



**UNIVERSIDAD DE BURGOS**

ESCUELA DE DOCTORADO

ESTUDIO Y CARACTERIZACIÓN MORFOLÓGICA DE LOS PATRONES  
DE CRESTAS DEL TRIGÓNIDO Y TALÓNIDO EN EL ESMALTE  
Y EN LA DENTINA DE LOS HOMININOS DEL PLEISTOCENO  
DE LA SIERRA DE ATAPUERCA (BURGOS) MEDIANTE TÉCNICAS  
DE MICROTOMOGRFÍA COMPUTARIZADA.

COMPARATIVA CON OTROS GRUPOS HUMANOS  
E INFERENCIAS EVOLUTIVAS

TESIS DOCTORAL

MARINA MARTÍNEZ DE PINILLOS GONZÁLEZ

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*Dibujo de la portada realizado en acuarela por el artista Fernando Fueyo Gómez, titulado La sierra de Atapuerca en Burgos.*





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PROGRAMA DE DOCTORADO INTERUNIVERSITARIO  
EN EVOLUCIÓN HUMANA, PALEOECOLOGÍA DEL CUATERNARIO  
Y TÉCNICAS DE GEOFÍSICA APLICADAS A LA INVESTIGACIÓN

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MARINA MARTÍNEZ DE PINILLOS GONZÁLEZ

Dirigido por:

Dra. María Martínón Torres  
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**HACE CONSTAR:**

Que el presente trabajo de investigación titulado “Estudio y caracterización morfológica de los patrones de crestas del trigónido y talónido en el esmalte y en la dentina de los homínidos del Pleistoceno de la sierra de Atapuerca (Burgos) mediante técnicas de microtomografía computarizada. Comparativa con otros grupos humanos e inferencias evolutivas” y llevado a cabo por **Dña. MARINA MARTÍNEZ DE PINILLOS GONZÁLEZ** dentro del Programa de Doctorado Interuniversitario de Evolución Humana, Paleocología del Cuaternario y Técnicas Geofísicas Aplicadas a la Investigación, cumple todos los requisitos necesarios para ser aprobado como Tesis Doctoral con la mención de Doctor Internacional, por acuerdo del Consejo de Departamento celebrado el día 28 de septiembre de 2017.

Burgos, a ..... de ..... de 2017

D. Joaquín Pacheco Bonrostro







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**HACEN CONSTAR:**

Que el presente trabajo de investigación titulado “Estudio y caracterización morfológica de los patrones de crestas del trigónido y talónido en el esmalte y en la dentina de los homínidos del Pleistoceno de la sierra de Atapuerca (Burgos) mediante técnicas de microtomografía computarizada. Comparativa con otros grupos humanos e inferencias evolutivas” y llevado a cabo por **Dña. MARINA MARTÍNEZ DE PINILLOS GONZÁLEZ** dentro del Programa de Doctorado Interuniversitario de Evolución Humana, Paleoecología del Cuaternario y Técnicas Geofísicas Aplicadas a la Investigación, cumple todos los requisitos necesarios para ser aprobado como Tesis Doctoral con la mención de Doctor Internacional, por acuerdo del Consejo de Departamento celebrado el día 28 de septiembre de 2017.

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Dra. María Martínón Torres

Dr. José María Bermúdez de Castro Risueño

Dra. María Rebeca García González







*Al pequeño gran milagro de la vida.*

*A Luca.*



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## RESUMEN



## RESUMEN

Los dientes son una valiosa fuente de caracteres morfológicos con importancia taxonómica y filogenética. Además, su alto componente de expresión genética, los convierte en la “caja fuerte” del código genético. En esta tesis doctoral hemos caracterizado y comparado morfológicamente el patrón de crestas del talónido y del trigónido existentes en el esmalte y la dentina para la mayoría de homínidos del Pleistoceno europeo. Además, para comprender la polaridad de dichos caracteres y contextualizar la evolución de las poblaciones europeas, hemos analizado también otros especímenes de diversos yacimientos de África, Asia y Oriente Medio. El total de nuestra muestra de estudio consta de 274 molares que han sido analizados mediante la técnica de la microtomografía axial computarizada (micro CT), y en la que hemos estudiado la variabilidad intra- e inter-poblacional en la expresión de las crestas del trigónido y el talónido. Asimismo, hemos analizado sus frecuencias de expresión y el grado de correlación existente entre la morfología del esmalte y de la dentina para este carácter. Los datos obtenidos demuestran que los patrones de crestas del trigónido son taxonómica y filogenéticamente útiles. Las altas frecuencias de crestas del trigónido continuas muestran una mayor afinidad fenética entre la Sima de los Huesos y *H. neanderthalensis*, frente a las bajas frecuencias de *H. antecessor* y *H. sapiens*. En consonancia con los análisis genéticos de la Sima de los Huesos, nuestros resultados refuerzan la hipótesis de que esta población pertenece al linaje neandertal, lo que implica adelantar cronológicamente el momento en que *H. sapiens* y *H. neanderthalensis* se separaron y reevaluar la posición filogenética de *H. antecessor*. Así, nuestros datos confirman la particularidad morfológica de esta especie, cuya mezcla de caracteres primitivos y derivados con respecto al género *Homo* la posiciona cerca nodo de divergencia de *H. sapiens* y *H. neanderthalensis*. Finalmente, los resultados de nuestra investigación apuntan a una colonización menos lineal del continente europeo, donde posiblemente representaría una de las sucesivas oleadas migratorias que, en el Pleistoceno Inferior, se adentrarían en Europa desde el suroeste asiático. Posteriormente, se sucederían nuevas y distintas incursiones en momentos diferentes que podrían explicar la variabilidad poblacional del Pleistoceno Medio europeo.

**Palabras clave:** Holoceno; Pleistoceno; evolución humana; Europa; sierra de Atapuerca; Sima de los Huesos; *Homo antecessor*; *H. neanderthalensis*; *Homo sapiens*; microCT; morfología dental; crestas del talónido; crestas del trigónido.



## ABSTRACT

Teeth are an important source of morphological traits with taxonomic and phylogenetic value. In addition, their high component of genetic expression makes them the “black box” of genetic code. Through this PhD dissertation we have characterized and compared the pattern of expression of talonid and trigonid crests at the enamel and dentine for most European Pleistocene hominins. In addition, to understand the polarity of these morphological features and to contextualize the evolution of European populations, we have also analyzed other specimens from Africa, Asia and the Middle East. Our total sample consists of 274 molars that have been analyzed by means of micro-computed tomography (micro CT). We present the intra- and inter-population variability in the expression of the trigonid and talonid crests in these groups and assess the correlation between the enamel and dentine surfaces. Our data ratify that the trigonid crests patterns are taxonomically and phylogenetically useful. Sima de los Huesos and *H. neanderthalensis* are phenetically closer in their high frequencies of continuous trigonid crests. This pattern contrasts with the lower frequencies of *H. antecessor* and *H. sapiens*. Our results reinforce the hypothesis that the Sima de los Huesos population belongs to the Neanderthal lineage and, in accordance with recent paleogenetic studies, pushes back the split of *H. sapiens* and *H. neanderthalensis* and compels to reassess the phylogenetic position of *H. antecessor*. Our study confirms that *H. antecessor* has a unique morphological mosaic of primitive and derived features regarding the *Homo* clade and would support its position close to the node of divergence of *H. sapiens* and *H. neanderthalensis*. Finally, our results point to a less linear settlement of Europe, where *H. antecessor* might represent one of the successive hominin waves into this continent, possibly from Western Eurasia. Subsequent dispersals at different times could explain the variability of the European Middle Pleistocene population.

**Keywords:** Holocene; Pleistocene; human evolution; Europe; sierra de Atapuerca; Sima de los Huesos; *Homo antecessor*; *H. neanderthalensis*; *Homo sapiens*; microCT; dental morphology; talonid crests; trigonid crests.



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INTRODUCCIÓN





## 1. INTRODUCCIÓN

### 1.1. ANTROPOLOGÍA DENTAL: LA MORFOLOGÍA DENTAL COMO HERRAMIENTA PARA EL ESTUDIO DE LAS POBLACIONES.

La morfología dental es una fuente importante de información desde el punto de vista funcional (Benazzi et al., 2011, 2013), taxonómico (Bailey, 2002a; Gómez-Robles et al., 2012; Martínón-Torres et al., 2012) y filogenético (Bermúdez de Castro et al., 1999a; Martínón-Torres et al., 2007b; Gómez-Robles et al., 2013). Una de las características principales de los dientes es la dureza de su tejido, lo que implica una mejor conservación que cualquier otra parte esquelética y por tanto una mayor perdurabilidad en el registro fósil, siendo con frecuencia los únicos restos recuperados en un yacimiento. Otra característica, no menos importante, es que los dientes no están sometidos a procesos de remodelación ósea como ocurre con los huesos quienes además pueden verse afectados por factores externos. Es decir, que una vez finalizada la etapa de amelogénesis (formación del esmalte) y dentinogénesis (formación de la dentina), el tamaño y la forma de la corona dental tan sólo se verán modificados por procesos de desgaste. Esta peculiaridad hace que los dientes posean una importante carga genética (Scott y Turner II, 1997) gracias a la cual se puede inferir semejanzas entre los fósiles -rasgos fenéticos- que ayudan a establecer parentesco entre las poblaciones a las que pertenecen (Irish, 1998a). Un ejemplo de ello es la pervivencia, o no, de determinados caracteres morfológicos discretos altamente hereditarios (p. ej., cresta media del trigónido, cresta oblicua, diente en forma de “pala”) que permiten inferir el parentesco entre especies (Wood et al., 1983; Scott y Turner II, 1997; Bailey y Lynch, 2005; Guatelli-Steinberg y Irish, 2005; Pilbrow, 2006; Martínón-Torres et al., 2007a). Por todo ello, la antropología dental es una herramienta útil y eficaz para el análisis y caracterización de poblaciones pasadas y para la realización de estudios de proximidad filogenética entre ellas.

En el siglo XIX numerosos investigadores se dieron cuenta de la importancia de los dientes como fuente de información para estudios ontogenéticos y filogenéticos, desarrollándose así investigaciones en el ámbito de la histología y de la morfología dental (Schreger, 1800; Retzius, 1836; Owen, 1840). Sin embargo las primeras teorías sobre morfogénesis y desarrollo filogenético de los dientes vinieron de la mano de E.D. Cope, H.F. Osborn y W.K. Gregory, entre otros (p. ej., Cope, 1883, 1888; Osborn, 1888,

1895; Gregory, 1921). Ya a comienzos del siglo XX, una de las mayores aportaciones en el campo de la antropología dental fueron los trabajos que A. Hrdlička (p. ej., Hrdlička, 1911, 1921) y posteriormente A. A. Dahlberg (Dahlberg, 1945, 1971, 1991) realizaron sobre la importancia de los rasgos morfológicos dentales como herramienta para el estudio de las poblaciones. A. Hrdlička estudió la forma en pala de los incisivos superiores de poblaciones modernas y creó una escala para cada uno de los grados de desarrollo de dicho carácter (Hrdlička, 1920). Años más tarde, A. A. Dahlberg establecía un sistema de clasificación de diversos rasgos mediante el uso de placas de referencia (Dahlberg, 1956). A partir de entonces, la morfología y la morfometría de los dientes fue ganando peso en el ámbito de estudio de la evolución humana, ofreciendo información sobre relaciones filogenéticas e historia evolutiva (Korenhof, 1960, 1961, 1966, 1978, 1982; Johanson et al., 1982; Wood y Abbott, 1983; Wood et al., 1983; Grine, 1984; Bermúdez de Castro, 1986, 1988; Wood y Uytterschaut, 1987; Wood y Engleman, 1988; Uytterschaut y Wood, 1989).

Sin embargo, un avance importante en el estudio y clasificación de la morfología dental tiene lugar en 1991 cuando, basándose en las placas de referencia creadas por A. A. Dahlberg en 1956, Turner y colaboradores establecen el método ASUDAS (Arizona State University Dental Anthropology System) (Turner et al., 1991). Esta metodología de clasificación de caracteres morfológicos discretos comienza a ser empleada de manera sistemática, no sólo para el estudio de poblaciones modernas (Irish, 1997; Scott y Turner II, 1997; Stringer et al., 1997; Coppa et al., 1998; Irish, 1998a; Cucina et al., 1999) sino también para el análisis y caracterización de especies fósiles (Bailey, 2000, 2002a; b; Guatelli-Steinberg y Irish, 2005; Bailey, 2006; Martínón-Torres, 2006; Bailey et al., 2011).

En la actualidad, los avances tecnológicos están permitiendo abrir nuevas líneas de investigación en el campo de la paleontología que están aportando importante información en el ámbito de la evolución humana (Benazzi et al., 2014; Martin-Francés et al., 2015; Sala et al., 2016; Li et al., 2017). En el caso particular de los dientes, el uso de las técnicas de microtomografía axial computarizada (microCT) nos ha permitido caracterizar morfológica y cuantitativamente los tejidos que los conforman (esmalte, dentina y cemento), obteniendo, de forma no destructiva, cortes histológicos virtuales y reconstrucciones tridimensionales de gran resolución (Kono y Suwa, 2008; Olejniczak et al., 2008a; b; Skinner et al., 2008a; Bailey et al., 2011; Martínón-Torres et al., 2011b; Prado-Simón et al., 2012b; Martínón-Torres et al., 2014; Zanolli et al., 2014; Xing et al., 2015; Zanolli et al., 2015; Fornai et al., 2016; Skinner et al., 2016; Weber et al.,

2016). Los estudios morfológicos clásicos se complementan ahora con la obtención de una serie de nuevas variables con un alto potencial taxonómico y filogenético.

Por todo ello, y puesto que los dientes son una fuente de información primordial a la hora de reconstruir el escenario evolutivo en el que las especies han evolucionado (Turner, 1987; Bermúdez de Castro et al., 1999b; Irish y Guatelli-Steinberg, 2003; Martín-Torres, 2006), la presente tesis doctoral pretende aportar información sobre el origen del poblamiento europeo y las posibles interrelaciones entre grupos, mediante determinados caracteres morfológicos considerados filogenéticamente útiles.

## 1.2. ODONTOGÉNESIS: DESARROLLO Y FORMACIÓN DE LA CORONA.

En el proceso de formación de un diente intervienen varios factores. Así, la morfología de la corona empieza a desarrollarse en una membrana basal o membrana praeformativa, que acabará convirtiéndose en la unión esmalte-dentina, sobre la que finalmente se depositará el esmalte (Butler, 1995).

El aparato masticador de un embrión en desarrollo se encuentra recubierto por un tejido denominado epitelio. Durante la sexta semana de vida intrauterina, la proliferación de las células ectodérmicas basales de la boca primitiva producen un engrosamiento del epitelio bucal que formarán la *banda epitelial primaria* o *epitelio oral* que se dividirá en la *lámina vestibular* y la *lámina dental* (Hillson, 1996). Poco después, en la lámina dental comienzan a producirse crecimientos epiteliales dentro del ectomesénquima que darán lugar a los gérmenes dentales cuyo desarrollo pasará por tres etapas bien diferenciadas: etapa de yema, etapa de casquete y etapa de campana (Figura 1.2.1.).

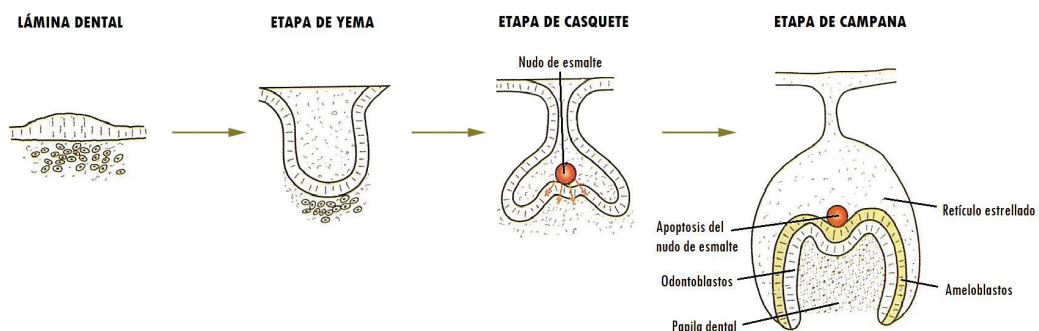


Figura 1.2.1. Proceso de odontogénesis. Imagen modificada de [www.uaz.edu.mx/histo/MorfoEmbrio/Carlson/Cap13/13\\_16.jpg](http://www.uaz.edu.mx/histo/MorfoEmbrio/Carlson/Cap13/13_16.jpg)

Durante la primera etapa, las células epiteliales de la lámina dental proliferan dentro del ectomesénquima y adquieren una forma redondeada. En la siguiente fase o etapa de casquete, tendrá lugar el desarrollo de las estructuras que originarán la matriz de esmalte, la dentina y el cemento (Infante, 2009). Durante esta fase se formará el nudo de esmalte primario que será la base de la corona dental y se eliminará posteriormente por apoptosis. Alrededor del nudo de esmalte primario tendrá lugar el plegamiento inicial del diente (Jernvall et al., 1998; Jernvall y Jung, 2000). En la última fase o etapa de campana se definirá la forma final de la corona. En este estadio ya se diferencian claramente los elementos principales del germen dentario: el órgano dental u órgano de esmalte y la papila dental envueltos por el folículo o saco dental. El epitelio dental interno se pliega para dar lugar al futuro patrón de la corona dentaria. Las células de la papila dental se diferencian en odontoblastos, lo que estimula la diferenciación de ameloblastos por parte del epitelio interno del esmalte (Infante, 2009). Mientras en la dentición anterior (incisivos y caninos) el ápice del capuchón dental dará lugar a la única cúspide, en la dentición posterior (premolares y molares) aparecerán nudos de esmalte secundarios que formarán las futuras cúspides (Jernvall et al., 1994; Jernvall y Jung, 2000).

La evolución morfológica de la corona de los molares de los homínidos tiene su origen en los molares tribosfénicos característicos de los mamíferos ancestrales (Figura 1.2.2.). E.D. Cope y H.F. Osborn fueron los primeros en intentar explicar la evolución de la morfología dental de los molares (Cope, 1883, 1887, 1888; Osborn, 1888, 1895). H.F. Osborn propuso una nomenclatura basándose en prefijos y sufijos que denominaban el tipo y la localización de cada elemento dental. De esta manera, el *trígono* en los molares superiores y el *trigónido* en los molares inferiores hacían referencia a la estructura dental triangular formada por las tres cúspides principales denominadas *protocono*, *paracono* y *metacono* en los superiores y *protocónido*, *paracónido* y *metacónido* en los inferiores, aunque en la mayoría de los primates el paracónido termina desapareciendo quedando únicamente dos cúspides principales (Scott y Turner II, 1997). Los trabajos de E.D. Cope y H.F. Osborn hablan de una forma cónica de los dientes primitivos a los que se les añadió una cúspide mesial y otra distal. Dicha posición lineal originaria quedó alterada por el desplazamiento de ambas cúspides accesorias hacia la cara bucal en los molares superiores y hacia la cara lingual en los inferiores, confiriendo una morfología triangular al diente. Adicionalmente, aparecerán nuevas cúspides secundarias en la zona distal de dicha estructura triangular que recibirán el nombre de *talón* en los molares superiores y *talónido* en los molares inferiores. El desarrollo del *hipocono* en los

molares superiores ha sido considerado como un paso evolutivo clave en la adaptación y diversificación de muchos grupos de mamíferos (Hunter y Jernvall, 1995). En los molares inferiores, el talónido está formado por las cúspides denominadas *hipocónido*, *entocónido* e *hipoconúlido*, donde esta última tiende a reducirse y/o desaparecer en el género *Homo* a partir del Pleistoceno Medio (Scott y Turner II, 1997). Sin duda alguna, esta compleja evolución en el patrón de cúspides de la superficie oclusal de los molares, favoreció la capacidad de cortar y moler el alimento al mismo tiempo, lo que supuso una apomorfía clave en la diversificación de muchas especies de mamíferos (Luo, 2007).

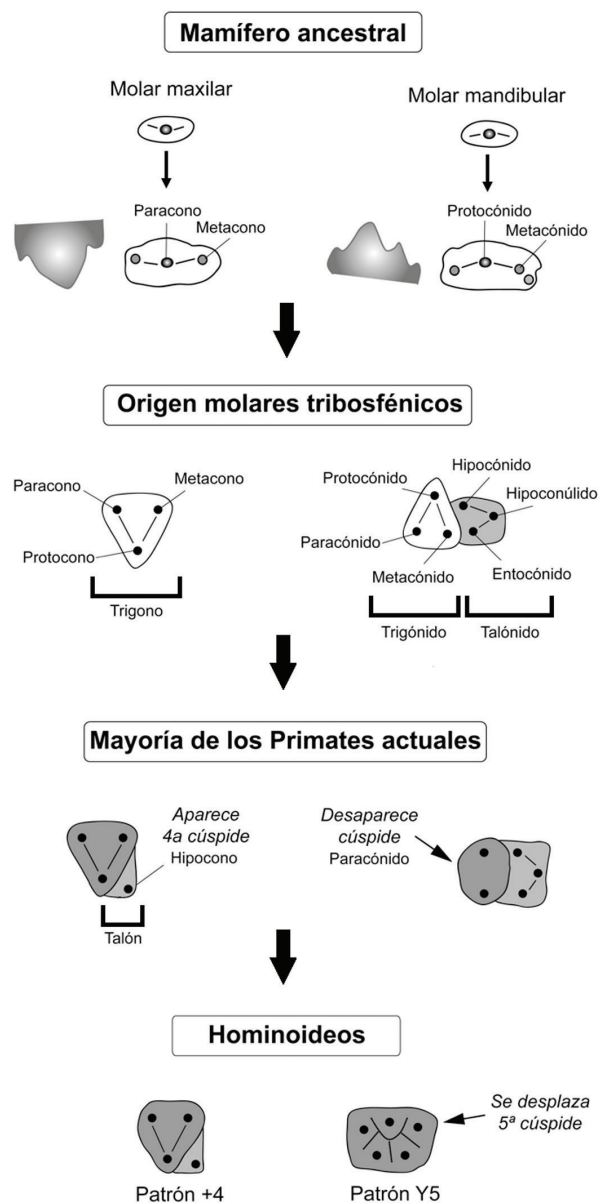


Figura 1.2.2. Origen y evolución morfológica de los molares tribosfénicos. Imagen modificada de Pérez-Pérez et al., 2010.

