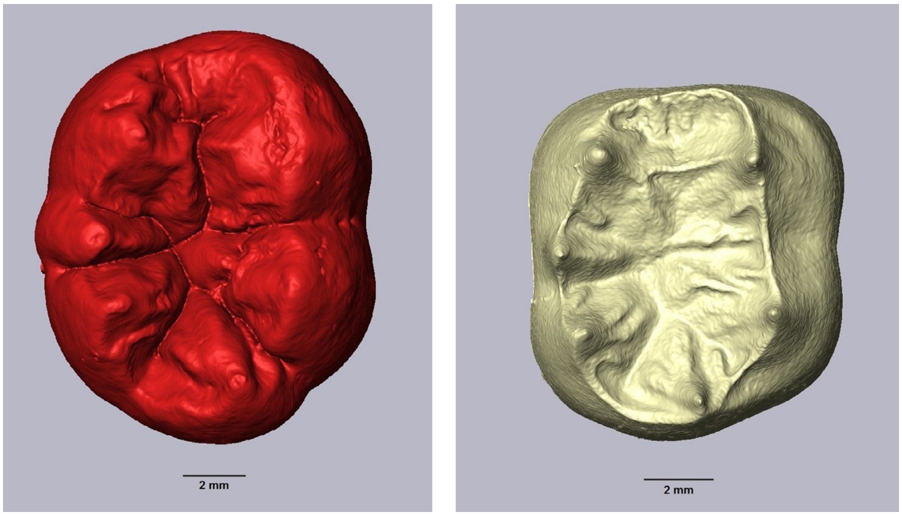

Fig. 10. (Color online.) Enamel and dentine surface of a M_1 (EQ-H5) with lack of correspondence (see text for specific mention). Virtual reconstruction of dentine and enamel computer models on micro-computed tomography.
Fig. 10. (Couleur en ligne.) Surface de l'émail et de la dentine d'une M_1 (EQ-H5) avec absence de correspondance (voir le texte pour plus de détails). Reconstruction virtuelle de modèles informatiques pour l'émail et la dentine à partir de données microtomographiques.

Table 11
Comparison between the data of our samples and those from Bailey et al. (2011) regarding continuous or discontinuous MdTC.
Tableau 11
Comparaison entre les données issues de nos échantillons et celles présentées dans Bailey et al. (2011) en ce qui concerne les MdTC continues ou discontinues.

	This study						Bailey's data			
	SH sample		*H. neanderthalensis*		*H. sapiens*		*H. neanderthalensis*		*H. sapiens*	
	n	%	*n*	%	*n*	%	*n*	%	*n*	%
Enamel (OES)										
MdTC continuous (grade 2-3, Bailey et al., 2011)	40	93.02	33	97.05	11	39.28	61	100	8	11.76
MdTC discontinuous (grade 1, Bailey et al., 2011)	3	6.97	1	2.94	3	10.71	–	–	13	19.11
Dentine (EDJ)										
MdTC continuous (grade 2-3, Bailey et al., 2011)	40	93.02	33	97.05	13	46.42	72	98.63	24	35.29
MdTC discontinuous (grade 1, Bailey et al., 2011)	3	6.97	1	2.94	6	21.42	1	1.36	8	11.76

OES: outer enamel surface; EDJ: enamel-dentine junction; SH: Sima de los Huesos; MdTC: middle and distal trigonid crest.

