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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 $M_3$s compared to $M_1$s and $M_2$s. 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.



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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 $M_3$s par rapport aux $M_1$s et $M_2$s. 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