### 1.3. ESCENARIO EVOLUTIVO EN EUROPA DURANTE EL PLEISTOCENO INFERIOR Y MEDIO.

El periodo cronológico en el que vivieron los antepasados de nuestro propio género se conoce como Pleistoceno. Dicho periodo se divide en tres etapas bien diferenciadas: Pleistoceno Inferior (2,5 Ma-780 ka), Pleistoceno Medio (780-130 ka) y Pleistoceno Superior (130-10 ka). Durante las últimas décadas, el notable incremento del registro fósil, así como los importantes hallazgos en paleogenética (Reich et al., 2010; Gómez-Sánchez et al., 2014; Meyer et al., 2014, 2016; Mathieson et al., 2015), han permitido obtener datos relevantes que, por un lado han reabierto el debate sobre la taxonomía y filogenia de determinadas especies ya existentes (p. ej., *H. heidelbergensis*), y por otro están ayudando a plantear diferentes hipótesis sobre el escenario evolutivo más plausible para el Pleistoceno europeo.

En Europa existen varios yacimientos con presencia humana durante el Pleistoceno Inferior como son Sima del Elefante en Atapuerca (Burgos, España), con una antigüedad de entorno a 1,2 Ma (Carbonell et al., 2008a; Bermúdez de Castro et al., 2011b); Barranco León y Fuente Nueva 3 en la cuenca de Guadix-Baza (Granada, España) con una cronología de 1,4 Ma (Oms et al., 2011; Toro-Moyano et al., 2013); Monte Poggiolo y Pirro Nord (Italia) de entre 1 y 1,5 Ma (Arzarello et al., 2016), Kozarnika (Bulgaria) entorno a 1,5 Ma (Sirakov et al., 2010) y Dmanisi (Georgia) con 1,8 Ma (Gabunia y Vekua, 1995a; b). Sin embargo, a día de hoy, *H. antecessor* junto con *H. georgicus* son las dos únicas especies humanas reconocidas científicamente para este periodo cronológico en Europa (Bermúdez de Castro et al., 1997a; Gabunia et al., 2002). El primer hallazgo tuvo lugar en 1994 en el nivel TD6 del yacimiento de la Gran Dolina en la sierra de Atapuerca (Burgos, España), y en la actualidad el hipodigma de *H. antecessor* supera los 150 restos fósiles humanos pertenecientes a un número mínimo de ocho individuos (Bermúdez de Castro et al., 2017) y asociados a más de 600 herramientas líticas. Las últimas dataciones llevadas a cabo en el yacimiento de la Gran Dolina han permitido obtener para el nivel TD6 una cronología aproximada de 900-800 ka (Arnold et al., 2015; Moreno et al., 2015).

A pesar de la fragmentación debida a la actividad de canibalismo practicada por la especie (Fernández-Jalvo et al., 1999), el buen estado de conservación de los restos fósiles hallados en TD6 permitió realizar importantes estudios que llevaron a considerar, en un primer momento, a los homínidos de TD6 como el antepasado común de sapiens y neandertales (Bermúdez de Castro et al., 1997a). Esta hipótesis se basó en

la existencia de ciertas sinapomorfias (novedad evolutiva compartida entre especies) encontradas en los fósiles de *H. antecessor* tales como la posición anterior y vertical del canal incisivo, la escama del hueso temporal convexa y alta, y una morfología facial moderna con una marcada fosa canina (Arsuaga et al., 1999b), que llevó a proponer un origen africano para los restos humanos de la Gran Dolina-TD6 (Bermúdez de Castro et al., 1997a; Rosas y Bermúdez de Castro, 1999). Años después, el estudio detallado de las muestras dentales de la población de la Sima de los Huesos y de los homínidos de la Gran Dolina-TD6, condujo a los investigadores a plantear la posibilidad de una discontinuidad poblacional europea entre las especies del Pleistoceno Inferior y Medio (Bermúdez de Castro et al., 2003a). De esta manera, los homínidos que habitaban en Europa durante el Pleistoceno Inferior habrían sido reemplazados o genéticamente absorbidos por la llegada de otros grupos humanos, hace aproximadamente 600-500 ka, con posible origen africano y responsables de la inclusión del Modo 2 en nuestro continente (Carbonell et al., 1999b; Bermúdez de Castro et al., 2003a).

Años más tarde, Martínón-Torres y colaboradores (2007a) realizaron un análisis exhaustivo de numerosas muestras dentales y llegaron a la conclusión de que *H. antecessor* presentaba una mezcla de rasgos dentales propios de poblaciones Euroasiáticas, de *H. erectus* de Asia, de poblaciones del Pleistoceno Medio de Europa y de *H. neanderthalensis*. Ciertas sinapomorfias compartidas única y exclusivamente con el linaje neandertal (Bailey, 2004; Martínón-Torres, 2006; Gómez-Robles et al., 2007) fue lo que llevó a los investigadores a sugerir algún tipo de relación filogenética entre *H. antecessor* y el linaje neandertal, reflejando una herencia común proveniente de una misma población madre. Investigaciones recientes (Bermúdez de Castro et al., 2010a; Dennell et al., 2010, 2011; Martínón-Torres et al., 2011a; Bermúdez de Castro y Martínón-Torres, 2013), apoyan la hipótesis planteada sobre los estudios craneales, mandibulares y dentales previos (Arsuaga et al., 1999b; Carbonell et al., 2005; Martínón-Torres, 2006; Martínón-Torres et al., 2006; Gómez-Robles et al., 2007; Martínón-Torres et al., 2007a; Bermúdez de Castro et al., 2008) que sugieren una mayor influencia asiática que africana para las poblaciones del Pleistoceno Inferior y Medio de Europa. De este modo, es posible que durante el Pleistoceno Inferior se hubiera producido uno o más eventos de especiación en la parte más occidental de Eurasia, dando lugar a diversas poblaciones que habrían migrado hacia Europa en periodos diferentes.

Desde que en 1907 se hallara la mandíbula de Mauer, cerca de la ciudad de Heidelberg en Alemania (Schoetensack, 1908), el registro fósil existente en Europa para el periodo cronológico del Pleistoceno Medio ha aumentado notablemente



a merced de diversos descubrimientos en Reino Unido, Francia, Alemania, Italia o España entre otros (p. ej., de Lumley y de Lumley, 1971; Bîlly y Vallois, 1977; Green et al., 1989). El descubrimiento de dicha mandíbula llevó a la asignación de una nueva especie conocida como *H. heidelbergensis* y considerada, hasta el hallazgo de los fósiles de la Gran Dolina-TD6, como la especie más antigua de Europa. A partir de aquel momento, todos los fósiles humanos encontrados a lo largo del Pleistoceno Medio en Europa fueron asignados a la especie *H. heidelbergensis*. Actualmente, las poblaciones que habitaron el continente europeo hace aproximadamente medio millón de años son bien conocidas, sobre todo gracias al yacimiento de la Sima de los Huesos situado en la sierra de Atapuerca (Burgos, España) (Aguirre et al., 1990; Arsuaga et al., 1997) cuya antigüedad se estima en  $427 \pm 12$  ka (Arnold et al., 2014). En dicho yacimiento se ha encontrado cerca de 7.000 restos fósiles pertenecientes a, al menos, 28 individuos con edades comprendidas entre los 2 y los 35 años (Bermúdez de Castro et al., 2004b). El perfecto estado de conservación de dichos restos ha permitido obtener importantes datos para caracterizar a los homínidos que habitaron en la sierra de Atapuerca durante el Pleistoceno Medio y que, a día de hoy, constituyen una de las mayores acumulaciones del registro fósil mundial para dicho periodo.

Sin embargo, en la actualidad la especie *H. heidelbergensis* sigue siendo un taxón controvertido. Aún no existe un consenso entre los investigadores que proponían el uso de dicha nomenclatura única y exclusivamente para las poblaciones que habitaron en Europa y cuya evolución terminaba con los neandertales clásicos (Arsuaga et al., 1997b; Rosas y Bermúdez de Castro, 1998; Wood y Richmond, 2000; Antón, 2003), y aquellos que consideraban *H. heidelbergensis* como un taxón “Afro-Europeo” siendo el antepasado común de sapiens y neandertales (Wood, 1992; Rightmire, 1996, 1998, 2001; Mounier et al., 2009). Aunque, sin duda, ambas partes coincidían en que los homínidos del Pleistoceno Medio europeo evolucionaron hacia los neandertales clásicos, mientras que los grupos humanos que habitaron el continente africano durante dicho periodo cronológico dieron lugar a nuestra especie, *H. sapiens*. Los últimos avances en paleogenética, han permitido secuenciar el ADN mitocondrial y nuclear de los homínidos de la Sima de los Huesos (Meyer et al., 2014, 2016). Esto ha permitido, por un lado corroborar lo que algunos investigadores venían sugiriendo sobre la secuencia ancestro-descendiente con continuidad reproductiva para los grupos humanos del Pleistoceno Medio Europeo y los neandertales (Arsuaga et al., 1993, 1997b; Hublin, 1998; Hawks y Wolpoff, 2001), y por otro atribuir los fósiles de la Sima de los Huesos a la misma especie evolutiva que *H. neanderthalensis*. No obstante, es

importante señalar que precisamente el holotipo de la especie de *H. heidelbergensis* (la mandíbula de Mauer) carece de muchos de los caracteres morfológicos apomórficos que agrupan a la mayor parte de los homínidos del Pleistoceno Medio Europeo y que, por tanto, es el que menos se aproxima fenéticamente a los neandertales clásicos. Por tanto, teniendo en cuenta todos estos datos, y sabiendo que la población de la Sima de los Huesos representa más del 80% del registro fósil para los grupos humanos del Pleistoceno Medio europeo, consideramos que la utilidad taxonómica y filogenética de *H. heidelbergensis* es confusa e innecesaria.

#### **1.4. CARACTERIZACIÓN Y ANÁLISIS MORFOLÓGICO DENTAL MEDIANTE MICROTOMOGRAFÍA AXIAL COMPUTARIZADA PARA UN MEJOR CONOCIMIENTO DEL POBLAMIENTO EUROPEO DURANTE EL PLEISTOCENO. RESUMEN DE LAS PUBLICACIONES.**

Las nuevas técnicas de microtomografía axial computarizada (microCT) junto con los programas de reconstrucción virtual tridimensional se han convertido en una herramienta esencial en el ámbito de la paleoantropología. Es frecuente que los restos óseos recuperados en los yacimientos presenten cambios en su morfología debido a los procesos tafonómicos (fragmentación, rotura, deformación, etc.) acontecidos durante su enterramiento. Estas nuevas técnicas han permitido la reconstrucción de especímenes dañados y el acceso a las estructuras internas, hasta ahora desconocidas, obteniendo así una nueva batería de datos para su análisis (Gunz et al., 2009; Berge y Goullaras, 2010; Bermúdez de Castro et al., 2010b; Vialet et al., 2010; Freidline et al., 2013; Benazzi et al., 2014; Spoor et al., 2015).

La aplicación de técnicas microtomográficas y de visionado 3D en los fósiles, ha supuesto el despegue de nuevas líneas de investigación a partir de datos de los que hasta ahora no se tenía acceso, dejando atrás, en su mayoría, los estudios histológicos que requerían técnicas destructivas. En antropología dental, los estudios clásicos se limitaban al análisis de la forma y caracteres morfológicos externos de la corona (Nager, 1960; Korenhof, 1961, 1982; Suzuki y Sakai, 1973; Corruccini, 1978; Carlsen, 1987). Sin embargo, desde hace escasamente una década, se han desarrollado líneas de investigación que abordan estudios morfométricos e histológicos de los tejidos que conforman los dientes, demostrando su importante valor taxonómico y filogenético (Macchiarelli et al., 2006; Skinner et al., 2008a, 2009; Bayle et al., 2009a; Bermúdez

de Castro et al., 2010b; Braga et al., 2010; Bailey et al., 2011; Prado-Simón, 2012; Prado-Simón et al., 2012a; b; Zanolli et al., 2012; Bailey et al., 2014; Kaifu et al., 2015; Zanolli et al., 2015; Zanolli, 2015; Skinner et al., 2016).

Puesto que los fósiles de Atapuerca son los más representativos a la hora de entender la evolución del género *Homo* en Europa durante el Pleistoceno Inferior y Medio, el estudio de su dentición está siendo cada vez más importante. Por tanto, con este trabajo de investigación pretendemos, por un lado, realizar inferencias evolutivas revisando taxonómica y filogenéticamente las distintas especies estudiadas basándonos en la morfología dental analizada, y por otro, comprobar las distintas hipótesis existentes a día de hoy sobre el escenario evolutivo europeo durante el Pleistoceno, proponiendo un asentamiento menos lineal del continente con varias migraciones y/o cruzamiento entre grupos.

Esta tesis doctoral se presenta dentro de la modalidad de tesis por artículos. A continuación exponemos un resumen de dichas publicaciones en donde, a diferencia del orden cronológico detallado en el índice, mantenemos el orden secuencial y lógico de creación. Esto se debe a que en numerosas ocasiones los artículos forman parte de un volumen general, demorando la fecha oficial de publicación.

Nuestro primer trabajo de investigación titulado *Inventory of trigonid crest patterns at the enamel-dentine junction of the Sima de los Huesos molars (Atapuerca)*, se centró en la caracterización de la expresión de un rasgo morfológico dental -conocido como cresta media del trigónido- que aparece en los molares inferiores de ciertos homínidos. El patrón de expresión de este rasgo se ha considerado típico de los neandertales, y por tanto es útil para la clasificación de dientes aislados y su posible atribución a *H. neanderthalensis* o a *H. sapiens* (Bailey et al., 2011; Martín-Torres et al., 2012). Uno de los inconvenientes más importantes que nos surgió a la hora de estudiar dicho carácter morfológico, fue el de establecer criterios únicos de clasificación para poder compararlo con otras muestras ya estudiadas. Además, el análisis interno de los dientes fósiles de la población de la Sima de los Huesos, no sólo nos obligó a reconsiderar las clasificaciones tradicionales que se utilizaban para categorizar las crestas del trigónido (Korenhof, 1982; Turner et al., 1991), sino que nos ayudó a plantear un nuevo y provisional sistema de clasificación para la dentina.

Por ello, en la segunda publicación titulada *Trigonid crests expression in Atapuerca-Sima de los Huesos lower molars: internal and external morphological expression*

*and evolutionary inferences*, desarrollamos la clasificación definitiva o scoring system para cubrir toda la variabilidad existente en la dentina. Es decir, elaboramos un “muestuario” de todos los tipos de crestas del trigónido, que a día de hoy sirven de referencia a otros investigadores para comparar sus colecciones. Igualmente analizamos el grado de concordancia existente entre el esmalte y la dentina y, a pesar de que la variabilidad de crestas del trigónido es mayor en la dentina que en el esmalte, nuestros resultados concuerdan con los de otros investigadores (Skinner et al., 2008b; Bailey et al., 2011) en la existencia de una gran correlación entre ambas estructuras.

Sabiendo que determinados rasgos morfológicos son de utilidad taxonómica y filogenética a la hora de diferenciar especies, nuestro tercer estudio *-Talonid crests expression at the enamel-dentine junction of hominin lower permanent and deciduous molars-* consistió en la caracterización y análisis de la cresta del talónido. Con esta investigación pudimos comprobar cómo de nuevo, nuestros resultados respaldan las diferencias apuntadas por otros autores entre los linajes sapiens y neandertal, así como las afinidades que los homínidos de la Sima de los Huesos presentan con *H. neanderthalensis* (Bermúdez de Castro, 1986, 1993; Bermúdez de Castro et al., 1999b; Bailey, 2002b; Bailey et al., 2011; Martín-Torres et al., 2012). Además, observamos cómo los dientes de la población de la Sima de los Huesos reunían, por un lado, muchos de los rasgos considerados típicos de los neandertales -superando en algunos casos su grado de expresión máxima- y por otro, presentaban características morfológicas particulares y exclusivas de dicha población.

El trabajo titulado *Characterization of the enamel-dentine junction of the hominin permanent lower molars from Arago (Tautavel, France)* se centró en caracterizar, por primera vez, la morfología interna de los molares del Pleistoceno Medio del yacimiento de Arago, en Tautavel (Francia) cuyas últimas dataciones han ofrecido una cronología similar a las aportadas para la Sima de los Huesos (Falguères et al., 2015). Sabiendo que el patrón de crestas del trigónido es útil a la hora de establecer relaciones taxonómicas y filogenéticas (Scott y Turner II, 1997; Bailey, 2002a; Martín-Torres, 2006), consideramos interesante conocer el patrón existente en los homínidos de Arago y así compararlos con diferentes poblaciones del Pleistoceno europeo. Finalmente, nuestros resultados revelaron que la muestra de Arago exhibía patrones de crestas típicos del linaje neandertal aunque con una menor variabilidad en los tipos, lo cual podría estar condicionado por el pequeño tamaño muestral y por tanto no representar la variabilidad real de la población original.

Los siguientes trabajos de investigación se realizaron de manera simultánea y se centraron en aportar datos que nos ayudaran a entender la posición filogenética en la que se encontraban *H. antecessor* desde que, en 1997, se propusiera como una especie nueva (Bermúdez de Castro et al., 1997a).

Primero publicamos *Homo antecessor: The state of the art eighteen years later*, en el que se recopilan los principales resultados obtenidos hasta la fecha. Desde 1994 -cuando se halló el primer resto fósil humano en el nivel TD6 de la Gran Dolina- hasta hoy, han pasado más de veinte años en el que se han realizado innumerables estudios. Además, los avances tecnológicos y el notable incremento del registro fósil en África y Eurasia a lo largo de estas dos décadas, han dado lugar a diversas interpretaciones sobre la posición filogenética de *H. antecessor* y los posibles escenarios evolutivos. Mediante este trabajo, argumentamos que esta especie se define por un mosaico único de caracteres. Por un lado presenta caracteres primitivos con respecto al género *Homo* y, por otro, comparte rasgos derivados con los humanos modernos, *H. neanderthalensis* y poblaciones humanas del Pleistoceno Medio de Europa y China. Estos datos nos ayudan a pensar que, posiblemente hacia la mitad del Pleistoceno Inferior se produjera un evento de especiación entre África y la zona más occidental de Eurasia que daría lugar a un nuevo clado del género *Homo*, del cual *H. antecessor* sería una rama lateral que se asentaría en Europa tras separarse de dicha población ancestral.

Paralelamente al trabajo anterior, llevamos a cabo otros dos estudios para intentar comprender mejor la posición filogenética de los homínidos de la Gran Dolina-TD6. El primero de ellos -*Comparative analysis of the trigonid crest patterns in Homo antecessor molars at the enamel and dentine surfaces*- se centró en comparar y analizar las afinidades existentes entre las poblaciones europeas del Pleistoceno mediante la caracterización del patrón de crestas del trigónido. Para ello, por un lado, dimos a conocer por primera vez el patrón de crestas exhibidas en los molares de *H. antecessor*, y por otro, realizamos un análisis comparativo con el resto de homínidos. Nuestros resultados demostraron que *H. antecessor* exhibía ya, aunque en bajas frecuencias, el patrón de crestas medias del trigónido continuas considerado típico del *H. neanderthalensis*. Este hecho permite afirmar que dicho rasgo morfológico no puede ser considerado una autapomorfía del linaje neandertal propiamente dicha, sino un rasgo surgido en el Pleistoceno Inferior pero convertido en típico del linaje neandertal por sus altas frecuencias de expresión. Así, mientras que las bajas frecuencias de este carácter en *H. antecessor* indican que estarían fenéticamente más cerca de *H. sapiens*; las elevadas frecuencias en la población de la Sima de los Huesos y *H. neanderthalensis*, ratifican nuevamente sus similitudes.

En el artículo *Virtual reconstruction of the Early Pleistocene mandible ATD6-96 from Gran Dolina-TD6-2 (Sierra de Atapuerca, Spain)* abordamos el tema de la filogenia de los homínidos del Pleistoceno Inferior de la sierra de Atapuerca. Mediante la reconstrucción virtual de la hemimandíbula conseguimos obtener nuevas variables con importante valor taxonómico y filogenético. Así, el análisis morfológico concluyó que *H. antecessor* exhibe un patrón derivado con respecto al género *Homo*, por presentar una morfología parabólica de la arcada alveolar cuyo índice se acerca a los valores medios de neandertales y de la población de la Sima de los Huesos. Sin embargo, el alto porcentaje de la longitud de la arcada alveolar frente a la longitud total, confirmó que *H. antecessor* también poseía una estructura mandibular primitiva dentro del género *Homo*. Por último, y puesto que los homínidos de TD6 presentan claras afinidades con las poblaciones euroasiáticas de Pleistoceno, nuestras conclusiones apoyan la teoría de que *H. antecessor* representaría una de las sucesivas oleadas de población que se asentaron en Europa como resultado de un evento cladogenético acaecido en África o el oeste Eurasiático a finales del Pleistoceno Inferior.

Finalmente, en el último artículo *-Early Pleistocene hominin deciduous teeth from the Homo antecessor Gran Dolina TD6 bearing level (Sierra de Atapuerca, Spain)-* estudiamos las características morfométricas de los dientes deciduos recuperados durante las campañas de excavación del 2003 al 2007. Dicho análisis nos permitió identificar y describir nuevos rasgos, en su mayoría primitivos, exhibidos por esta población. Asimismo, nuestros resultados ratifican estudios anteriores sobre la combinación única de caracteres primitivos y derivados de *H. antecessor*. La dentición decidua de los homínidos de TD6 muestra rasgos primitivos con respecto al género *Homo* (p. ej., el desarrollo de una fóvea anterior y posterior en el segundo molar inferior), que unidos a otros caracteres más modernos (p. ej., la presencia de un tubérculo molar bien marcado o la notable reducción del talónido en los primeros molares), confieren a esta especie su particular patrón morfológico. Con este trabajo hemos aumentado el listado de rasgos primitivos y derivados con respecto al género *Homo* exhibidos por *H. antecessor*, que ayudarán a conocer mejor el estatus evolutivo de dicha especie.



# 02

OBJETIVOS Y ESTRUCTURA DE  
LA TESIS





## 2.1. OBJETIVOS

Los objetivos de esta tesis doctoral se resumen en los siguientes puntos:

1. Caracterizar y comparar el patrón de expresión de crestas del trigónido y talónido en el esmalte y la dentina de los molares inferiores de las distintas especies homínidas del Pleistoceno Inferior, Medio y Superior analizadas mediante microtomografía axial computarizada.

1.1. Desarrollar un sistema de clasificación común para la expresión de crestas del trigónido y talónido en el esmalte y la dentina basándonos en una amplia muestra de homínidos del Pleistoceno y humanos actuales.

1.2. Describir y caracterizar la variabilidad de expresión de crestas en los molares inferiores de la población de la Gran Dolina-TD6 y Sima de los Huesos de Atapuerca.

1.3. Estudiar el grado de correlación existente entre la morfología externa (esmalte) e interna (dentina) para todos los especímenes analizados.

1.4. Caracterizar la variabilidad intra e interpoblacional de la expresión de estas crestas en las poblaciones de estudio.

2. Realizar inferencias evolutivas (taxonomía y filogenia) de las distintas poblaciones estudiadas atendiendo a la expresión de las crestas del trigónido y talónido analizadas en esta tesis doctoral.