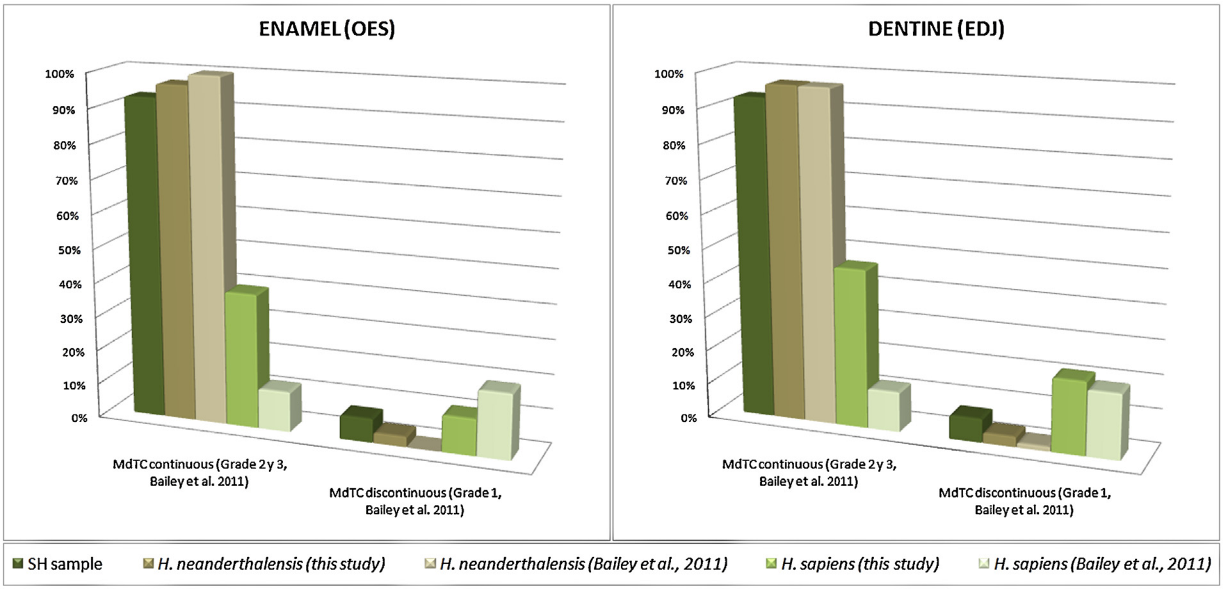

Fig. 11. Illustrations of differences among specimens for grades of presence of middle trigonid crest (MdTC) at the outer enamel and enamel-dentine junction surfaces.
Fig. 11. Illustration des différences entre les spécimens selon les degrés de présence des crêtes du trigonide intermédiaires (MdTC) au niveau de l'OES et de la EDJ.

that those types are not present in any other hominin group, they should be considered as derived (and maybe autopomorphic) features for the SH hominin group, and they would ratify the highly derived state of this population with regard to *H. neanderthalensis* (Gómez-Robles and Polly, 2012; Gómez-Robles et al., 2007, 2008; Martinón-Torres et al., 2012).

6. Conclusions

In agreement with Bailey et al. (2011) and because the EDJ exhibits a greater number of trigonid crest types than the enamel, we developed a comprehensive scoring system to characterize trigonid crest patterning in the Sima de los Huesos lower molar sample. Our analysis reveals higher variability of trigonid crest expression at the EDJ compared to the OES; however, our results confirm the general concordance between the two surfaces with regard to the expression of continuous mesial/middle and distal trigonid crests (Bailey et al., 2011; Skinner et al., 2008b). Thus, the manifestation of the trigonid crest patterns at the enamel is mostly determined by the development of the EDJ. This fact is particularly relevant as it allows prediction of the type of trigonid crest pattern at the OES in the case of excessively worn teeth. This also maximizes the number of teeth that can be analyzed, enlarging the sample size particularly in the case of the scarce fossil human remains.

In concordance with previous studies based on the OES morphology, our study confirms that SH displays trigonid crest patterns that have been classically considered as typical of *H. neanderthalensis* and significantly different from *H. sapiens*. However, it has also shown some trigonid crest types that were present neither in the *H. neanderthalensis* sample nor in the *H. sapiens* sample. Analysis of other Pleistocene hominins will improve the taxonomic and phylogenetic information about these traits, as well as, to make possible evolutionary inferences about the expression of these traits in relation with other ancestral hominins.

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