2.1. Relación existente entre *H. antecessor* y los homínidos del Pleistoceno Medio y Superior de Europa; Pleistoceno Inferior y Medio de África y Asia y *H. sapiens*.

2.2. Relación existente entre la población de la Sima de los Huesos y *H. neanderthalensis*.

2.3. Relación existente entre la población de la Sima de los Huesos con otros homínidos del Pleistoceno Medio de Europa y Pleistoceno Inferior y Medio de África y Asia.

3. Revisión del escenario evolutivo de las poblaciones del Pleistoceno europeo a la luz de la morfología analizada para los molares inferiores.

## 2.2. ESTRUCTURA DE LA TESIS

La presente tesis ha sido estructurada siguiendo el modelo de tesis doctoral mediante compendio de publicaciones. De esta manera, la tesis queda dividida en ocho capítulos siguiendo el esquema detallado a continuación.

El primer capítulo, **Introducción General**, abarca brevemente la historia de la antropología dental y el uso de la morfología dental como herramienta para el estudio de las poblaciones, así como una explicación de los procesos odontogénicos que influyen en el desarrollo y formación de la corona dental. Asimismo, para una mejor comprensión de esta tesis doctoral, hacemos una revisión sobre el poblamiento europeo durante el Pleistoceno Inferior y Medio. Finalmente, añadimos un resumen que sintetiza las diferentes publicaciones incluidas en el presente trabajo y que han ayudado a comprender dicho escenario evolutivo. Un segundo capítulo de **Objetivos y Estructura** en el que se establecen los propósitos principales de esta tesis doctoral. En el tercer capítulo, **Material**, presentamos las muestras incluidas en este estudio y contextualizadas en su marco arqueológico y cronológico. Asimismo, hacemos una breve reseña a los dientes analizados como muestra bibliográfica de comparación pertenecientes a diversos yacimientos de Europa, África, Asia y Oriente Medio y cuyos datos han sido publicados previamente. Igualmente, adjuntamos una tabla con los principales datos de las piezas dentales analizadas en la presente tesis doctoral. El cuarto capítulo hace referencia a la **Metodología** utilizada, explicando los principios y utilidades de la microtomografía axial computarizada que junto con los softwares de tratamiento de imagen y el uso de análisis estadísticos, nos ha permitido segmentar y analizar el material que conforma la muestra de estudio. El capítulo quinto de **Resultados** es el cuerpo de esta tesis doctoral e incluye seis publicaciones indexadas en el Science Citation Index (SCI) junto con otros dos trabajos de investigación realizados durante la preparación de esta tesis doctoral pero no incluidos en el SCI.

Además, presentamos un apartado de resultados inéditos en donde aportamos los datos obtenidos tras el análisis estadístico de comparativa. El capítulo sexto consta de una **Discusión** global en el que abordamos las cuestiones de taxonomía y filogenia de las especies estudiadas, al igual que realizamos una revisión del escenario evolutivo de las poblaciones del Pleistoceno europeo basándonos en los caracteres analizados en la presente tesis doctoral. El capítulo séptimo, **Conclusiones**, sintetiza los aspectos más relevantes obtenidos en este trabajo de investigación. Finalmente, el capítulo octavo referente a la **Bibliografía** detalla cada una de las citas utilizada en la elaboración de esta tesis doctoral. En el apartado de **Anexos** hemos incluido otras publicaciones y trabajos presentados en Congresos Nacionales e Internacionales durante el periodo de realización de la tesis doctoral y relacionados con la misma.



03

MATERIAL



### 3. MATERIAL

La muestra de estudio de la presente tesis doctoral cubre la práctica totalidad de los fósiles dentales humanos conocidos a día de hoy para el Pleistoceno europeo, así como un significativo número de molares de época holocena. Además, para contextualizar la evolución de estas poblaciones y comprender la polaridad de los caracteres observados, hemos incluido como muestra comparativa los dientes humanos de otros yacimientos importantes de África y Oriente Medio, así como los datos disponibles en la literatura sobre la morfología de la superficie amelo-dentinaria en otros homínidos (ver Tabla 3). A continuación hacemos una breve descripción de cada uno de los yacimientos analizados en esta tesis doctoral donde he realizado personalmente la segmentación de las piezas dentales, así como una breve reseña de otros yacimientos de Europa, África, Asia y Oriente Medio disponibles en la literatura científica y que se han incluido como muestra bibliográfica de comparación.

#### 3.1. YACIMIENTOS DE LA SIERRA DE ATAPUERCA

##### 3.1.1. GRAN DOLINA-TD6

A unos 15 km al este de la ciudad de Burgos se encuentra la sierra de Atapuerca, una suave elevación montañosa a 1.079 m sobre el nivel del mar. La sierra de Atapuerca se sitúa en un lugar estratégico en la Península Ibérica conocido como Corredor de la Bureba, un pasillo natural que comunica las cuencas del Ebro y del Duero y que durante más de un millón de años ha servido de paso para homínidos y animales que transitaban entre ambas cuencas (Ortega et al., 2013). La sierra de Atapuerca está formada por roca caliza y en su interior se localiza un complejo sistema kárstico con más de 4 km de galerías y cavidades subterráneas (Ortega, 2009; Ortega et al., 2010, 2014).

Entre los yacimientos de la sierra de Atapuerca que contienen restos fósiles humanos, se encuentra la Gran Dolina. Este yacimiento, situado en la parte noroeste de la Trincheras del Ferrocarril, posee una secuencia estratigráfica de aproximadamente 25 m de profundidad y 18 m de anchura (Bermejo et al., 2017). El yacimiento de Gran Dolina se divide en once unidades estratigráficas (Gil et al., 1987) que cubren un intervalo temporal de más de un millón de años, desde el nivel inferior (TD1) con



$1.25 \pm 0.13$  Ma (Moreno et al., 2015) hasta el nivel superior (TD11) con 0.24 Ma (Berger et al., 2008). Las dos primeras unidades estratigráficas (TD1 y TD2) son facies de interior que, al depositarse cuando la cueva aún estaba cerrada, son arqueológica y paleontológicamente estériles. El resto de las unidades (TD3 a TD11) representan, en su mayoría, rellenos provenientes del exterior compuestos principalmente por barro, brechas, sedimentos laminados y espeleotemas (Parés y Pérez-González, 1999; Campaña et al., 2016, 2017).

En 1993 y tras la realización de un sondeo vertical de 6 m<sup>2</sup> a lo largo de toda la secuencia estratigráfica del yacimiento, se hallaron en el denominado Estrato Aurora del nivel TD6 restos fósiles humanos asociados a herramientas muy rudimentarias (Carbonell et al., 1995). Durante los dos años siguientes de excavación sistemática en los apenas 20 cm de grosor del Estrato Aurora, el número de fósiles aumentó notablemente hasta alcanzar la cifra de 90 restos humanos (Bermúdez de Castro et al., 1997a), 268 piezas líticas de sílex, arenisca, caliza y cuarzo clasificados como Modo 1 (Carbonell et al., 1995, 1999a) así como varios miles de restos de pequeños y grandes vertebrados (Cuenca-Bescós et al., 1999; García y Arsuaga, 1999; Made, 1999). Estudios posteriores de los restos fósiles humanos certificaban la combinación única de caracteres primitivos y derivados con respecto al género *Homo*. Esto permitió que en 1997 dichos restos fueran asignados a una especie nueva: *Homo antecessor* (Bermúdez de Castro et al., 1997a).

Los primeros análisis de paleomagnetismo confirmaron la existencia del cambio de polaridad magnética Matuyama/Brunhes en la zona superior de la unidad estratigráfica TD7, a unos 117 cm por encima del Estrato Aurora, indicando una antigüedad mayor de 780 ka para el nivel TD6 (Parés y Pérez-González, 1995, 1999). De esta manera, los niveles comprendidos entre TD8 y TD11 fueron depositados durante el Pleistoceno Medio, mientras que los niveles de TD1 a TD7 tuvieron lugar durante el Pleistoceno Inferior. Posteriores dataciones mediante la combinación de Resonancia Paramagnética Electrónica (Electro Spin Resonance, ESR) y series de Uranio (U-series) sugirieron para TD6 un rango de edad comprendido entre los 780-857 ka (Falguères et al., 1999; Falguères, 2003), lo que estaría correlacionado con el Estadio Isotópico Marino (Marine Isotope Stages, MIS) 19-21. Mediante la técnica de Termoluminiscencia (TL), (Berger et al., 2008) se analizaron muestras tomadas 1 m por debajo del cambio de polaridad Matuyama/Brunhes y se obtuvo una datación de  $960 \pm 12$  ka. Años más tarde, un nuevo estudio detallado de la magnetoestratigrafía, establecía una edad en torno a los 900 ka para el nivel TD6 (Parés et al., 2013). Tanto los

resultados de la Termoluminiscencia como los de la Magnetoestratigrafía, coinciden en que el depósito sedimentario del nivel TD6 habría tenido lugar durante el MIS 25. Mediante la aplicación de técnicas alternativas de datación por luminiscencia como la Luminiscencia Óptica Estimulada por Transferencia Térmica (Thermally Transferred Optically Stimulated Luminescence, TT-OSL), la Luminiscencia Infrarroja Estimulada por Post-Infrarrojos (Post-Infrared Infrared Stimulated Luminescence, pIR-IRSL) y la Luminiscencia Óptica Estimulada (Optically Stimulated Luminescence, OSL), Arnold y colaboradores (2015) analizaron granos de cuarzo y obtuvieron un nuevo rango de datación de  $846 \pm 57$  ka. La última datación sistemática de la secuencia completa del yacimiento de Gran Dolina se llevó a cabo mediante ESR sobre cuarzos ópticamente blanqueados. Los análisis permitieron obtener un rango cronológico de entre 880-800 ka para el nivel TD6, sugiriendo que el conjunto de restos fósiles humanos se depositaron durante el MIS 21 (Moreno García, 2011; Moreno et al., 2015).

Métodos de datación relativos como la bioestratigrafía han ayudado a reforzar las cronologías establecidas mediante otras técnicas de datación absolutas. La existencia de roedores como *Mymomys savini*, *Iberomys huescarensis* y *Pliomis episcopalis* permitió establecer una cronología para el Estrato Aurora cercana al periodo final del Pleistoceno Inferior (Cuenca-Bescós et al., 1999). Además, el estudio de ciertos fósiles de anfibios y reptiles en el nivel TD6 (Blain et al., 2008) junto con el análisis palinológico que demuestra la existencia de taxones mediterráneos como *Pistacea*, *Celtis*, *Olea* y *Ceratonia* asociados a *Quercus*, *Pinus* y algunas especies de la familia *Cupressaceae* (García Antón, 1998), sugieren que los homínidos del Pleistoceno Inferior de la Gran Dolina habitaron la sierra de Atapuerca con un clima mediterráneo de condiciones húmedas y templadas (Rodríguez et al., 2011).

Entre los años 2003 y 2007 se llevó a cabo una nueva excavación cercana al sondeo original que permitió aumentar la superficie de excavación de TD6 en unos 13 m<sup>2</sup>. Como resultado de esta ampliación, se pudo redefinir la secuencia estratigráfica de TD6, quedando el Estrato Aurora subdividido en seis unidades litoestratigráficas diferentes (Bermúdez de Castro et al., 2008). Todo ello permitió superar el medio millar de herramientas líticas y aumentar el hipodigma de *H. antecessor* con más de 150 restos fósiles humanos craneales y post-craneales que, a día de hoy, han permitido realizar estudios de diversa índole (Martín-Torres et al., 2007b; Lacruz et al., 2013; Bermúdez de Castro y Martín-Torres, 2014; Martín-Torres et al., 2014; Bermúdez de Castro et al., 2015; Gómez-Robles et al., 2015). Aunque las estimaciones sobre el

número mínimo de individuos (MNI) de los restos humanos encontrados en el Estrato Aurora han ido cambiando con el tiempo (Bermúdez de Castro et al., 1999c, 2006, 2008, 2010b), los últimos análisis hablan de al menos 8 individuos (Bermúdez de Castro et al., 2017), cuyas edades fueron estimadas mediante estándares de humanos modernos actuales entre los tres y los diecisiete años (Bermúdez de Castro et al., 1999c). A pesar de que los restos fósiles humanos aparecen fragmentados a causa de una actividad de canibalismo continuada en el tiempo (Fernández-Jalvo et al., 1999; Carbonell et al., 2010; Saladié et al., 2012), el favorable estado de conservación ha permitido realizar estudios paleopatológicos que han evidenciado procesos traumáticos y de estrés a los que los homínidos del Pleistoceno Inferior de la sierra de Atapuerca estuvieron sometidos (Martín-Francés et al., 2015, 2016). En el año 2012, Carretero y colaboradores basándose en estudios anteriores sobre la medición de la clavícula, el radio (Carretero et al., 1999) y un segundo metatarso (Lorenzo et al., 1999), establecieron una estatura media para los homínidos de TD6 en  $172.6 \pm 1.8$  cm. Ese mismo año, Pablos y colaboradores (2012) tras el análisis y estudio de un astrágalo y un cuarto metatarso, establecieron una estatura mínima de  $167.6 \pm 4.7$  cm para las hembras y de  $173.4 \pm 5.1$  cm para los machos de *H. antecessor*.

Las investigaciones llevadas a cabo a partir de los restos humanos de TD6 han aportado importantes datos sobre el mosaico de caracteres primitivos y derivados de *H. antecessor* (Carretero et al., 1999; Lorenzo et al., 1999; Bermúdez de Castro et al., 2003c; Martín-Torres et al., 2007b; Bermúdez de Castro et al., 2008, 2010b, 2012; Pablos et al., 2012; Lacruz et al., 2013; Bermúdez de Castro et al., 2015; Gómez-Robles et al., 2015; Bermúdez de Castro et al., 2017; Martínez de Pinillos et al., 2017). Estos estudios junto con las investigaciones de diferentes fósiles de Eurasia y África (Abbate et al., 1998; Asfaw et al., 2002; Manzi et al., 2003; Macchiarelli et al., 2004; Lumley y Lordkipanidze, 2006; Kappelman et al., 2008; Martín-Torres et al., 2008; Carretero et al., 2009; Krause et al., 2010; Vialet et al., 2010; Roksandic et al., 2011; Liu et al., 2013, 2015; Xing et al., 2014, 2015) han aportado una cantidad considerable de información que favorece la idea de que *H. antecessor* pudo haber compartido con las poblaciones del Pleistoceno Medio y Superior europeo un ancestro común evolucionado en África o en Asia occidental. Además, en el año 2007 y a tan sólo 100 m de la Gran Dolina, se descubrió en el yacimiento conocido como Sima del Elefante, uno de los restos fósiles humanos más antiguos de Europa (Carbonell et al., 2008a). El fragmento de mandíbula (ATE9-1) encontrado en el nivel 9 de dicho yacimiento fue datado en torno a 1.2 Ma y asignado, en un primer momento, a la especie *H. antecessor* (Carbonell et al., 2008a).

Poco después, y ante la ausencia de información suficiente como para incluir a dicho espécimen dentro de un grupo taxonómico ya conocido, se decidió clasificar dicha mandíbula como *Homo* sp. (Bermúdez de Castro et al., 2011b). Todo parece indicar que, tanto la especie representada por ATE9-1 como los homínidos del yacimiento de la Gran Dolina-TD6, podría ser el resultado de uno o más eventos cladogenéticos acaecidos a finales del Pleistoceno Inferior en la parte más occidental de Eurasia (Bermúdez de Castro et al., 2007; Martín-Torres et al., 2007a; Bermúdez de Castro et al., 2008; Endicott et al., 2010; Bermúdez de Castro et al., 2011b; Martín-Torres et al., 2011a; MacDonald et al., 2012; Bermúdez de Castro y Martín-Torres, 2013; Mosquera et al., 2013; Bermúdez de Castro y Martín-Torres, 2014; Bermúdez de Castro et al., 2015).

La muestra de Gran Dolina-TD6 incluida en la presente tesis doctoral consta de tres dientes deciduos y once permanentes correspondientes a un fragmento mandibular derecho con sus tres molares, una hemimandíbula izquierda y cinco dientes aislados (ver Tabla 3).

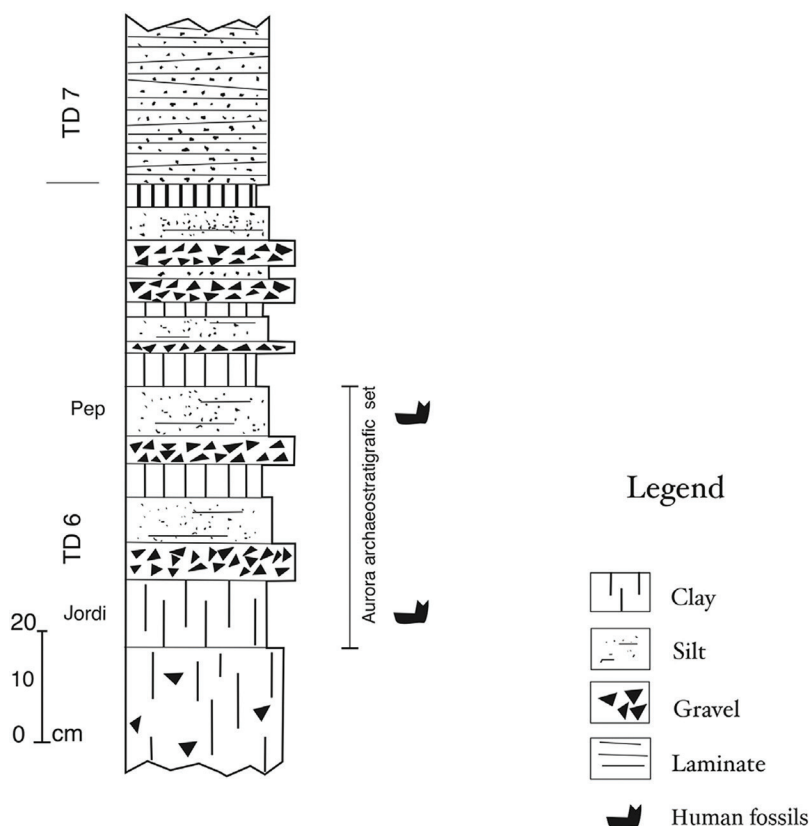


Figura 3.1.1. Secuencia litoestratigráfica de la zona superior de la unidad TD6 de la Gran Dolina (Bermúdez de Castro et al., 2017).

### 3.1.2. SIMA DE LOS HUESOS

La Sima de los Huesos es un yacimiento que forma parte del sistema kárstico de la sierra de Atapuerca cuya entrada tiene lugar en la cavidad conocida como Cueva Mayor (Ortega et al., 2014). Nada más entrar a dicha cavidad nos encontramos con el yacimiento de El Portalón, cuyos depósitos sedimentarios han permitido documentar un registro cronológico que va desde finales del Pleistoceno Superior hasta la época medieval (Carretero et al., 2008; Ortega et al., 2008). Prosiguiendo nuestro camino hacia la Sima de los Huesos, tras dejar El Portalón, hemos de descender por una rampa hasta encontrarnos con una gran sala conocida como Sala del Coro en la que se unen tres galerías: Galería del Betún, Galería Baja, cuyo trayecto termina en el yacimiento de la Sima del Elefante, y Galería del Silo cuyo camino permite llegar hasta la Sima de los Huesos. Tras recorrer 0.5 km de galerías y gateras, para acceder al yacimiento de la Sima de los Huesos hay que descender una pendiente vertical de más de 13 m, seguidos de una rampa de 10 m conocida como Rampa de la Sima de los Huesos y comúnmente dividida en Rampa Alta, Rampa Media y Rampa Baja, que finaliza en una sala de 32 m<sup>2</sup> o Cámara de la Sima de los Huesos, donde se encuentra la mayor parte de los restos fósiles hallados en el yacimiento (Arsuaga et al., 1990, 1991, 1993, 1997b; Cuenca-Bescós et al., 1997; García et al., 1997; Arsuaga et al., 1999a; García et al., 2007; Arsuaga et al., 2014).

Aunque en 1983 se realizó un breve muestreo que proporcionó dientes humanos, no fue hasta un año después cuando se excavó de manera sistemática el yacimiento. Desde 1984 hasta comienzos de los años 90, el trabajo consistió en la evacuación y evaluación de los sedimentos removidos (Aguirre et al., 1990). A partir de 1991 y hasta la actualidad, se lleva excavando *in situ* los niveles inalterados que han permitido recuperar la mayor acumulación de fósiles humanos del mundo en un mismo lugar (Arsuaga et al., 1997a; c).

Los depósitos sedimentarios que componen la Sima de los Huesos se subdividen en 12 unidades lito-estratigráficas (LU-1 a LU-12), donde únicamente las unidades 6 y 7 albergan los restos humanos y de carnívoros, entre los que abunda el *Ursus deningeri*. La LU-6 está compuesta por arcillas plásticas de color marrón-rojizo con gran densidad de restos fósiles y una abundancia de intra-clastos de espeleotemas. La datación realizada sobre un fragmento de espeleotema depositado directamente sobre un cráneo humano hallado en la LU-6, permitió obtener un rango cronológico aproximado de  $434 \pm 36$  ka, concordando con los datos biocronológicos obtenidos

para el conjunto faunístico de la LU-6 y LU-7 (García y Arsuaga, 2011). Mientras, la LU-7 compuesta por sedimentos arcillosos con cuarzos, feldespatos y filosilicatos fue transportada al interior de la cavidad como *debris* y alberga, en su mayoría, restos de grandes carnívoros que fundamentalmente se corresponden con los huesos de *Ursus deningeri* previamente acumulados en la Rampa (Arsuaga et al., 2014). Análisis previos basados en series de Uranio y ESR, sugerían una cronología de 600-200 ka para los restos humanos de la Sima de los Huesos (Bischoff et al., 1997, 2003, 2007). Sin embargo, recientes investigaciones basadas en la combinación de técnicas de datación por luminiscencia, tales como TT-OSL y pIR-IRSL, llevadas a cabo mediante análisis de granos de cuarzo y feldespato provenientes de la LU-7, han proporcionado una edad mínima de  $427 \pm 12$  ka para la acumulación de fósiles humanos de la Sima de los Huesos (Arnold et al., 2014).

Desde el primer fósil humano hallado en 1976 (Aguirre et al., 1976) hasta la actualidad, se han recuperado más de 6.500 restos en donde todas las regiones anatómicas están representadas. Esto, entre otras cosas, ha permitido obtener una estatura media de 163.6 cm para los individuos de la Sima de los Huesos (Carretero et al., 2012). Bermúdez de Castro y colaboradores (2004) estimaron un número mínimo de 28 individuos de ambos sexos y con edades comprendidas entre los cuatro y los treinta y cinco años. Además, sugerían que debido a la homogeneidad de la muestra y al haber sido recuperados en la misma unidad lito-estratigráfica, los homínidos de la Sima de los Huesos pertenecían a una misma población biológica. Esta hipótesis de un único paleo-deme (p-deme), queda de nuevo reforzada en el trabajo de Arsuaga y colaboradores (2014) donde se explica que fósiles recuperados en distintas partes del yacimiento encajan entre sí y no presentan signos de haber sido transportados durante diferentes eventos. Igualmente, la posibilidad de que los restos humanos hubieran podido ser arrastrados al interior por corrientes de lodo, queda descartada debido a la ausencia de clastos del exterior y presencia de frágiles formaciones calcíticas internas. El hecho excepcional de encontrar perfectamente representada una única población biológica, ofrece una oportunidad única a la hora de analizar la variabilidad intra-poblacional e investigar los procesos de hominización.

En cuanto al origen de la acumulación de los homínidos de la Sima de los Huesos, diversos estudios tafonómicos y sedimentológicos se han llevado a cabo a lo largo de todos estos años (Arsuaga et al., 1990, 1997c; Andrews y Jalvo, 1997; Bocquet-Appel y Arsuaga, 1999; Aguirre, 2002; Sala et al., 2014, 2015a; b; Aranburu et al., 2017). Los resultados parecen indicar que los fósiles humanos de Sima de los Huesos no

serían fruto de una trampa natural ni de un cubil de carnívoros, sino más bien una acumulación intencionada de carácter antrópico. Además, el hallazgo en 1998 de un bifaz, que a día de hoy sigue siendo la única herramienta lítica recuperada en el yacimiento, ha sido interpretada como un posible comportamiento simbólico de esta población (Carbonell et al., 2003).

Los análisis faunísticos y palinológicos llevados a cabo en el yacimiento, junto con los estudios basados en isótopos estables, han contribuido a conocer el nicho ecológico en el que habitaban los homínidos del Pleistoceno Medio de la sierra de Atapuerca. Estas investigaciones han descrito un paisaje típicamente mediterráneo de bosques abiertos (Cuenca-Bescós et al., 1997, 2010; García Antón, 1998; García y Arsuaga, 2011; Rodríguez et al., 2011).

La excepcionalidad y singularidad de la muestra fósil de la Sima de los Huesos ha permitido realizar innumerables estudios multidisciplinarios (paleopatológicos, tafonómicos, paleodemográficos, genéticos, morfológicos, métricos, etc.) que han contribuido no sólo a caracterizar mejor a la población del Pleistoceno Medio de la sierra de Atapuerca, sino que a día de hoy están aportando información muy valiosa en el debate taxonómico y filogenético de las poblaciones del Pleistoceno Medio Europeo y el origen de los neandertales (Bermúdez de Castro y Pérez, 1995; Arsuaga et al., 1997b; Carretero et al., 1997; Arsuaga et al., 1999a; Bermúdez de Castro et al., 2001, 2003b, 2004a; b; Rosas y Bastir, 2004; Gómez-Olivencia et al., 2007; Martínez et al., 2008; Lozano et al., 2009; Bonmatí et al., 2010; Gracia et al., 2010; Gómez-Robles et al., 2012; Martín-Torres et al., 2012; Prado-Simón et al., 2012b; Gracia-Téllez et al., 2013; Martín-Torres et al., 2013b; Arsuaga et al., 2014; Meyer et al., 2014; Arsuaga et al., 2015; Martín-Francés Martín de la Fuente, 2015; Pablos et al., 2017; Sala et al., 2015b; Meyer et al., 2016; Quam et al., 2016; Rodríguez et al., 2016).

La muestra de los dientes del yacimiento de la Sima de los Huesos incluidos en esta tesis doctoral está formada por sesenta y cuatro molares permanentes y dos deciduos, correspondientes a diferentes individuos (ver Tabla 3).

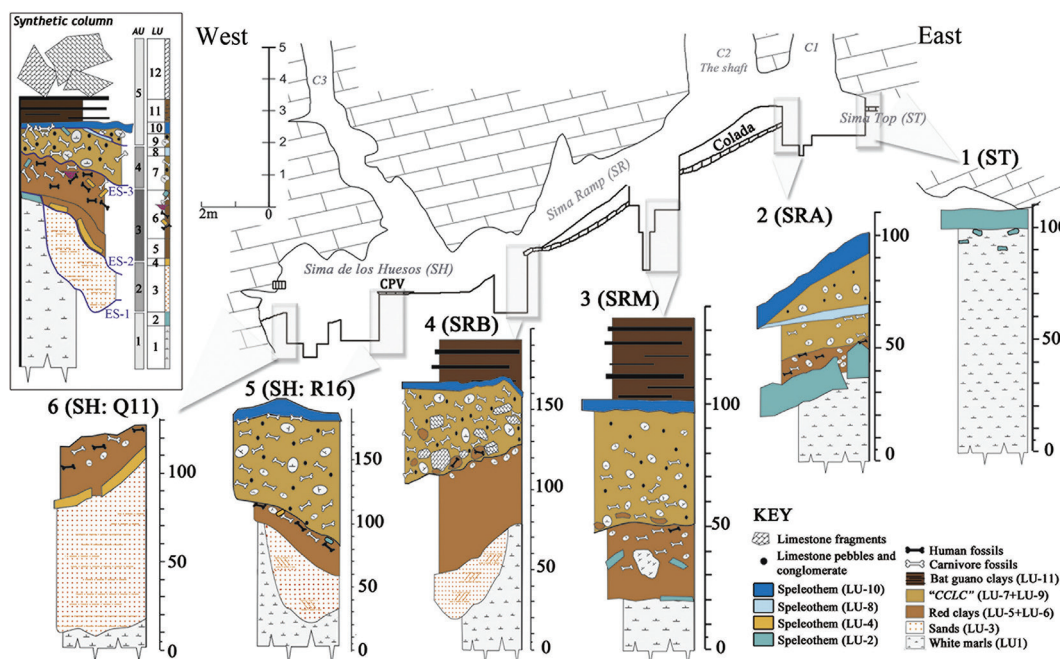


Figura 3.1.2. Sección de la Sima de los Huesos con diferentes columnas estratigráficas analizadas en el yacimiento (Aranburu et al., 2017).

## 3.2. MUESTRA COMPARATIVA ORIGINAL

### 3.2.1. PLEISTOCENO INFERIOR

#### 3.2.1.1. BARRANCO LEÓN

El yacimiento conocido como Barranco León forma parte de un conjunto de yacimientos situados en la región de Orce, al noroeste de Granada. Los 140 m<sup>2</sup> excavados durante más de treinta años, han proporcionado un enorme complejo de industria lítica compuesto por más de 1.200 artefactos de sílex, caliza y cuarcita (Fajardo, 2008), así como evidencias antrópicas en el uso de herramientas sobre huesos de grandes mamíferos (Turq et al., 1996; Gibert et al., 1998; Toro-Moyano et al., 2003, 2009, 2011; Palmqvist et al., 2005; Martínez-Navarro et al., 2010; Espigares et al., 2013). Las dataciones llevadas a cabo mediante ESR han proporcionado una cronología entre 1.02-1.73 Ma (Duval, 2008) que, en combinación con el paleomagnetismo (Oms et al., 2000, 2011; Gibert et al., 2006; Agustí et al., 2007; Scott et al., 2007) y los datos biocronológicos (Maul et al., 1998; Agustí et al., 2010; Oms et al., 2011), han ofrecido una aproximación en torno a 1.4 Ma. Sin embargo, lo más destacado de este yacimiento



es el hallazgo de un molar deciduo inferior izquierdo (BL02-J54-100) analizado en la presente tesis doctoral (ver Tabla 3) que, según las dataciones aportadas, pertenecería a día de hoy, al homínido más antiguo de Europa occidental (Toro-Moyano et al., 2013).



Figura 3.2.1. Localización de los yacimientos con fósiles del Pleistoceno Inferior analizados en la presente tesis doctoral.

### 3.2.2. PLEISTOCENO MEDIO

#### 3.2.2.1. ARAGO

La Caune de l'Arago en Tautavel es una cavidad situada al sur de Francia, en la zona del Pirineo Oriental. Las primeras excavaciones fueron llevadas a cabo por el Profesor H. de Lumley en 1964 y hasta la fecha, este yacimiento ha proporcionado más de 140 fósiles humanos -fragmentos postcraneales, 5 mandíbulas y 123 dientes- asociados a un gran número de especies animales e innumerables restos de industria lítica del Modo 2 (de Lumley y Barsky, 2004). El potencial del yacimiento está formado por una secuencia estratigráfica de 10 m de espesor (de Lumley et al., 2014), donde nuevas dataciones obtenidas mediante ESR y series de Uranio han ayudado a comprender mejor los depósitos sedimentarios (Falguères et al., 2015). Todos los fósiles humanos provienen de 15 unidades arqueostratigráficas que van desde los 550 ka (nivel inferior de la Unidad Q) a los 400 ka (nivel superior de la Unidad C), aunque la mayoría proceden de las unidades F y G (de Lumley M.-A., 2015).

La muestra incluida en la presente tesis doctoral -cinco molares permanentes y un deciduo (ver Tabla 3)- proviene de las unidades F, G y C cuya cronología aproximada es de 450-350 ka (de Lumley M.-A., 2015; Falguères et al., 2015). Estas nuevas dataciones confirman la contemporaneidad de los restos fósiles humanos del yacimiento de Arago con los homínidos de la Sima de los Huesos de Atapuerca datados en  $427 \pm 12$  ka (Arnold et al., 2014). Es por ello por lo que los fósiles humanos de la Caune de l'Arago son una importante fuente de información para investigar la evolución humana en Europa durante el Pleistoceno Medio (de Lumley M.-A., 2015).

### **3.2.2.2. MONTMAURIN-LA NICHE**

El sistema kárstico de Montmaurin está formado por ocho cavidades. Entre 1946 y 1961, L. Méroc y su equipo comenzaron las excavaciones de los depósitos sedimentarios del complejo de cuevas de Montmaurin, en el valle de Seygouade cerca del Pirineo francés (Méroc, 1948; Baylac et al., 1950). Dentro de este complejo kárstico se encuentra la cueva de La Niche, una chimenea vertical donde en 1949 R. Commas y colaboradores encontraron restos craneales y post-craneales asociados a una industria premusteriense (Baylac et al., 1950; Cammas y Tavano, 1986). Entre los fósiles destacados se encuentra una mandíbula casi completa perteneciente a un individuo adulto considerado preneandertal (Vallois, 1955, 1956; Billy y Vallois, 1977) cuyos molares han sido incluidos en nuestra muestra de estudio (ver Tabla 3). En un primer momento, el análisis del material arqueológico y estratigráfico permitió asociar los fósiles humanos al periodo interglaciar Riss-Würn o MIS 5 (Vallois, 1956; Tavano, 1982; Cammas y Tavano, 1986; Tavano et al., 1990). Sin embargo, un nuevo estudio del contexto geomorfológico y faunístico de la cavidad ha hecho posible atribuir la acumulación con restos humanos al MIS 7 (Crégut-Bonnouere et al., 2010).

### **3.2.2.3. TIGHENIF**

El yacimiento de Tighenif, también conocido como Ternifine, está situado a 20 km al este de Mascara (Argelia). Su descubrimiento tuvo lugar entre 1954 y 1955, gracias a las excavaciones llevadas a cabo por C. Arambourg y R. Hoffstetter (Arambourg, 1954, 1955, 1957; Arambourg y Hoffstetter, 1954). En el yacimiento se han encontrado restos de fauna (Geraads, 1981; Geraads et al., 1986), industria lítica (Balout y Tixier, 1956; Balout et al., 1967; Djemmali, 1985) y fósiles humanos cuya datación mediante estudios biocronológicos se ha estimado entorno a los 700 ka (Geraads et al., 1986). Estos últimos se corresponden con una hemimandíbula adulta (Tighenif 2), dos mandíbulas adultas prácticamente completas (Tighenif 1 y 3), nueve dientes aislados (tres deciduos

y seis permanentes) y un fragmento de parietal (Tighenif 4), lo que sugiere un número mínimo de 5 individuos: cuatro adultos y un inmaduro (Arambourg y Hoffstetter, 1963; Tillier, 1980; Schwartz y Tattersall, 2003). Los homínidos de Tighenif fueron originalmente clasificados por Arambourg en 1954 como *Atlanthropus mauritanicus* (Arambourg, 1954). Posteriormente, y debido a ciertas similitudes con los restos chinos de Zhoukoudian, se decidió incluir a los fósiles de Tighenif dentro del hipodigma de *H. erectus* (Howell, 1960; Le Gros Clark, 1964; Rightmire, 1990). Por su parte, J.J. Hublin y C. Stringer no sólo defendían la clasificación de los homínidos de Tighenif como *H. mauritanicus*, sino que consideraban que los fósiles de la Gran Dolina-TD6 deberían estar incluidos dentro de ese mismo taxón (Hublin, 2001; Stringer, 2003). Sin embargo, un posterior estudio llevado a cabo por Bermúdez de Castro y colaboradores (2007) en el que comparaban los restos fósiles de ambos yacimientos, permitió concluir que a pesar de compartir ciertos rasgos plesiomórficos con respecto al género *Homo*, la dentición de TD6 presentaban caracteres morfológicos derivados típicos de las poblaciones pleistocenas euroasiáticas, mientras que la morfología dental de los homínidos de Tighenif era más parecida a las poblaciones del Pleistoceno Inferior de África. De esta manera, los autores afirmaban que los homínidos de Tighenif y Gran Dolina-TD6 pertenecían a dos especies diferentes: *H. ergaster mauritanicus* y *H. antecessor* respectivamente. Años después, una revisión del hipodigma de *H. heidelbergensis* sugería que las similitudes morfológicas existentes entre esta especie y los fósiles de Tighenif, garantizaba la asignación a dicho taxón (Mounier et al., 2009; Stringer, 2012; Zanolli y Mazurier, 2013). Sin embargo, algunos caracteres derivados



Figura 3.2.2. Localización de los yacimientos con fósiles del Pleistoceno Medio analizados en la presente tesis doctoral.

presentes en Tighenif parecían situar a dichos homínidos más cerca de *H. sapiens* que de *H. neanderthalensis* (Schwartz y Tattersall, 2000, 2010; Mounier et al., 2009; Zanolli et al., 2010). En la actualidad, la problemática sobre la asignación taxonómica de estos restos fósiles humanos sigue vigente.

La muestra incluida en la presente tesis doctoral consta de los tres molares pertenecientes a la hemimandíbula izquierda de Tighenif 2 y cuatro molares pertenecientes a la mandíbula de Tighenif 1 (ver Tabla 3).

### **3.2.3. FINAL DEL PLEISTOCENO MEDIO / PLEISTOCENO SUPERIOR**

En este apartado, y puesto que algunos de los especímenes analizados en la presente tesis doctoral pertenecen a la transición entre el Pleistoceno Medio y el Superior, hemos creído conveniente agruparlos bajo el mismo epígrafe para facilitar la comprensión de la muestra estudiada.

#### **3.2.3.1. *HOMO NEANDERTHALENSIS***

##### **3.2.3.1.1. KRAPINA**

El yacimiento de Krapina es un abrigo rocoso situado a 40 km al noroeste del Zagreb (Croacia) descubierto en 1899 por el geólogo, paleontólogo y arqueólogo D. Gorjanović-Kramberger, encargado de llevar a cabo las excavaciones de manera sistemática desde 1899 hasta 1905. De los 11 m de acumulación sedimentaria, Gorjanović-Kramberger diferenció nueve niveles estratigráficos con abundantes restos de fauna y fósiles humanos de *H. neanderthalensis* asociados a industria Musteriense (Gorjanović-Kramberger, 1899, 1901, 1902, 1904, 1905). La mayor parte de los más de 850 restos craneales y postcraneales de neandertales proceden de los niveles 3 y 4 -conocidos como *Hominid Zone*- así como de los niveles 5, 6 y 7. Tal acumulación ha posibilitado la asignación de al menos 24 individuos de ambos sexos con edades comprendidas entre tres y veintisiete años y con un rango de mortalidad mayor de entre quince y dieciocho años (Smith, 1976; Trinkaus, 1978; Wolpoff, 1979; Radovčić et al., 1988; Schwartz y Tattersall, 2002; Gardner y Smith, 2006). En 1995, diversos análisis realizados a través de series de Uranio y ESR permitieron obtener una edad aproximada para los depósitos con acumulación humana de entorno a los  $130 \pm 12$  ka (MIS 5e) (Rink et al., 1995).

El yacimiento de Krapina, al igual que el de la Sima de los Huesos, constituye una muestra excepcional en el estudio de la evolución humana. El registro fósil de Krapina cuenta con más de 20 individuos de la especie *H. neanderthalensis* de todas las edades y de ambos sexos que conforman una única población. Esta colección nos proporciona una oportunidad excepcional de estudiar y comparar los grados de variabilidad no sólo intra-poblacional, sino también inter-poblacional con otras poblaciones fósiles como la del yacimiento de la Sima de los Huesos.

La muestra fósil del yacimiento Krapina utilizada en la presente tesis doctoral, está compuesta por treinta molares: veinticuatro permanentes y siete deciduos, correspondientes a diferentes individuos (ver Tabla 3).

#### **3.2.3.1.2. ENGIS**

Engis es una cavidad situada cerca de la ciudad de Liège (Bélgica). En 1829 el médico y naturalista belga P.C. Schmerling descubrió diversos restos humanos entre los que destacaban un cráneo casi completo de un individuo adulto (Engis 1), varios fragmentos craneales y un maxilar de un individuo inmaduro (Engis 2) así como algún fragmento craneal y postcraneal (Engis 3) que a día de hoy están desaparecidos (Schmerling, 1833). Años después, E. Dupont encontró un cúbito (Engis 4) (Dupont, 1872). En 1936, C. Fraipont recopiló todos los datos existentes sobre el yacimiento, y tras un estudio detallado de los restos fósiles humanos concluyó que Engis 1 pertenecía a un *H. sapiens* del Paleolítico Superior, mientras que Engis 2 era el cráneo infantil de un individuo de la especie *H. neanderthalensis* de época Musteriense (Fraipont, 1936), datos que posteriormente fueron corroborados por otros autores (Fenart y Empereur-Buisson, 1970; Tillier, 1983a). Un reciente estudio basado en la histología dental del individuo de Engis 2 establecen su edad de muerte entorno a los tres años (Smith et al., 2010).

En la presente tesis doctoral solamente hemos incluido el primer molar inferior derecho de Engis 2 (ver Tabla 3), al ser el único espécimen del que obtuvimos las imágenes virtuales para proceder a su reconstrucción y posterior análisis.

#### **3.2.3.1.3. GIBRALTAR, DEVIL'S TOWER**

Devil's Tower es una estrecha cavidad situada a 9 m sobre el nivel del mar cerca de la zona este de Forbes's Quarry (Gibraltar) con una datación perteneciente al MIS 3 (Garrod et al., 1928; Vogel y Waterbolk, 1964; Tillier, 1982). Descubierta en 1917 por el Abate H. Breuil (Breuil, 1922), no fue hasta 1926 cuando se iniciaron las

campañas de excavación por D. Garrod (Garrod et al., 1928). Ese mismo año, en la boca de la cueva, se encontraron diversos fósiles humanos -un parietal, un frontal, un temporal, un maxilar y una mandíbula- asociados a huesos de animales y a industria Musteriense. Un estudio preliminar de los restos realizado por L. Buxton y E. Smith (Garrod et al., 1928), determinó que el cráneo pertenecía a un único individuo de la especie *H. neanderthalensis*, cuya edad de muerte estaba entorno a los cinco años. Años más tarde, dicho cráneo fue designado como Gibraltar 2 (Oakley et al., 1971). Sin embargo, en 1982, A.M. Tillier propuso que los restos pertenecían a dos individuos diferentes: uno de tres años y otro de cinco (Tillier, 1982). Investigaciones posteriores basadas en un estudio dental y comparativo con individuos de edad conocida, pudieron determinar que los restos humanos hallados en Devil's Tower pertenecían a un único individuo de unos cuatro años de edad (Stringer et al., 1990; Stringer y Dean, 1997; Smith et al., 2010).

La muestra de Gibraltar Devil's Tower incluida en nuestro estudio consta de cinco molares: tres permanentes y dos deciduos (ver Tabla 3).

#### **3.2.3.1.4. EHRINGSDORF**

Entre 1908 y 1925, H. Fischer, E. Lindig y colaboradores hallaron en la cantera de Ehringsdorf, cerca de la ciudad de Weimar (Alemania), más de 35 fragmentos humanos, craneales y postcraneales (Schwartz y Tattersall, 2002), que representaban a un número mínimo de nueve individuos (Vlček et al., 1993). Los restos fósiles fueron hallados en los niveles inferiores de unos sedimentos travertinos de 15 m de grosor y asociados a especies animales propias de condiciones climáticas interglaciares. En un primer momento, las dataciones de los sedimentos y de la fauna asociada a los restos humanos favorecían una cronología cercana al último periodo interglaciar (MIS 5e) (Steiner, 1979). Sin embargo, posteriores investigaciones basadas en series de Uranio (Brunnacker et al., 1983; Blackwell y Schwarcz, 1986), análisis de ESR (Grün et al., 1988) y estudios microfaunísticos (Heinrich, 1981), proponían una cronología más cercana al penúltimo periodo interglaciar (MIS 7). Aunque a día de hoy la mayor parte de los investigadores consideran que los restos de Ehringsdorf pertenecen a neandertales tempranos (Street et al., 2006), en su día la asignación taxonómica de los restos fue ampliamente debatida entre los que consideraban que se trataba de la especie *H. neanderthalensis* (Virchow, 1920; Olivier y Tissier, 1975; Smith, 1984) y los que veían rasgos morfológicos más característicos de *H. sapiens* (Weidenreich, 1928; Vlček et al., 1993).

La muestra del yacimiento de Ehringsdorf estudiada en la presente tesis doctoral la conforman tres molares permanentes: uno aislado (Ehringsdorf I) y dos pertenecientes a un fragmento mandibular izquierdo (Ehringsdorf G1) (ver Tabla 3).

#### 3.2.3.1.5. HUNAS

Hunas es una cavidad situada a 520 m sobre el nivel del mar al sureste de Alemania, en la ciudad de Baviera. La cavidad fue descubierta en 1956 por F. Heller y fue estudiada durante los años sucesivos hasta 1964 (Heller y Schoch, 1983). Ante la posible destrucción del lugar por su utilización como cantera, las excavaciones se retomaron en 1983. Tres años después, el arqueólogo B. Kaulich encontró un diente humano *in situ* en la base del nivel estratigráfico F2 situado en la parte superior de una amplia secuencia sedimentaria con abundantes restos faunísticos y arqueológicos de cronología Musteriense (Groiß, 1986). El hallazgo de industria lítica del Paleolítico Medio en dicho nivel, le confería una edad relativa de no más de 40 ka. Ya en el año 2002, el descubrimiento de una capa de espeleotemas en los niveles inferiores de dicha secuencia sedimentaria, permitió datar por Uranio-Torio mediante la técnica de Ionización Térmica por Espectrometría de Masas (Thermal Ionization Mass Spectrometric, TIMS-U/Th) una estalagmita de 30 cm de altura con la que se obtuvieron fechas de entorno a  $79 \pm 8$  ka para la base y  $76 \pm 9$  ka para la parte superior (Rosendahl et al., 2006). De esta manera, la totalidad de los sedimentos del yacimiento de Hunas muestran un intervalo temporal de unos 50 ka (90-40 ka). Además, los parámetros morfológicos y métricos de la corona y de la raíz, el patrón de fisuras, el grosor del esmalte, las características radiológicas y el desgaste oclusal e interproximal, indicaban que el diente de Hunas se correspondía con un tercer molar inferior derecho de un neandertal (Alt et al., 2006).

La muestra del yacimiento de Hunas incluida en la presente tesis doctoral consta de un tercer molar permanente (ver Tabla 3).

#### 3.2.3.1.6. ABRI SUARD

La Chaise-de-Vouthon forma un conjunto de yacimientos pertenecientes al mismo complejo kárstico, situados en el municipio de Vouthon (Francia). Los yacimientos que la componen son: l'Abri Suard, l'Abri Bourgeois-Delaunay y l'Abri Duport, llamados así por los nombres de sus descubridores.

Abri Suard fue descubierto en 1870 y las primeras excavaciones fueron llevadas a cabo por P. David entre 1949 y 1959 y posteriormente por A. Debénath entre 1972

y 1975 (Coqueugniot et al., 1996). En total se hallaron más de cincuenta restos fósiles humanos, adultos e inmaduros, sin conexión anatómica (Piveteau et al., 1982) asociados a restos de animales e industria lítica (David y Prat, 1965; Moisan, 1992; Matilla, 2010). Los rasgos morfológicos que presentaban los restos humanos indicaban que se trataba de individuos de la especie *H. neanderthalensis* (Krukoff, 1970; Piveteau, 1970; Hublin, 1980; Tillier y Genet-Varci, 1980; Coqueugniot et al., 1996; Teilhol, 2003) con una cronología entorno al MIS 6 (Debénath, 1974a; b, 1977; Schvoerer et al., 1977; Schwarcz y Debénath, 1979; Blackwell et al., 1983).

La muestra del yacimiento Abri Suard utilizada para el análisis y estudio de la presente tesis doctoral, está formada por cinco molares: cuatro dientes permanentes aislados y un molar deciduo (ver Tabla 3).

#### **3.2.3.1.7. ABRI BOURGEOIS-DELAUNAY**

Abri Bourgeois-Delaunay fue descubierta en 1850 por los abades que dan nombre a la cavidad, y al igual que l'Abri Suard, forma parte del complejo de yacimientos de La Chaise-de-Vouthon. Las primeras excavaciones sistemáticas fueron llevadas a cabo por P. David entre 1936 y 1961, y seis años después sería A. Debénath quien se pusiera al frente de los sucesivos trabajos de excavación hasta 1983 (David, 1954; Debénath y Piveteau, 1969; Debénath, 1974b, 1977; Condemi, 2001; Condemi y Moncel, 2004). Abri Bourgeois-Delaunay es la cavidad más grande con 12 m de ancho y 25 m de profundidad. En ella se ha encontrado industria lítica (Matilla, 2010), restos de animales (David y Prat, 1965; Moisan, 1992; Armand, 1998) y 22 fragmentos craneales y postcraneales de niños y adultos de la especie *H. neanderthalensis* con una datación aproximada de 135 ka (Schwarcz y Debénath, 1979; Blackwell et al., 1983, 1990, 1992; Teilhol, 1999, 2001; Condemi, 2001; Condemi y Moncel, 2004; Debénath, 2006).

La muestra del yacimiento Abri Bourgeois-Delaunay consta de un primer molar permanente aislado (ver Tabla 3).

#### **3.2.3.1.8. REGOURDOU**

Regourdou es un yacimiento situado a 2 km de Montignac, en la Dordoña francesa, cercano a la cueva de Lascaux. En 1957, R. Constant y posteriormente E. Bonifay y colaboradores encontraron la mandíbula y el esqueleto parcial de un individuo (Regourdou 1) junto con fragmentos de pie de un segundo individuo (Regourdou 2) (Bonifay y Vandermeersch, 1962; Bonifay, 1964; Vandermeersch y Trinkaus, 1995; Bonifay et al., 2007). Posteriores excavaciones junto con la revisión



de los restos faunísticos del yacimiento han permitido recuperar nuevos fósiles humanos pertenecientes a Regourdou 1 (Madelaine et al., 2008; Cavanhié, 2009; Gómez-Olivencia et al., 2013; Maureille et al., 2015) Estudios detallados sobre Regourdou 1 demuestran que se trata de un individuo de entre veinte y treinta años con características morfológicas típicamente neandertales (Piveteau, 1959, 1963; Vandermeersch y Trinkaus, 1995; Maureille et al., 2001; Madelaine et al., 2008; Meyer et al., 2011; Gómez-Olivencia et al., 2012, 2013; Volpato et al., 2012; Meyer, 2013; Plavcan et al., 2014). Aunque el sexo “indeterminado” de Regourdou 1 (Vandermeersch y Trinkaus, 1995; Meyer et al., 2011) sigue siendo objeto de investigación, diferentes estudios indican que, a pesar del reducido tamaño de los huesos largos, pudiera tratarse de un individuo masculino (Piveteau, 1963; Vallois, 1965; Churchill y Formicola, 1997; Gómez-Olivencia et al., 2007), de unos 72 kg de peso y 162-164 cm de altura (Ruff et al., 1997; Carretero et al., 2012). Los primeros análisis estratigráficos y el estudio de los restos faunísticos del Nivel 4, sugerían que dicha acumulación se había producido durante una fase moderadamente cálida del último glacial, probablemente en el MIS 4 (Bonifay, 1964). Esta datación fue posteriormente confirmada tras el análisis de los restos de artiodáctilos existentes a lo largo de la secuencia estratigráfica del yacimiento, proponiendo el MIS 4 como estadio cronológico para los Niveles 3 y 4 (Delpech, 1996).

La muestra del yacimiento de Regourdou utilizada en esta tesis doctoral está formada por la mandíbula con los seis molares permanentes (ver Tabla 3).

### 3.2.3.1.9. ROC DE MARSAL

Roc de Marsal es un yacimiento paleolítico de la época Musteriense localizado a 5 km al suroeste de Les Eyzeis-de-Tayac, en la Dordoña francesa. En agosto de 1961, Jean Lafille encontró en los niveles inferiores restos de un individuo infantil asociados a industria Musteriense y asignado a *H. neanderthalensis* (Bordes y Lafille, 1962; Piveteau, 1962). Un análisis detallado del desarrollo dental basándose en los estándares modernos, proporcionó una estimación de edad de muerte del individuo entre los dos y medio y los cuatro años (Legoux, 1965; Tillier, 1983b; Madre-Dupouy, 1985, 1992; Tillier, 1996; Granat y Heim, 2003; Bayle et al., 2009a). El conjunto de análisis palinológicos (Van Campo y Bouchud, 1962), faunísticos (Vandermeersch, 1965) y arqueológicos (Turq, 1985; Thiebaut, 2003) establecen una datación aproximada para los restos humanos entre el MIS3 y el MIS4; sin embargo estudios posteriores hablan de un registro temporal más cercano al MIS4 y MIS 5a (Sandgathe et al., 2007, 2011; Tillier, 2007).

La muestra del yacimiento de Roc de Marsal utilizada en esta tesis está compuesta por dos molares permanentes (ver Tabla 3).



Figura 3.2.3.1. Localización de los yacimientos con fósiles de la especie *H. neanderthalensis* analizados en la presente tesis doctoral.

### 3.2.3.2. *HOMO SAPIENS*

#### 3.2.3.2.1. LAGAR VELHO

El abrigo de Lagar Velho es un yacimiento situado en el Valle de Lapedo (Portugal). A finales de noviembre de 1998, J. Mauricio y P. Suoto encontraron restos de un antebrazo perteneciente a un individuo inmaduro que, posteriormente, fue confirmado por C. Duarte y J. Zilhão como parte de un enterramiento humano del Paleolítico Superior. Poco después, el equipo de excavadores dirigido J. Zilhão, proporcionó pruebas de los primeros humanos modernos en el extremo más occidental del continente Europeo (Duarte et al., 1999). El esqueleto, perteneciente a un niño de aproximadamente cuatro años de edad, fue enterrado junto con restos de ocre y fragmentos de concha que pudieron ser datados por  $^{14}\text{C}$ , lo que permitió obtener una cronología de unos  $24.500 \pm 500$  yr BP (Duarte et al., 1999; Zilhão y Trinkaus, 2002; Zilhão, 2006). El hallazgo casi completo del individuo (>90% de los huesos) ha permitido realizar estudios detallados sobre su morfología craneal y postcraneal. Basándose en dichos estudios, algunos investigadores argumentan que el niño de Lagar Velho presenta un mosaico de caracteres neandertales y de humanos modernos que permiten confirmar que sería el resultado de un proceso de hibridación ocurrido durante décadas (Duarte et al., 1999; Trinkaus y Zilhão, 2002; Bayle et al.,

2010). Mientras, otros autores (Tattersall y Schwartz, 1999) rechazan tal afirmación asegurando que la mayoría de las características morfológicas del niño de Lagar Velho caen dentro del rango de humanos modernos. Sin embargo, las últimas investigaciones en el campo de la genética han ayudado a comprender que el cruzamiento e hibridación entre neandertales y *H. sapiens* existió en algún momento de nuestro pasado evolutivo (Callaway, 2010; Sankararaman et al., 2012, 2014; Sánchez-Quinto et al., 2012; Vernot y Akey, 2014, 2015). El estudio genético del individuo de Lagar Velho en un futuro, ayudaría a confirmar o desmentir las afirmaciones sobre el hibridismo de este espécimen.

La muestra del yacimiento de Lagar Velho incluida en la presente tesis doctoral está formada por dos molares: uno permanente y uno deciduo (ver Tabla 3).

#### **3.2.3.2.2. LA MADELEINE**

El abrigo rocoso de La Madeleine es un yacimiento situado en el municipio de Tursac, en la Dordoña francesa. Las primeras excavaciones llevadas a cabo por D. Peyrony en 1926 (Peyrony, 1926), sacaron a la luz el enterramiento de un individuo inmaduro de unos tres o cuatro años de edad perteneciente a la especie *H. sapiens* (Bayle et al., 2009b). El esqueleto se encontró con restos de ocre y abundantes ornamentos personales tallados en hueso, dientes y conchas (Peyrony, 1927; Capitan y Peyrony, 1928; Vanhaeren y d'Errico, 2001) cuyas dataciones mediante radiocarbono con el Acelerador de Espectrometría de Masas ( $^{14}\text{C}$  AMS) permitieron obtener una cronología entorno a  $10.190 \pm 100$  yr BP (Gambier et al., 2000).

La muestra del yacimiento de La Madeleine analizada en esta tesis está formada por la mandíbula con los cuatro molares deciduales (ver Tabla 3).

#### **3.2.3.2.3. QAFZEH**

Jebel Qafzeh es una cavidad situada a unos 3 km al sur de Nazaret (Israel) con sedimentos holocenos y del Paleolítico Medio y Superior. Las primeras excavaciones tuvieron lugar durante 1933 y 1935 bajo la dirección de R. Neuville y M. Stekelis (Neuville, 1951), siendo posteriormente retomadas por B. Vandermeersch y D. Bar-Yosef entre 1966 y 1979 (Vandermeersch, 1966, 1969a; b, 1970, 1972, 1981; Bar-Yosef y Vandermeersch, 1981). Cabe destacar la abundancia y riqueza de la fauna encontrada en el yacimiento (Avnimelech, 1937; Haas, 1972; Bouchud, 1974; Rabinovich y Tchernov, 1995; Rabinovich et al., 2004), así como el predominio de industria lítica de tipo Levallois (Hovers, 1997, 2009; Hovers y Raveh, 2000). En

referencia a los restos de *H. sapiens* hallados en la cavidad, se estima que entre los esqueletos casi completos y los dientes aislados encontrados, el número mínimo de individuos sería de unos catorce entre adultos, niños y adolescentes (Schwartz y Tattersall, 2003; Bar-Yosef Mayer et al., 2009). Diversos análisis llevados a cabo mediante técnicas de Termoluminiscencia, ESR y series de Uranio han sugerido una datación para los restos humanos del yacimiento de Qafzeh entorno a los 130-90 ka BP (Bar-Yosef y Vandermeersch, 1981; Schwarcz et al., 1988; Valladas et al., 1988; Grün y Stringer, 1991; Yokoyama et al., 1997).

Los dientes del yacimiento de Qafzeh incluidos en la presente tesis doctoral son ocho molares permanentes y cuatro deciduos (ver Tabla 3).

#### **3.2.3.2.4. EQUUS CAVE**

La cueva denominada Equus Cave se sitúa cerca de Taung, a unos 130 km al norte de la ciudad de Kimberley (Sudáfrica). Aunque los primeros restos fósiles fueron encontrados por F.E. Peabody en 1954 -siendo el hallazgo de un diente de caballo lo que dio nombre a la cavidad (Peabody, 1954)- las primeras excavaciones sistemáticas se llevaron a cabo por P. Beaumont y M. Shackley en 1978 (Grine y Klein, 1985). El potencial stratigráfico, compuesto por sedimentos del Pleistoceno Superior y del Holoceno (Butzer et al., 1978; Beaumont et al., 1984; Vogel y Partridge, 1984; Vogel et al., 1986), ha permitido obtener una gran cantidad de industria lítica y restos de animales, donde predominan los grandes mamíferos -con más de 45 especies diferentes- frente a la microfauna (Klein et al., 1991). En cuanto a los restos humanos, se encontraron doce dientes aislados y un fragmento mandibular izquierdo con dos molares pertenecientes a la especie *H. sapiens*. El fragmento mandibular fue hallado por C.K. Brain y K.W. Butzer en 1971, mientras que de los dientes aislados, cuatro se encontraron durante las excavaciones de P. Beaumont y M. Shackley en 1978 y los otros ocho durante la excavación de P. Beaumont en 1982. Tanto la mandíbula (EQ-H71/33) como ocho de los dientes (EQ-H5 a EQ-H12) pertenecen al Pleistoceno Superior con una cronología de entre 94.000-33.000 yr BP, mientras que los cuatro dientes restantes (EQ-H1 a EQ-H4) son de época holocena con una datación máxima de 7.500 yr BP (Grine y Klein, 1985).

Los molares de Equus Cave analizados en esta tesis pertenecen al Pleistoceno Superior y se corresponden con dos dientes aislados (EQ-H5 y EQ-H8) y el tercer molar mandibular (EQ-H71/33) (ver Tabla 3).

### 3.2.4. HOLOCENO

#### 3.2.4.1. EL MIRADOR

La cueva de El Mirador es un yacimiento situado en la ladera sur de la sierra de Atapuerca (Burgos, España). Los primeros trabajos de expedición de la cavidad se llevaron a cabo en 1970 por el Grupo Espeleológico Edelweiss (Ortega y Martín, 2012) y desde 1999 hasta la actualidad se continúa excavando por el Equipo de Investigación de Atapuerca. Durante los diez primeros años, los trabajos se centraron en un primer sondeo de 6 m<sup>2</sup> en el centro de la cavidad. Esto permitió documentar una secuencia estratigráfica de 20 m de profundidad: 14 m de sedimentos pleistocenos y 6 m de sedimentos holocenos (Vergès et al., 2016). Numerosas investigaciones han contribuido a conocer mejor el registro arqueológico y paleontológico de la secuencia del Holoceno (Vergès et al., 2002, 2008; Moral del Hoyo et al., 2003; Angelucci et al., 2009; Martín et al., 2009, 2016; Carrancho et al., 2013, 2016; Ceperuelo et al., 2015; Lozano et al., 2017; Modesto-Mata et al., 2017; Expósito y Burjachs, 2016).

La muestra utilizada en la presente tesis doctoral hace referencia a los restos humanos de dos épocas bien diferenciadas en dos sondeos diferentes: el Calcolítico y la Edad del Bronce (Ceperuelo et al., 2014, 2015; Gómez-Sánchez et al., 2014; Lozano et al., 2017; Mathieson et al., 2015; Modesto-Mata et al., 2017). Los niveles MIR3 y MIR4 fueron depositados durante las ocupaciones humanas del Bronce (Vergès et al., 2002, 2016). En este primer conjunto de 6 m<sup>2</sup> situados en la zona central de la cavidad, se hallaron seis individuos de diferentes sexos y edades (Lozano et al., 2017). Estos cuerpos fueron canibalizados y abandonados en el interior de la cueva durante el Bronce Inicial (4.400-4.100 cal BP), siendo enterrados por otros grupos humanos en el Bronce Medio o Final (Cáceres et al., 2007). El segundo conjunto conocido como “Cueva del Laminador” se corresponde con la excavación llevada a cabo en el año 2009 en una cámara natural de unos 14 m<sup>2</sup> situada al noroeste de la cavidad. En ella se encontró un segundo enterramiento colectivo de época calcolítica datados entorno a 4.760-4.200 cal BP (Gómez-Sánchez et al., 2014; Mathieson et al., 2015). A pesar de que algunos de los cuerpos se encontraron en posición anatómica, otros fueron removidos y mezclados por la acción clandestina de diversos excavadores que accedieron a la cueva durante la década de los 80. El número mínimo de individuos es de 23 y sus edades están comprendidas entre los dos y los cuarenta años (Lozano et al., 2015).

La muestra del yacimiento de El Mirador incluida en la presente tesis doctoral consta de veintidós dientes: trece molares aislados de la Edad del Bronce (once permanentes y dos deciduos) y nueve molares de época calcolítica pertenecientes a una mandíbula con los primeros y segundos molares y el tercer molar derecho, una hemimandíbula izquierda con el tercer molar y hemimandíbula derecha con los tres molares (ver Tabla 3).

#### **3.2.4.2. MUESTRAS CONTEMPORÁNEAS**

La muestra de *H. sapiens* se ha completado con varias colecciones contemporáneas que pertenecen a poblaciones españolas y que han sido englobadas en la base de datos de la presente tesis doctoral bajo el nombre de Muestras Contemporáneas (ver Tabla 3). La importancia de estas muestras es que se conoce el sexo y la edad exacta de los individuos a los que pertenece cada pieza dental. Por un lado, la Colección de Referencia del CENIEH está formada por más de 250 piezas dentales donadas por particulares y por diferentes clínicas odontológicas de diversas ciudades españolas y de la Sociedad Española de Periodoncia. De esta colección, la muestra utilizada en nuestro estudio se compone de 20 molares permanentes (cuatro primeros, diez segundos y seis terceros) pertenecientes a once mujeres y nueve hombres con un rango de edad de entre veintitrés y setenta y dos años. Por otro lado, y gracias a la colaboración del Dr. Bernardo Perea Pérez, se ha utilizado la Colección Antropológica depositada en la Escuela de Medicina Legal y Forense de la Universidad Complutense de Madrid. Esta colección se obtuvo tras el cierre de dos cementerios madrileños -el de Carabanchel y el Antiguo de Alcorcón- y está formada por 84 esqueletos (veinticuatro mujeres y sesenta hombres) de individuos adultos con sexo, edad y patologías conocidos. Los esqueletos pertenecen a individuos nacidos durante la primera mitad del siglo XX en diferentes provincias españolas. Para nuestro estudio hemos utilizado 35 molares permanentes (doce primeros, dieciséis segundos y siete terceros) pertenecientes a quince mujeres y veinte hombres con un rango de edad de entre veintiuno y cincuenta y cinco años.



Figura 3.2.3.2. Localización de los yacimientos con fósiles de la especie *H. sapiens* analizados en la presente tesis doctoral. La estrella amarilla hace referencia a *H. sapiens* de época Holocena.

### 3.3. MUESTRA BIBLIOGRÁFICA DE COMPARACIÓN

La muestra bibliográfica de comparación utilizada en la presente tesis doctoral proviene de diversos yacimientos pleistocenos de Europa, África, Asia y Oriente Medio cuya morfología externa e interna ha sido previamente publicada por sus correspondientes autores. Los datos aportados en los diferentes artículos junto con las imágenes virtuales del esmalte y de la dentina, nos ha permitido realizar nuestra propia clasificación de los diferentes tipos de crestas, y con ello interpretar y contextualizar la evolución de las poblaciones europeas para comprender la polaridad de los caracteres observados.

Los yacimientos de los que hemos obtenido la muestra bibliográfica de comparación son: Mala Balanica, en Serbia (Roksandic et al., 2011; Skinner et al., 2016); Buia, en Eritrea (Zanolli et al., 2014); Yiyuan, al Este de China (Xing et al., 2016); Hexian, al este de China (Xing et al., 2014; Liu et al., 2017); Zhoukoudian, al norte de China (Xing et al., 2014); Xujiayao, al norte de China (Xing et al., 2015); Sangiran Dome, en Java (Zanolli et al., 2012, 2015, Zanolli, 2013, 2015) y Qesem Cave, en Israel (Fornai et al., 2016; Hershkovitz et al., 2016; Weber et al., 2016).



Figura 3.3. Localización de los yacimientos estudiados como parte de la muestra bibliográfica de comparación.



Tabla 3. Lista detallada de todos los molares que forman parte del material de estudio de la presente tesis doctoral.

ESPECIE / GRUPO	YACIMIENTO	LOCALIZACIÓN	CRONOLOGÍA	ESPECÍMEN	INDIVIDUO	PIEZA DENTAL	BASE DATOS
-	Barranco León	España	1,73-1,02 Ma	BL02-J54-100	-	m <sub>1</sub> izq.	CENIEH
<i>H. antecessor</i>	Gran Dolina-TD6	España	900-800 ka	ATD6-5	I	M <sub>1</sub> drch.	CENIEH
<i>H. antecessor</i>	Gran Dolina-TD6	España	900-800 ka	ATD6-94	V	M <sub>1</sub> drch.	CENIEH
<i>H. antecessor</i>	Gran Dolina-TD6	España	900-800 ka	ATD6-112	VIII	M <sub>1</sub> drch.	CENIEH
<i>H. antecessor</i>	Gran Dolina-TD6	España	900-800 ka	ATD6-96	VI	M <sub>1</sub> izq.	CENIEH
<i>H. antecessor</i>	Gran Dolina-TD6	España	900-800 ka	ATD6-5	I	M <sub>2</sub> drch.	CENIEH
<i>H. antecessor</i>	Gran Dolina-TD6	España	900-800 ka	ATD6-113	VII	M <sub>2</sub> izq.	CENIEH
<i>H. antecessor</i>	Gran Dolina-TD6	España	900-800 ka	ATD6-144	-	M <sub>2</sub> drch.	CENIEH
<i>H. antecessor</i>	Gran Dolina-TD6	España	900-800 ka	ATD6-96	VI	M <sub>2</sub> izq.	CENIEH
<i>H. antecessor</i>	Gran Dolina-TD6	España	900-800 ka	ATD6-5	I	M <sub>3</sub> drch.	CENIEH
<i>H. antecessor</i>	Gran Dolina-TD6	España	900-800 ka	ATD6-113	VII	M <sub>3</sub> izq.	CENIEH
<i>H. antecessor</i>	Gran Dolina-TD6	España	900-800 ka	ATD6-96	VI	M <sub>3</sub> izq.	CENIEH
<i>H. antecessor</i>	Gran Dolina-TD6	España	900-800 ka	ATD6-93	-	m <sub>1</sub> drch.	CENIEH
<i>H. antecessor</i>	Gran Dolina-TD6	España	900-800 ka	ATD6-112	VIII	m <sub>1</sub> drch.	CENIEH
<i>H. antecessor</i>	Gran Dolina-TD6	España	900-800 ka	ATD6-112	VIII	m <sub>2</sub> drch.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-2	II	M <sub>1</sub> drch.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-14	IV	M <sub>1</sub> izq.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-21	VII	M <sub>1</sub> izq.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-22	III	M <sub>1</sub> izq.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-101	III	M <sub>1</sub> drch.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-141	X	M <sub>1</sub> drch.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-272	XXIII	M <sub>1</sub> drch.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-286	XXIII	M <sub>1</sub> izq.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-556	X	M <sub>1</sub> izq.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-561	XXVI	M <sub>1</sub> drch.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-576	XIX	M <sub>1</sub> izq.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-829	XVIII	M <sub>1</sub> izq.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-943	XVIII	M <sub>1</sub> drch.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-1458	XXIV	M <sub>1</sub> izq.	CENIEH

<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-1459	XIV	M <sub>1</sub> izq.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-1759	VI	M <sub>1</sub> izq.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-2276	XIV	M <sub>1</sub> drch.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-2438	XXIV	M <sub>1</sub> drch.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-3175	XX	M <sub>1</sub> drch.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-3933	XXV	M <sub>1</sub> drch.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-3934	XXV	M <sub>1</sub> izq.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-4318	XX	M <sub>1</sub> izq.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-142	II	M <sub>2</sub> drch.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-169	X	M <sub>2</sub> izq.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-271	III	M <sub>2</sub> drch.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-273	III	M <sub>2</sub> izq.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-284	XIV	M <sub>2</sub> drch.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-557	XXIII	M <sub>2</sub> izq.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-941	XVIII	M <sub>2</sub> izq.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-946	XX	M <sub>2</sub> izq.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-1752	XVIII	M <sub>2</sub> drch.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-1756	XXVI	M <sub>2</sub> drch.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-1761	XXIII	M <sub>2</sub> drch.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-2270	XXVI	M <sub>2</sub> izq.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-2272	XIV	M <sub>2</sub> izq.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-2396	XXIV	M <sub>2</sub> izq.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-3176	XXVII	M <sub>2</sub> izq.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-3179	II	M <sub>2</sub> izq.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-3890	XX	M <sub>2</sub> drch.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-3889	XXV	M <sub>2</sub> drch.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-6579	XXV	M <sub>2</sub> izq.	CENIEH
<i>SH hominins*</i>	Sima de los Huesos	España	427 ± 12 ka	AT-11	XIII	M <sub>2</sub> izq.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-13	VII	M <sub>3</sub> izq.	CENIEH
<i>SH hominins</i>	Sima de los Huesos	España	427 ± 12 ka	AT-30	XXVI	M <sub>3</sub> drch.	CENIEH

SH hominins	Sima de los Huesos	España	427 ± 12 ka	AT-100	IV	M <sub>3</sub> izq.	CENIEH
SH hominins	Sima de los Huesos	España	427 ± 12 ka	AT-143	II	M <sub>3</sub> drch.	CENIEH
SH hominins	Sima de los Huesos	España	427 ± 12 ka	AT-598	-	M <sub>3</sub> izq.	CENIEH
SH hominins	Sima de los Huesos	España	427 ± 12 ka	AT-599	-	M <sub>3</sub> drch.	CENIEH
SH hominins	Sima de los Huesos	España	427 ± 12 ka	AT-811	IV	M <sub>3</sub> drch.	CENIEH
SH hominins	Sima de los Huesos	España	427 ± 12 ka	AT-942	-	M <sub>3</sub> drch.	CENIEH
SH hominins	Sima de los Huesos	España	427 ± 12 ka	AT-1468	-	M <sub>3</sub> drch.	CENIEH
SH hominins	Sima de los Huesos	España	427 ± 12 ka	AT-1473	-	M <sub>3</sub> izq.	CENIEH
SH hominins	Sima de los Huesos	España	427 ± 12 ka	AT-1945	-	M <sub>3</sub> izq.	CENIEH
SH hominins	Sima de los Huesos	España	427 ± 12 ka	AT-1959	-	M <sub>3</sub> drch.	CENIEH
SH hominins	Sima de los Huesos	España	427 ± 12 ka	AT-2271	XXVIII	M <sub>3</sub> izq.	CENIEH
SH hominins	Sima de los Huesos	España	427 ± 12 ka	AT-2273	-	M <sub>3</sub> izq.	CENIEH
SH hominins	Sima de los Huesos	España	427 ± 12 ka	AT-2277	XXVIII	M <sub>3</sub> drch.	CENIEH
SH hominins	Sima de los Huesos	España	427 ± 12 ka	AT-2385	XXIV	M <sub>3</sub> izq.	CENIEH
SH hominins	Sima de los Huesos	España	427 ± 12 ka	AT-2438	XXIV	M <sub>3</sub> drch.	CENIEH
SH hominins	Sima de los Huesos	España	427 ± 12 ka	AT-2760	-	M <sub>3</sub> izq.	CENIEH
SH hominins	Sima de los Huesos	España	427 ± 12 ka	AT-2777	-	M <sub>3</sub> drch.	CENIEH
SH hominins	Sima de los Huesos	España	427 ± 12 ka	AT-3182	-	M <sub>3</sub> drch.	CENIEH
SH hominins	Sima de los Huesos	España	427 ± 12 ka	AT-3943	XXV	M <sub>3</sub> drch.	CENIEH
SH hominins	Sima de los Huesos	España	427 ± 12 ka	AT-6580	XXV	M <sub>3</sub> izq.	CENIEH
SH hominins	Sima de los Huesos	España	427 ± 12 ka	AT-947	XVIII	m <sub>2</sub> izq.	CENIEH
SH hominins	Sima de los Huesos	España	427 ± 12 ka	AT-2398	XVIII	m <sub>2</sub> drch.	CENIEH
MP hominins Europe	Arago	Francia	400-350 ka	A-40	-	M <sub>1</sub> drch.	CENIEH
MP hominins Europe	Arago	Francia	400-350 ka	A-68	-	M <sub>2</sub> drch.	CENIEH
MP hominins Europe	Arago	Francia	392 ± 43 ka	A-10	-	M <sub>2</sub> drch.	CENIEH
MP hominins Europe	Arago	Francia	392 ± 43 ka	A-32	-	M <sub>2</sub> izq.	CENIEH
MP hominins Europe	Arago	Francia	438 ± 31 ka	A-106	-	M <sub>3</sub> izq.	CENIEH
MP hominins Europe*	Arago	Francia	-	A-5	-	m <sub>2</sub> izq.	CENIEH
MP hominins Europe	Montmaurin	Francia	200 ka	Montmaurin	I	M <sub>1</sub> drch.	LAMIS
MP hominins Europe	Montmaurin	Francia	200 ka	Montmaurin	I	M <sub>1</sub> izq.	LAMIS

<i>MP hominins Europe</i>	Montmaurin	France	200 ka	Montmaurin	I	M <sub>2</sub> drch.	LAMIS
<i>MP hominins Europe</i>	Montmaurin	France	200 ka	Montmaurin	I	M <sub>2</sub> izq.	LAMIS
<i>MP hominins Europe</i>	Montmaurin	France	200 ka	Montmaurin	I	M <sub>3</sub> drch.	LAMIS
<i>MP hominins Europe</i>	Montmaurin	France	200 ka	Montmaurin	I	M <sub>3</sub> izq.	LAMIS
<i>MP hominins Africa</i>	Tighenif	Argelia	700 ka	Tighenif 1	I	M <sub>2</sub> drch.	IC2MP
<i>MP hominins Africa</i>	Tighenif	Argelia	700 ka	Tighenif 1	I	M <sub>2</sub> izq.	IC2MP
<i>MP hominins Africa</i>	Tighenif	Argelia	700 ka	Tighenif 1	I	M <sub>3</sub> drch.	IC2MP
<i>MP hominins Africa</i>	Tighenif	Argelia	700 ka	Tighenif 1	I	M <sub>3</sub> izq.	IC2MP
<i>MP hominins Africa</i>	Tighenif	Argelia	700 ka	Tighenif 2	II	M <sub>1</sub> izq.	IC2MP
<i>MP hominins Africa</i>	Tighenif	Argelia	700 ka	Tighenif 2	II	M <sub>2</sub> izq.	IC2MP
<i>MP hominins Africa</i>	Tighenif	Argelia	700 ka	Tighenif 2	II	M <sub>3</sub> izq.	IC2MP
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D77	E	M <sub>1</sub> drch.	NESPOS®
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D79	L	M <sub>1</sub> drch.	NESPOS®
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D80	-	M <sub>1</sub> drch.	NESPOS®
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D84	N	M <sub>1</sub> drch.	NESPOS®
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D105	-	M <sub>1</sub> drch.	NESPOS®
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D81	P	M <sub>1</sub> izq.	NESPOS®
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D82	M	M <sub>1</sub> izq.	NESPOS®
<i>H. neanderthalensis*</i>	Krapina	Croacia	130 ± 12 ka	Krapina D168	Q	M <sub>1</sub> izq.	NESPOS®
<i>H. neanderthalensis*</i>	Krapina	Croacia	130 ± 12 ka	Krapina D1	L	M <sub>2</sub> drch.	NESPOS®
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D3	M	M <sub>2</sub> izq.	NESPOS®
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D86	-	M <sub>2</sub> izq.	NESPOS®
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D107	-	M <sub>2</sub> izq.	NESPOS®
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D2	N	M <sub>2</sub> drch.	NESPOS®
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D6	-	M <sub>2</sub> izq.	NESPOS®
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D10	E	M <sub>2</sub> drch.	NESPOS®
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D104	-	M <sub>2</sub> drch.	NESPOS®
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D4	K	M <sub>3</sub> izq.	NESPOS®

<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D5	M	M <sub>3</sub> izq.	NESPOS®
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D9	-	M <sub>3</sub> izq.	NESPOS®
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D85	L	M <sub>3</sub> izq.	NESPOS®
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D106	-	M <sub>3</sub> izq.	NESPOS®
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D7	L	M <sub>3</sub> drch.	NESPOS®
<i>H. neanderthalensis</i> *	Krapina	Croacia	130 ± 12 ka	Krapina D8	-	M <sub>3</sub> drch.	NESPOS®
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D108	E	M <sub>3</sub> drch.	NESPOS®
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D62	B	m <sub>2</sub> izq.	NESPOS®
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D63	Q	m <sub>2</sub> izq.	NESPOS®
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D64	P	m <sub>2</sub> izq.	NESPOS®
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D65	-	m <sub>2</sub> izq.	NESPOS®
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D66	C	m <sub>2</sub> izq.	NESPOS®
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D67	P	m <sub>1</sub> izq.	NESPOS®
<i>H. neanderthalensis</i>	Krapina	Croacia	130 ± 12 ka	Krapina D68	-	m <sub>2</sub> drch.	NESPOS®
<i>H. neanderthalensis</i>	Engis	Bélgica	50-30 ka	Engis 2	II	M <sub>1</sub> drch.	ESRF®
<i>H. neanderthalensis</i>	Devil's Tower	Gibraltar	50-30 ka	Gibraltar 2	-	M <sub>1</sub> drch.	ESRF®
<i>H. neanderthalensis</i>	Devil's Tower	Gibraltar	50-30 ka	Gibraltar 2	-	M <sub>1</sub> izq.	ESRF®
<i>H. neanderthalensis</i>	Devil's Tower	Gibraltar	50-30 ka	Gibraltar 2	-	M <sub>2</sub> izq.	ESRF®
<i>H. neanderthalensis</i>	Devil's Tower	Gibraltar	50-30 ka	Gibraltar 2	-	m <sub>1</sub> drch.	ESRF®
<i>H. neanderthalensis</i>	Devil's Tower	Gibraltar	50-30 ka	Gibraltar 2	-	m <sub>2</sub> drch.	ESRF®
<i>H. neanderthalensis</i>	Ehringsdorf	Alemania	243-123 ka	Ehringsdorf I 1048/69	-	M <sub>1</sub> izq.	NESPOS®
<i>H. neanderthalensis</i> *	Ehringsdorf	Alemania	243-123 ka	Ehringsdorf G1 1010/69	-	M <sub>1</sub> izq.	NESPOS®
<i>H. neanderthalensis</i> *	Ehringsdorf	Alemania	243-123 ka	Ehringsdorf G1 1010/69	-	M <sub>2</sub> izq.	NESPOS®
<i>H. neanderthalensis</i>	Hunas	Alemania	90-40 ka	Hunas 1	-	M <sub>3</sub> drch.	NESPOS®
<i>H. neanderthalensis</i>	Abri Suard	Francia	191 ka	Abri Suard S5	-	M <sub>1</sub> izq.	NESPOS®
<i>H. neanderthalensis</i>	Abri Suard	Francia	191 ka	Abri Suard S14-7	-	M <sub>1</sub> drch.	NESPOS®
<i>H. neanderthalensis</i>	Abri Suard	Francia	191 ka	Abri Suard S49	-	M <sub>1</sub> drch.	NESPOS®
<i>H. neanderthalensis</i>	Abri Suard	Francia	191 ka	Abri Suard S43	-	M <sub>3</sub> drch.	NESPOS®

<i>H. neanderthalensis</i>	Abri Suard	Francia	191 ka	Abri Suard S15-5	-	m <sub>2</sub> drch.	NESPOS®
<i>H. neanderthalensis</i>	Abri Bourgeois-Delaunay	Francia	135 ka	Abri BDJ4C9	-	M <sub>1</sub> izq.	NESPOS®
<i>H. neanderthalensis</i>	Regourdou	Francia	71 ka	Regourdou 1	I	M <sub>1</sub> drch.	NESPOS®
<i>H. neanderthalensis</i>	Regourdou	Francia	71 ka	Regourdou 1	I	M <sub>1</sub> izq.	NESPOS®
<i>H. neanderthalensis</i>	Regourdou	Francia	71 ka	Regourdou 1	I	M <sub>2</sub> drch.	NESPOS®
<i>H. neanderthalensis</i>	Regourdou	Francia	71 ka	Regourdou 1	I	M <sub>2</sub> izq.	NESPOS®
<i>H. neanderthalensis</i>	Regourdou	Francia	71 ka	Regourdou 1	I	M <sub>3</sub> drch.	NESPOS®
<i>H. neanderthalensis</i>	Regourdou	Francia	71 ka	Regourdou 1	I	M <sub>3</sub> izq.	NESPOS®
<i>H. neanderthalensis</i>	Roc de Marsal	Francia	82-71 ka	Roc de Marsal	I	M <sub>1</sub> drch.	NESPOS®
<i>H. neanderthalensis</i>	Roc de Marsal	Francia	82-71 ka	Roc de Marsal	I	M <sub>1</sub> izq.	NESPOS®
<i>H. sapiens</i>	Equus Cave	Sud África	94-33 ka	EQ-H5	V	M <sub>1</sub> drch.	ESRF®
<i>H. sapiens</i>	Equus Cave	Sud África	94-33 ka	EQ-H8	VIII	M <sub>1</sub> izq.	ESRF®
<i>H. sapiens*</i>	Equus Cave	Sud África	94-33 ka	EQ-H71/33	XIII	M <sub>3</sub> izq.	ESRF®
<i>H. sapiens</i>	Qafzeh	Israel	130-90 ka	Qafzeh 10	X	M <sub>1</sub> drch.	ESRF®
<i>H. sapiens</i>	Qafzeh	Israel	130-90 ka	Qafzeh 10	X	M <sub>1</sub> izq.	ESRF®
<i>H. sapiens</i>	Qafzeh	Israel	130-90 ka	Qafzeh 15	XV	M <sub>1</sub> drch.	ESRF®
<i>H. sapiens</i>	Qafzeh	Israel	130-90 ka	Qafzeh 15	XV	M <sub>1</sub> izq.	ESRF®
<i>H. sapiens</i>	Qafzeh	Israel	130-90 ka	Qafzeh 10	X	M <sub>2</sub> drch.	ESRF®
<i>H. sapiens</i>	Qafzeh	Israel	130-90 ka	Qafzeh 10	X	M <sub>2</sub> izq.	ESRF®
<i>H. sapiens</i>	Qafzeh	Israel	130-90 ka	Qafzeh 15	XV	M <sub>2</sub> drch.	ESRF®
<i>H. sapiens</i>	Qafzeh	Israel	130-90 ka	Qafzeh 15	XV	M <sub>2</sub> izq.	ESRF®
<i>H. sapiens</i>	Qafzeh	Israel	130-90 ka	Qafzeh 15	XV	m <sub>1</sub> drch.	ESRF®
<i>H. sapiens</i>	Qafzeh	Israel	130-90 ka	Qafzeh 15	XV	m <sub>1</sub> izq.	ESRF®
<i>H. sapiens</i>	Qafzeh	Israel	130-90 ka	Qafzeh 15	XV	m <sub>2</sub> drch.	ESRF®
<i>H. sapiens</i>	Qafzeh	Israel	130-90 ka	Qafzeh 15	XV	m <sub>2</sub> izq.	ESRF®
<i>H. sapiens</i>	Lagar Velho	Portugal	24.500 ± 500 yr BP	Lagar Velho 1	I	M <sub>1</sub> drch.	NESPOS®
<i>H. sapiens</i>	Lagar Velho	Portugal	24.500 ± 500 yr BP	Lagar Velho 1	I	m <sub>2</sub> drch.	NESPOS®

<i>H. sapiens</i>	La Madeleine	Francia	10.190 ± 100 yr BP	La Madeleine	I	m <sub>1</sub> drch.	NESPOS®
<i>H. sapiens</i>	La Madeleine	Francia	10.190 ± 100 yr BP	La Madeleine	I	m <sub>1</sub> izq.	NESPOS®
<i>H. sapiens</i>	La Madeleine	Francia	10.190 ± 100 yr BP	La Madeleine	I	m <sub>2</sub> drch.	NESPOS®
<i>H. sapiens</i>	La Madeleine	Francia	10.190 ± 100 yr BP	La Madeleine	I	m <sub>2</sub> izq.	NESPOS®
<i>H. sapiens</i>	El Mirador	España	4.760-4.200 cal yr BP	MIR201-7	VIII	M <sub>1</sub> drch.	CENIEH
<i>H. sapiens</i>	El Mirador	España	4.760-4.200 cal yr BP	MIR202-T34	VI	M <sub>1</sub> drch.	CENIEH
<i>H. sapiens</i>	El Mirador	España	4.760-4.200 cal yr BP	MIR202-T34	VI	M <sub>1</sub> izq.	CENIEH
<i>H. sapiens</i>	El Mirador	España	4.400-4.100 cal yr BP	MIR4 P22 294	I	M <sub>1</sub> izq.	CENIEH
<i>H. sapiens</i>	El Mirador	España	4.400-4.100 cal yr BP	MIR4 P22 205	IV	M <sub>1</sub> izq.	CENIEH
<i>H. sapiens</i>	El Mirador	España	4.400-4.100 cal yr BP	MIR4 P22 108	II	M <sub>1</sub> izq.	CENIEH
<i>H. sapiens</i>	El Mirador	España	4.400-4.100 cal yr BP	MIR4 P22 285	V	M <sub>1</sub> drch.	CENIEH
<i>H. sapiens</i>	El Mirador	España	4.400-4.100 cal yr BP	MIR4 P22 190	V	M <sub>1</sub> izq.	CENIEH
<i>H. sapiens</i>	El Mirador	España	4.760-4.200 cal yr BP	MIR201-7	VIII	M <sub>2</sub> drch.	CENIEH
<i>H. sapiens</i>	El Mirador	España	4.760-4.200 cal yr BP	MIR202-T34	VI	M <sub>2</sub> drch.	CENIEH
<i>H. sapiens</i>	El Mirador	España	4.760-4.200 cal yr BP	MIR202-T34	VI	M <sub>2</sub> izq.	CENIEH
<i>H. sapiens</i>	El Mirador	España	4.400-4.100 cal yr BP	MIR4 P22 230	VI	M <sub>2</sub> izq.	CENIEH
<i>H. sapiens</i>	El Mirador	España	4.400-4.100 cal yr BP	MIR4 P22 205	IV	M <sub>2</sub> izq.	CENIEH
<i>H. sapiens</i>	El Mirador	España	4.400-4.100 cal yr BP	MIR4 P22 108	II	M <sub>2</sub> izq.	CENIEH
<i>H. sapiens</i>	El Mirador	España	4.400-4.100 cal yr BP	MIR4 P22 285	V	M <sub>2</sub> drch.	CENIEH
<i>H. sapiens</i>	El Mirador	España	4.760-4.200 cal yr BP	MIR201-7	VIII	M <sub>3</sub> drch.	CENIEH
<i>H. sapiens</i>	El Mirador	España	4.760-4.200 cal yr BP	MIR201-P37	-	M <sub>3</sub> izq.	CENIEH
<i>H. sapiens</i>	El Mirador	España	4.760-4.200 cal yr BP	MIR202-T34	VI	M <sub>3</sub> drch.	CENIEH
<i>H. sapiens</i>	El Mirador	España	4.400-4.100 cal yr BP	MIR4 P22 230	VI	M <sub>3</sub> izq.	CENIEH
<i>H. sapiens</i>	El Mirador	España	4.400-4.100 cal yr BP	MIR4 P22 205	IV	M <sub>3</sub> izq.	CENIEH
<i>H. sapiens</i>	El Mirador	España	4.400-4.100 cal yr BP	MIR4 P22 294	I	m <sub>1</sub> izq.	CENIEH
<i>H. sapiens</i>	El Mirador	España	4.400-4.100 cal yr BP	MIR4 P22 294	I	m <sub>2</sub> izq.	CENIEH
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	IZ3	-	M <sub>1</sub> drch.	CENIEH
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	HER8	-	M <sub>1</sub> izq.	CENIEH

<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	AC87	-	M <sub>1</sub> izq.	CENIEH
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	BL4	-	M <sub>1</sub> izq.	CENIEH
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM16	XVI	M <sub>1</sub> izq.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM38	XXXVIII	M <sub>1</sub> izq.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM48	XLVIII	M <sub>1</sub> izq.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM10	X	M <sub>1</sub> izq.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM28	XXVIII	M <sub>1</sub> izq.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM38	XXXVIII	M <sub>1</sub> drch.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM51	LI	M <sub>1</sub> drch.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM53	LIII	M <sub>1</sub> drch.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM67	LXVII	M <sub>1</sub> drch.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM26	XXVI	M <sub>1</sub> drch.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM44	XLIV	M <sub>1</sub> drch.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM65	LXV	M <sub>1</sub> drch.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	AC7	-	M <sub>2</sub> drch.	CENIEH
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	AG1	-	M <sub>2</sub> drch.	CENIEH
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	AC33	-	M <sub>2</sub> drch.	CENIEH
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	AC12	-	M <sub>2</sub> izq.	CENIEH
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	AC10	-	M <sub>2</sub> izq.	CENIEH
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	ISC2	-	M <sub>2</sub> izq.	CENIEH
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	BA12	-	M <sub>2</sub> izq.	CENIEH
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	IZ14	-	M <sub>2</sub> izq.	CENIEH
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	CR20080000017	-	M <sub>2</sub> izq.	CENIEH
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	CR20080000113	-	M <sub>2</sub> izq.	CENIEH
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM3	III	M <sub>2</sub> izq.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM3	III	M <sub>2</sub> drch.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM58	LVIII	M <sub>2</sub> izq.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM58	LVIII	M <sub>2</sub> drch.	UCM



<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM22	XXII	M <sub>2</sub> drch.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM67	LXVII	M <sub>2</sub> drch.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM59	LIX	M <sub>2</sub> izq.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM65	LXV	M <sub>2</sub> izq.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM9	IX	M <sub>2</sub> izq.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM10	X	M <sub>2</sub> izq.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM69	LXIX	M <sub>2</sub> izq.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM24	XXIV	M <sub>2</sub> izq.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM28	XXVIII	M <sub>2</sub> izq.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM38	XXXVIII	M <sub>2</sub> izq.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM44	XLIV	M <sub>2</sub> izq.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM57	LVII	M <sub>2</sub> izq.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	IA19	-	M <sub>3</sub> izq.	CENIEH
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	JB1	-	M <sub>3</sub> izq.	CENIEH
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	CR20080000092	-	M <sub>3</sub> izq.	CENIEH
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	CR20080000117	-	M <sub>3</sub> drch.	CENIEH
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	CR20080000118	-	M <sub>3</sub> izq.	CENIEH
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	CR20080000123	-	M <sub>3</sub> izq.	CENIEH
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM18	XVIII	M <sub>3</sub> izq.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM65	LXV	M <sub>3</sub> izq.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM30	XXX	M <sub>3</sub> izq.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM31	XXXI	M <sub>3</sub> izq.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM38	XXXVIII	M <sub>3</sub> izq.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM4	IV	M <sub>3</sub> drch.	UCM
<i>H. sapiens</i>	Muestra Contemporánea	España	Muestra actual	UCM37	XXXVII	M <sub>3</sub> drch.	UCM
<i>H. ergaster</i>	Buia	Eritrea	1 Ma	MA 93	-	M <sub>1/2</sub> izq.	Zanolli et al., 2014
<i>H. erectus</i>	Sangiran Dome	Java	800-500 ka	NG0802.3	-	M <sub>2</sub> drch.	Zanolli, 2013 y 2015
<i>H. erectus</i>	Sangiran Dome	Java	800-500 ka	NG92.3	-	M <sub>2/3</sub> izq.	Zanolli, 2013 y 2015

<i>H. erectus</i>	Sangiran Dome	Java	800-500 ka	NG92 D6 ZE 57s/d 76	-	M <sub>23</sub> drch.	Zanolli, 2013 y 2015
<i>H. erectus</i>	Sangiran Dome	Java	800-500 ka	NG0802.2	-	M <sub>23</sub> drch.	Zanolli, 2013 y 2015
<i>H. erectus</i>	Sangiran Dome	Java	800-500 ka	NG9107.2	-	M <sub>3</sub> izq.	Zanolli, 2013 y 2015
<i>H. erectus</i>	Sangiran Dome	Java	800-500 ka	PCG.2	-	m <sub>2</sub> drch.	Zanolli et al., 2012
<i>H. erectus</i>	Yiyuan	Este China	420-320 ka BP	Sh.y.072	III	M <sub>2</sub> izq.	Xing et al., 2016
<i>H. erectus</i>	Hexian	Este China	412 ± 25 ka	PA838	-	M <sub>2</sub> izq.	Xing et al., 2014
<i>H. erectus</i>	Hexian	Este China	412 ± 25 ka	PA839	-	M <sub>2</sub> izq.	Xing et al., 2014
<i>H. erectus</i>	Hexian	Este China	412 ± 25 ka	PA834-2	-	M <sub>3</sub> izq.	Xing et al., 2014
<i>H. erectus</i>	Hexian	Este China	413 ± 25 ka	PA831	-	M <sub>2</sub> izq.	Liu et al., 2017
<i>H. erectus</i>	Hexian	Este China	413 ± 25 ka	PA831	-	M <sub>3</sub> izq.	Liu et al., 2017
<i>H. erectus</i>	Zhoukoudian	Norte China	770 ± 80 ka	PA 70	-	M <sub>2</sub> izq.	Xing et al., 2014
-	Xujijayao	Norte China	370-260 ka	PA 1500	IV	M <sub>3</sub> drch.	Xing et al., 2015
-	Qesem Cave	Israel	300 ka	QC12	-	M <sub>2</sub> drch.	HersHKovitz et al., 2016; Weber et al., 2016
-	Qesem Cave	Israel	300 ka	QC13	-	M <sub>3</sub> izq.	HersHKovitz et al., 2016
-	Qesem Cave	Israel	301 ka	QC2	-	m <sub>2</sub> izq.	Fornai et al., 2016
<i>H. heidelbergensis</i> s.l.	Mala Balanica	Serbia	400 ka	BH-1	-	M <sub>1</sub> izq.	Roksandic et al., 2011; Skinner et al., 2016
<i>H. heidelbergensis</i> s.l.	Mala Balanica	Serbia	400 ka	BH-1	-	M <sub>2</sub> izq.	Roksandic et al., 2011; Skinner et al., 2016
<i>H. heidelbergensis</i> s.l.	Mala Balanica	Serbia	400 ka	BH-1	-	M <sub>3</sub> izq.	Roksandic et al., 2011; Skinner et al., 2016

\* molares cuyo estado de conservación o reconstrucción 3D no ha permitido una correcta visualización de los caracteres morfológicos

- sin asignación

MP (Middle Pleistocene); CENIEH (Centro Nacional de Investigación sobre Evolución Humana); LAMIS (Laboratoire d'Anthropologie Moléculaire et Imagerie de Synthèse); IC2MP (Institut de Chimie des Milieux et Matériaux de Poitiers); NESPOS (Neanderthal Studies Professional Online Service); ESRF (European Synchrotron Radiation Facility); UCM (Universidad Complutense de Madrid)



# 04

METODOLOGÍA



## 4. METODOLOGÍA

### 4.1. PRINCIPIOS Y UTILIDADES DE LA MICROTOMOGRAFÍA AXIAL COMPUTARIZADA

El término tomografía proviene del griego “*τομον*” que significa corte o sección y “*γραφίς*” que significa imagen o grafía. Aunque el primer sistema de microtomografía por rayos X fue concebido y construido por J. Elliott en 1980 (Elliott y Dover, 1982), no fue hasta 1998 cuando la microtomografía axial computarizada (microCT) revolucionó el campo de la radiología, tal y como lo hizo la tomografía convencional a principios de los 70s, cuando los doctores G. Hounsfield y J. Ambrose lo utilizaron por primera vez como herramienta diagnóstica (Hounsfield, 1973). La microtomografía es una técnica no destructiva basada en la detección de rayos X a través del objeto escaneado que permite realizar secciones virtuales de micras de espesor y reconstrucciones tridimensionales en alta resolución de sus estructuras externas e internas (Pereira, 2004; Arana Fernández de Moya et al., 2006; Patoni et al., 2006; Calzado y Geleijns, 2010). A diferencia de la radiografía convencional que obtiene una única imagen de proyección, la tomografía consigue múltiples imágenes o cortes tomográficos.

La técnica del microCT se basa en la proyección tangencial de un haz colimado de rayos X hacia el objeto de estudio. Cuando dicho haz de electrones atraviesa el objeto la absorción y atenuación del haz, que dependen directamente de la densidad del objeto, es absorbida por un detector y convertida en una señal electrónica (Figura 4.1.1). Tras la repetición de este proceso desde múltiples ángulos, se obtiene una primera imagen tomográfica. Una vez reconstruida esta primera imagen, el objeto a escanear avanza una unidad de medida ya establecida y el ciclo vuelve a empezar consiguiendo un segundo corte tomográfico. El proceso se repite hasta que el objeto de estudio es escaneado por completo (Figura 4.1.2). A partir de entonces, todas las imágenes obtenidas y registradas en un ordenador reconstruyen una imagen bidimensional en escala de grises.

Para poder obtener una calidad de imagen óptima, es importante tener en cuenta una serie de factores. Estos factores son: el coeficiente de absorción o atenuación y el tamaño del voxel. El primero o coeficiente de absorción es el cociente obtenido entre la energía incidente y la absorbida por el objeto escaneado que dependerá de la densidad del mismo. La medición de la densidad del objeto se basa en una escala de

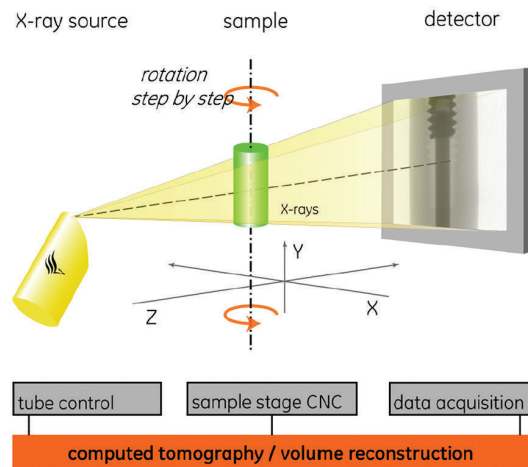


Figura 4.1.1. Representación gráfica del mecanismo de acción de un aparato de microtomografía.

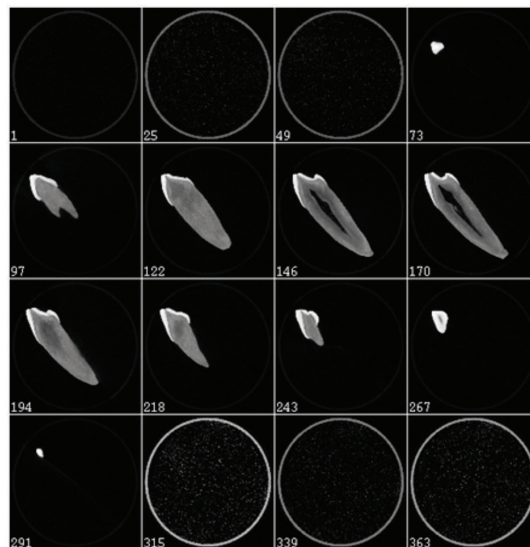


Figura 4.1.2. Ejemplo de diferentes secciones virtuales de un diente obtenidas con un microCT.

grises denominada Unidades Hounsfield (UH), cuyos límites están entre -1000 UH para el aire, 0 UH para el agua y +1000 UH para el hueso. En el caso de los dientes, la alta densidad del tejido adamantino (esmalte) puede alcanzar un valor superior a los 3000 UH. Puesto que el ojo humano no es capaz de distinguir unos niveles de grises tan altos, aquellos tejidos con un amplio rango de densidades, como es el caso de los dientes, son transformados por el ordenador en una escala con un mayor número de tonalidades de grises. En cuanto al segundo factor o tamaño de voxel (por su abreviatura del inglés, *volumetric pixel*) lo primero que tenemos que tener en cuenta es que una

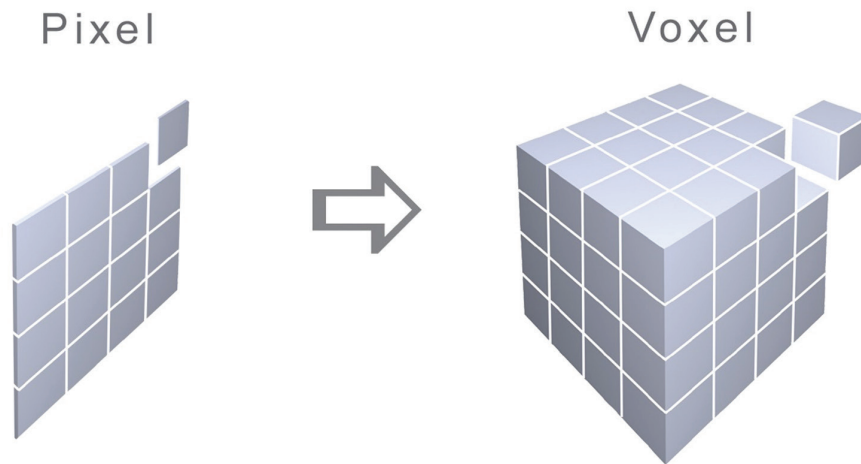


Figura 4.1.3. Representación gráfica de un conjunto de píxeles (4x4) y voxels (4x4x4) que forman una matriz de imagen.

imagen tomográfica está formada por píxeles. Un píxel (unidad mínima que compone un elemento bidimensional) forma parte de un elemento de volumen denominado voxel (unidad cúbica mínima que compone un objeto tridimensional), cuyo conjunto se conoce como matriz de imagen (Figura 4.1.3). Cada píxel tiene asignado un valor o coeficiente de absorción que depende directamente de la penetración del haz a través del objeto escaneado, por lo que cada píxel representa la densidad del objeto en una localización exacta, es decir, en un eje de coordenadas X e Y concreto. Por tanto, al unirse una serie de secciones contiguas equidistantes, se puede construir un mapa tridimensional que muestra las variaciones de densidad en el objeto.

Una vez obtenidos todos los cortes (*stack de imágenes*) microtomográficos, estos pueden ser exportados en diferentes formatos. Los más comunes son los ficheros de imágenes TIF (Tagged Images Format) y DICOM (Digital Imaging and Communication in Medicine), ambos utilizados para la reconstrucción del material de nuestra muestra de estudio. El programa del equipo del microtomografía genera un documento llamado *Header*, que contiene toda la información del escaneo (p.ej., tamaño del voxel, kilovoltaje, número de cortes tomográficos) necesaria a la hora de introducir los parámetros en un software de reconstrucción 3D para el correcto post-procesado de las imágenes. Sin embargo, la gran ventaja del formato DICOM es que cada uno de los ficheros generados posee toda la información del escaneo, con lo que se evita cometer errores o pérdida de información.



Durante los últimos años, la aplicación de la técnica del microCT ha permitido incrementar notablemente la información que se puede recabar de un registro tanpreciado y escaso como es el de los fósiles humanos sin dañar la muestra (Sporer et al., 2000; Olejniczak, 2006; Bailey et al., 2011; Martín-Torres et al., 2011b; Skinner et al., 2013; Martín-Francés et al., 2015; Xing et al., 2015; Zanolli, 2015; Quam et al., 2016).

#### 4.2. ESCANEADO DE LA MUESTRA DE ESTUDIO

El proceso de escaneo de la mayoría de los dientes que forman parte de la presente tesis doctoral se llevó a cabo con diferentes equipos albergados en Instituciones de España, Italia y Francia. En el Centro Nacional de Investigación sobre Evolución Humana (CENIEH) en Burgos, España, se encuentran dos de los equipamientos: el MicroCT-80 Scanco Medical (utilizado desde el año 2008 hasta el año 2014) y el MicroCT GE Phoenix v|tome|x (adquirido a partir del año 2015). En la Universidad de Burgos se utilizó el Tomograph YXILON Compact Yxlon International X-Ray GmbH. En el Multidisciplinary Laboratory (MLAB) del 'Abdus Salam' International Centre for Theoretical Physics (ICTP) en Trieste, Italia, se escanearon muestras con el X-ray ICTP-ELETTRA microCT system. Y finalmente, en el Laboratoire d'Anthropologie Moléculaire et Imagerie de Synthèse de Toulouse y en el Centre de Microtomographie de Rayons X de l'Université de Poitiers, se realizaron los escáneres de las mandíbulas de Montmaurin y Tighenif respectivamente.

Puesto que las características técnicas de cada equipo son diferentes, los parámetros aplicados para el escaneo de las muestras también lo son. Estos no sólo dependen del grado de fosilización sino también de su tamaño y morfología. El software del equipo de microCT genera un documento -denominado *Header*- donde se recogen todos los parámetros (kilovoltaje, amperaje, tamaño del voxel, filtro, etc.) utilizados a la hora de escanear la muestra. Los parámetros utilizados durante el escaneo de los restos fósiles aparecen documentados en el apartado de metodología de cada una de las publicaciones incluidas en la presente tesis doctoral.

### 4.3. POST-PROCESADO DE LAS IMÁGENES

El microCT ofrece a los investigadores una técnica no destructiva para visualizar las características tanto del exterior como del interior de los objetos sólidos compactados, y ofrecer información digitalizada de sus características geométricas y propiedades tridimensionales. No obstante, se necesita un programa informático potente para procesar las imágenes en bruto y poder reconstruir, obtener y evaluar la infinidad de datos que se nos presentan. Hoy en día existen numerosos softwares (Amira®, Avizo®, Mimics®) que permiten importar el *stack de imágenes* tomográficas y/o microtomográficas para reconstruir los diferentes materiales. Visage Imaging Amira® fue el software utilizado para realizar la segmentación, reconstrucción y análisis del material de estudio de la presente tesis doctoral (Figura 4.3.1).

Visage Imaging Amira® es un programa de tratamiento de imágenes que permite importar series de imágenes 2D -como las obtenidas con el microCT- y reconstruirlas tridimensionalmente con precisión. El análisis de imágenes con este software permite la creación, observación, manipulación y control de modelos DICOM, ISQ, TIF, CAD y de otros archivos matriz procedentes de distintos tomógrafos. Su sistema, basado en módulos funcionales, puede ser adaptado para reunir unos requerimientos técnicos

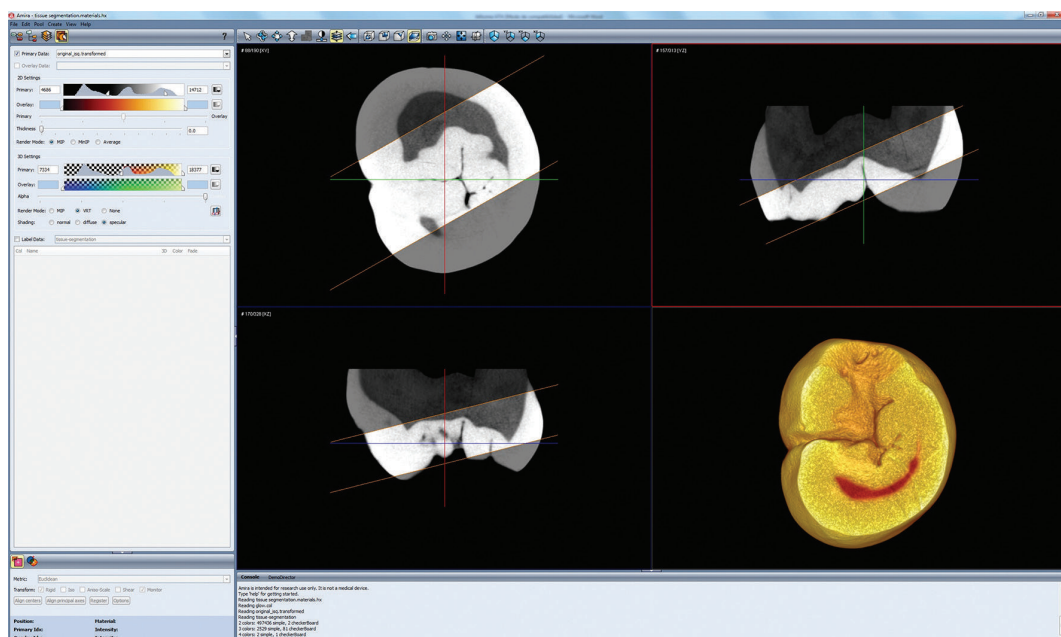


Figura 4.3.1. Visualización de un diente con el programa de reconstrucción Visage Imaging Amira®

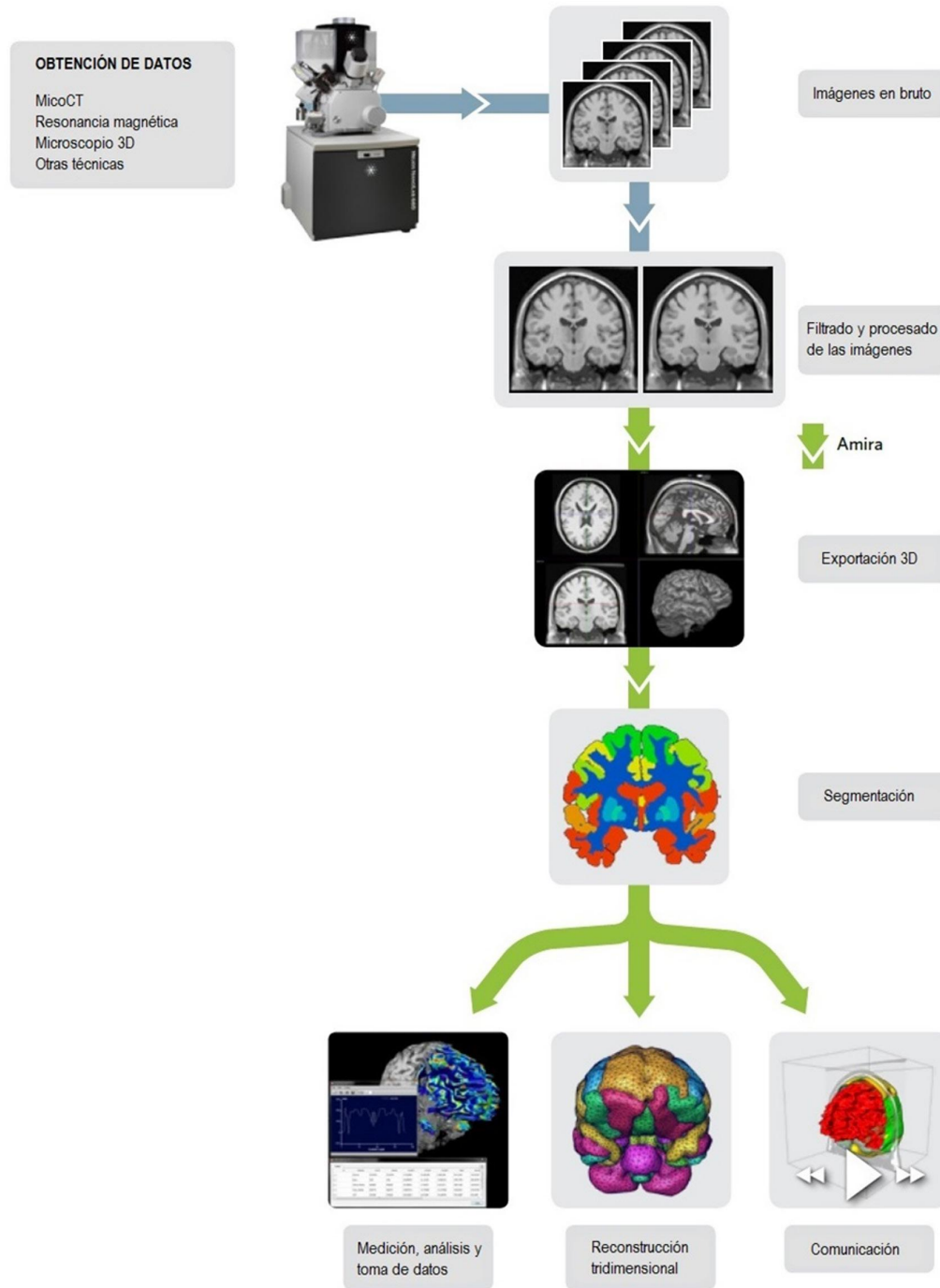


Figura 4.3.2. Pasos necesarios a la hora de trabajar imágenes con el software Visage Imaging Amira®

específicos conforme a las necesidades de aplicación. Esto, por un lado, ha facilitado la obtención de importantes datos (áreas, grosores, separación intratrabecular, dimensión fractal, etc.) a los que hasta ahora no se tenía acceso, pero además ha permitido aumentar la precisión y exactitud a la hora de realizar los análisis morfométricos y las evaluaciones anatómicas virtuales necesarias para la realización de la presente tesis doctoral. Pero, para ello, previamente se ha de efectuar una minuciosa labor de recopilación, procesamiento, análisis y reconstrucción tridimensional de los datos obtenidos a partir de las tomografías realizadas con el microCT (Figura 4.3.2).

El post-procesado de las imágenes es un trabajo minucioso no automatizado que requiere de un tratamiento individualizado para cada muestra. Por ello es fundamental la definición y optimización del protocolo llevado a cabo en el estudio del material. De esta forma se estandariza el método, se facilita la reproducibilidad entre diferentes investigadores o equipos, y se reducen errores y la consiguiente necesidad de reanalizar o rectificar a posteriori alguno de los laboriosos pasos ya realizados en el análisis de las imágenes.

De esta manera y dependiendo de la conservación de los restos, el primer paso tras la obtención de las imágenes en bruto, es la aplicación de una serie de **filtros** (Kuwahara, Median, Mean, Gauss, etc.) sobre las imágenes originales para mejorar el contraste y optimizar su visualización. Aunque en nuestro caso, gracias al estado de conservación de la muestra de estudio, no hemos hecho uso de ninguno de estos filtros, éstos se pueden aplicar desde el mismo software de reconstrucción 3D (Amira®) o mediante programas especializados en tratamiento de imágenes (Fiji). Posteriormente se procede a segmentar los diferentes materiales o tejidos -en nuestro caso esmalte y dentina- para su reconstrucción tridimensional.

En segundo lugar, se procede a **orientar** el diente en su posición anatómica alineándolo con los ejes de coordenadas, de tal manera que la cara mesial quede alineada con el eje de las X. Una vez orientado el diente, y para maximizar recursos, hemos establecido el **plano cervical** descrito por Olejniczak (2006) como el plano de corte.

El siguiente paso consiste en **segmentar** el diente. La segmentación se basa en asignar a cada píxel de la imagen un valor que indica a qué región o tejido pertenece dicho píxel, en nuestro caso esmalte o dentina. De esta manera, asignamos a cada tejido un material diferente que dependerá de la densidad de cada uno de ellos. El método conocido como *thresholding* es una herramienta útil a la hora de delimitar estructuras

con densidades homogéneas. Esta técnica permite crear umbrales de densidades que facilitan notablemente el postprocesado de las imágenes. Sin embargo, la corrección de imperfecciones (fracturas, artefactos, cálculo dental, etc.) siempre es necesaria y ha de realizarse manualmente para cada una de las imágenes tomográficas existentes. En algunos casos, normalmente con los restos fósiles, debido al grado de fosilización del material escaneado, esta minuciosa labor requiere mucho tiempo. Así, por ejemplo, la fosilización de algunas de las piezas dentales de *H. antecessor*, ha producido que los diferentes tejidos tengan la misma densidad dificultando la separación entre el blanco del esmalte y el gris de la dentina (Figura 4.3.3 imagen de la izquierda). Sin embargo, los dientes pertenecientes a las colecciones modernas suelen mostrar una clara diferenciación en la densidad de los tejidos, siendo posible distinguir en la escala de grises entre el blanco del esmalte y el gris de la dentina (Figura 4.3.3).

Una vez segmentado el diente generamos el **volumen** correspondiente al esmalte y a la dentina para proceder a realizar el análisis morfológico pertinente. Además, una importante ventaja que presenta la aplicación de un programa de reconstrucción 3D y el posterior tratamiento de imágenes, es que nos permite el ensamblaje virtual de las distintas piezas sin tocar el original, sirviendo además para corregir deformaciones y eliminar costras y capas de materiales que puedan enmascarar la morfología e incluso duplicar partes que no existen (Figura 4.3.4). Por tanto, a partir del microCT y con el software adecuado se pueden generar modelos tridimensionales digitales de gran precisión que reproducen la morfología original y permiten analizar la muestra sin dañarla. Todo esto es de gran utilidad en el campo de la paleoantropología donde la escasez de restos fósiles y su dificultad para estudiarlos, complica notablemente la obtención de importantes resultados.

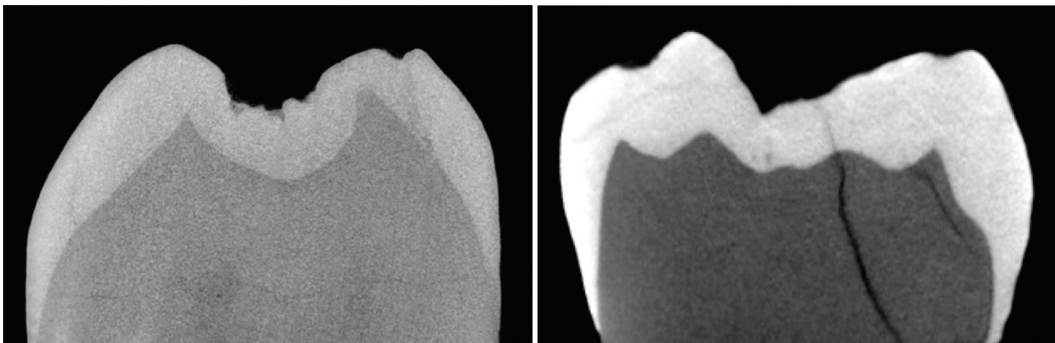


Figura 4.3.3. Imagen tomográfica de un molar perteneciente a *H. antecessor* (izquierda) y un molar perteneciente a *H. sapiens* de la Muestra Contemporánea (derecha).

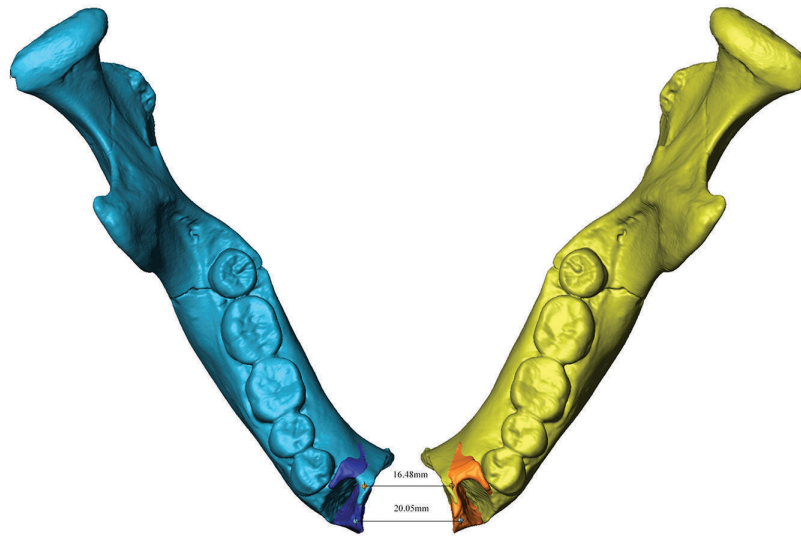


Figura 4.3.4. Reconstrucción de la mandíbula de *H. antecessor* (ATD6-96) mediante la duplicidad de la hemimandíbula original (see Bermúdez de Castro et al., 2016a)

#### 4.4. ANÁLISIS ESTADÍSTICOS

En la presente tesis doctoral hemos realizado diversos análisis estadísticos, como la prueba Chi-cuadrado y el Escalado Multidimensional No Métrico (NMDS) (PAST, Hammer et al., 2001) cuyos resultados se detallan en el capítulo siguiente. Para un correcto análisis e interpretación de los datos, tanto en el Chi-cuadrado como en el NMDS, hemos utilizado un único antímero y hemos excluido aquellos dientes con un grado de desgaste superior a 5 en la escala de Molnar (Molnar, 1971).

La prueba Chi-cuadrado es un método estadístico no paramétrico de contraste de hipótesis utilizado para probar la asociación entre dos variables. Es decir, es una prueba de hipótesis que determina si dos variables están o no relacionadas entre sí. Se utiliza para determinar si una muestra de estudio se ajusta o no a una distribución teórica, contrastando las frecuencias observadas con las frecuencias esperadas de acuerdo a una hipótesis nula. En nuestro caso hemos utilizado este análisis estadístico para comprobar el grado de correspondencia de los patrones de crestas existentes en el esmalte y la dentina entre diferentes especies de homínidos. Para ello, en el esmalte se han considerado los rasgos como presentes (cresta continua) o ausentes (cresta discontinua o ausente), y en la dentina como continuos, discontinuos y ausentes.

El NMDS es una técnica multivariante de interdependencia que trata de representar en un espacio geométrico de pocas dimensiones las proximidades existentes entre un conjunto de objetos. Es un método de ordenación adecuado para datos que están en una escala arbitraria. El objetivo del NMDS es reducir la dimensionalidad de los datos, de tal manera que una vez representados todos elementos, los que aparezcan más cerca, indiquen elementos más cercanos en la matriz de proximidades (García Pérez, 2005). El NMDS es una técnica ampliamente utilizada para detectar gradientes en comunidades biológicas. Con el uso del NMDS pretendemos observar las similitudes o diferencias (aproximación o separación) entre diferentes grupos humanos a través de los rasgos morfológicos analizados en la presente tesis doctoral.







05

RESULTADOS



**INVENTARIO DE LOS PATRONES DE CRESTAS DEL  
TRIGÓNIDO EN LA UNIÓN ESMALTE-DENTINA DE LOS  
MOLARES DE LA SIMA DE LOS HUESOS (ATAPUERCA)**

**INVENTORY OF TRIGONID CREST PATTERNS AT THE  
ENAMEL-DENTINE JUNCTION OF THE SIMA DE LOS HUESOS  
MOLARS (ATAPUERCA)**

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**Resumen**

Hasta el momento, el análisis de la superficie de la dentina en los molares inferiores dentro del género *Homo*, ha estado limitado a *Homo neanderthalensis* y *Homo sapiens*. En este estudio presentamos la tipología de crestas del trigónido que aparecen en los homínidos del Pleistoceno Medio de la Sima de los Huesos (SH), asignados a *Homo heidelbergensis*. La muestra ha sido escaneada con un microCT, así como digitalizada y analizada de manera tridimensional con el software Amira 5.3. Nuestro objetivo es caracterizar las expresiones de crestas

del trigónido en el esmalte (OES) y en la dentina (EDJ) de los homínidos de la SH, para evaluar la relación existente de dicho patrón morfológico dental entre ambas superficies. Aunque nuestros resultados muestran una mayor variabilidad de los patrones de crestas del trigónido en la dentina (14 tipos) con respecto al esmalte (4 tipos) –así como en los  $M_3s$  con respecto a los  $M_1s$  y  $M_2s$ – en casi todos los casos la existencia de una cresta continua en el esmalte se corresponde con una cresta continua en la dentina. Esta característica es ciertamente útil, ya que puede implicar la posibilidad de inferir el tipo de cresta del trigónido que existía en el esmalte de dientes desgastados. Nuestro análisis ratifica las similitudes encontradas en los patrones de crestas del trigónido entre la SH (*H. heidelbergensis*) y los Neanderthales, así como las diferencias con *H. sapiens*. Esta investigación permitirá conocer mejor la variabilidad intra-poblacional de la SH, así como explorar los orígenes del linaje Neanderthal.

**Palabras clave:** molares inferiores permanentes; Sima de los Huesos; *Homo heidelbergensis*; microtomografía; patrones de crestas del trigónido.

#### Abstract

Hitherto, the analysis of lower molars dentine surface, within de genus *Homo*, has been basically limited to *Homo neanderthalensis* and *Homo sapiens*. In this study, we present the analysis of the Middle Pleistocene permanent lower molar sample from the Sima de los Huesos (SH), assigned to *Homo heidelbergensis*. Crest expression was assessed from 3D models of the enamel and the dentine surfaces that were produced using microCT and the software Amira 5.3. Our aim is characterize the pattern of trigonid crest expression in the enamel and dentine to evaluate the concordance of this trait between both surfaces. The results reveal a greater variability in the expression of trigonid crests at the dentine (14 types) compared to the enamel (4 types). Despite this variability, in almost all cases the expression of a continuous trigonid crest at the enamel corresponds with the expression of a continuous trigonid crest at the dentine. This aspect is particularly useful as it may imply the possibility of predicting the type of trigonid crest pattern that would be at the enamel in the case of teeth that are too worn. Our study points to a higher variability in the trigonid crest expression in  $M_3s$  compared to  $M_1s$  and  $M_2s$ . Furthermore, 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*. This research will provide insight into the variability within the SH, as well as to explore the origins of the Neanderthal lineage.

**Keywords:** permanent lower molars; Sima de los Huesos; *Homo heidelbergensis*; microtomography; trigonid crest patterns.

#### INTRODUCTION

In this study, we aim to investigate the expression of trigonid crests at the EDJ of the Atapuerca-Sima de los Huesos lower molar sample by means of mCT. Sima

de los Huesos site is a small cavity of approximately 8m<sup>2</sup> x 4 m<sup>2</sup> 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., 2004). This extraordinary accumulation gives us the opportunity to study intrapopulation variability in a fossil population (Arsuaga et al., 1991; Arsuaga et al. 1993; Arsuaga et al. 1997; Bermúdez de Castro et al., 2004; Martínón-Torres et al., 2012). Sima de los Huesos hominins have been assigned to *Homo heidelbergensis*, a species that has been interpreted as ancestral to *Homo neanderthalensis*, although the exact relationship between both taxa is still matter of debate (Arsuaga et al., 1997; Hublin, 2009; Martínón-Torres et al., 2012) Our objective is to characterize the pattern of trigonid crest expression at the OES and EDJ of the SH sample in order to evaluate the concordance of expression between both surfaces and to explore possible evolutionary meanings of the expression of this feature as it was previously done based on the external morphology of the teeth.

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 (Martínón-Torres et al., 2012, 2007). 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., 2008). It is assumed that the morphology of the EDJ is largely responsible of the external morphology of a tooth (Korenhof, 1982; Nager, 1960; Schwartz et al., 1998; Scott and Turner II, 1997). However, the precise level of concordance between both surfaces is still under study (e.g., Bailey et al., 2011; Skinner et al., 2008; Skinner et al., 2009).

The expression of trigonid crests on the enamel surface human molars has revealed certain patterns of variation that seem to be taxonomically and phylogenetically informative (e.g., Bailey, 2002; Irish, 1998; Scott and Turner II, 1997; Turner II et al., 1991). 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 II, 1997; Turner II et al., 1991) and it can start from any lobe segment or from the marginal ridge complex as well (Bailey et al., 2011).

Following the pioneer work of Korenhof (Korenhof, 1982; Scott and Turner II, 1997), trigonid crests have recently been studied at the EDJ by means of microCT (Bailey et al., 2011; Skinner et al., 2008). 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 particu-

lar, the expression of conspicuous and continuous middle trigonid crests in lower molars has been interpreted as typical of *H. neanderthalensis* (Bailey, 2002; Martínón-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 human species (Bailey et al., 2011). However, evolutionary origin and timing of this distinctive Neanderthal pattern remains unclear as the EDJ expression of the trait has not been examined in geochronologically older hominin species.

## MATERIALS

### The Sima de los Huesos dental sample

Although the SH dental sample consists of 213 permanent molars, of which 123 are lower ones, we have only included in this study those that were isolated or included in a mandibular fragment small enough to fit in the micro-CT scan. In addition, and following Bailey et al. (2011), we excluded the teeth with wear degree higher than category 5 or those that exhibit moderate to extensive secondary dentine but the entire tooth is still completely surrounded by enamel (Molnar, 1971). Thus, the sample analyzed here consisted of 62 permanent lower molars from the Sima de los Huesos site (Table 1).

## METHODS

Each molar of the SH sample 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 75.8mm and a maximum scan length of 140mm, with image matrix from 512 x 512 to 4096 x 4096 pixels. Scans of the teeth from SH used a peak energy of 70 kV and intensity of scanning of 114 $\mu$ A. The sampletime of one projection is 800.000 $\mu$ s, and the microCT takes nearly 500 parallel projections for each 180°. The resultant slices thickness ranged from 18 to 36 micrometers ( $\mu$ m). 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.

### Terminological considerations

In this study, we will basically follow the terminology employed in Martínón-Torres et al., 2012, that combines terms and concepts from both Carlsen and Scott

and Turner II (Carlsen, 1987; Scott and Turner II, 1997) (Fig. 1). Thus, we consider that the main structures of a molar crown are cusps -with their corresponding lobes or ridges-, grooves and crests, and that these may be expressed or not at the dentine surface with the same score as at the enamel one (Skinner et al., 2008). In addition, we can also find secondary structures such as marginal ridges, cingula or tuberculum projections, and supernumerary structures, for which we will use the same terminology as Scott and Turner II (Scott and Turner II, 1997). Thereby, in accordance with the traditional literature (Cope, 1888; Osborn, 1888) and in order to avoid possible confusions, we will refer as a cusp what Carlsen (Carlsen, 1987) and Scott and Turner II (Scott and Turner II, 1997) referred as an entire lobe, and thus, we consider it like the occlusal projection of the crown (White and Folkens, 2005). A cusp can be divided in three different **segments** or lobes or ridges (hereof we will call it lobe) which can be mesial, middle -or essential- and distal (Scott and Turner II, 1997) depending on their anatomical position. The free apex on the top of the essential lobe will be called **cusp tip** (note that Carlsen, 1987, called it essential cusp, but Scott and Turner II, 1997, simply call it cusp). The shallow and longitudinal depressions in the surface of enamel will be called grooves (Carbó Ayala, 2005).

Arising from these concepts about the basic components of a molar, and according to Wu and Turner II (1993), we concur that when a complete crest connects the middle portions of the mesial cusps and it lies mesialward, but not on the marginal border, it is a middle trigonid crest (Wu and Turner II, 1993); otherwise it is a distal trigonid crest.

Although we acknowledge the atypical mesial position of some middle crests (Figure 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 that individual cusps are divided into three elements (mesial, middle and distal lobes) and that the middle or essential one is the one bearing the cusp tip. In this frame, 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; Martín-Torres et al., 2012). Anyhow, although we subscribe to the notion that there are mesial, middle and distal trigonid crests we believe that, at the OES, it is not possible to reliably differentiate a mesial (the one where at least one of the extremes goes clearly to the marginal ridge) from a middle trigonid. Thus, at the OES we will simply score a middle trigonid crest and a distal trigonid crest, following traditional literature and classic scoring systems (Korenhof, 1982; Scott and Turner II, 1997).

### Scoring procedures

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 clas-



sified as a distal trigonid crest (DTC), and over or mesial to this line as a middle (MdTC) or mesial trigonid crest (MeTC) (Fig. 3). If one of the ends of the crest that runs along the mesial 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 calls mesial trigonid crest, in our study is consider as 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. Based on observations of the study sample it is not possible at the OES to reliably differentiate a mesial (the one where one 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 II, 1997).

Although both antimeres were analyzed, we employed the unilateral count method (Turner II, 1987) and in case of asymmetry we have chosen the tooth with the highest degree of expression for the trait because we consider that is the one that has better expressed the genetic signal. Since the analyzed dental features are minimally affected by sexual dimorphism (Turner II 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 that may be useful for other researchers in forthcoming studies about these traits. We also present the frequencies and percentages of the trigonid crests pattern at both the OES and EDJ per molar class, and we will explore how the different EDJ types correspond with the expression of the trigonid crest at the OES. We considered that the trait is «present» when the crest is continuous. Otherwise we consider that the trait is absent (i.e., if the crest is absent or is discontinuous).

Furthermore, in those cases where an accessory cusp 7 (or metaconulid) is present and 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 and Table 2).

## RESULTS

### Trigonid crest types at the OES

If we calculate the frequency of expression of the trigonid crest types at the OES counting only one antimere per individual (Table 3), we observe that the totality of the  $M_1$  and  $M_2$  specimens analyzed present a **MdTC**, and for the nearly the totality of the  $M_3$ s specimens analyzed. Regarding **DTC** at the OES, and unlike

what we can observe in the previous case, now this trigonid crest pattern is present only in some of the  $M_3$ s.

#### *Trigonid crest types at the EDJ*

In the dentine of the SH molar sample, the variety of different trigonid crest types and combinations is clearly higher and more complex than the ones established on enamel. Contrary to what occurred with the enamel, at the EDJ we were able to be more precise in discerning the origin of the crests and in differentiating a mesial trigonid crest (MeTC) from a middle trigonid crest (MdTC). Table 4 presents comprehensive typology and description of all types, which are also illustrated in schematic form (Fig. 4).

Table 5 shows us the frequencies and percentages of the MeTC, MdTC and DTC for each dental class if we choose only one antimere per individual. Regarding **MeTC**, the largest number is displayed by the  $M_3$ s, followed by  $M_2$ s and ending with no MeTCs for the  $M_1$ s. Meanwhile, for the **MdTC** we can observe that the highest percentage correspond to the  $M_1$ s with the totality of the sample, followed by the  $M_2$ s and  $M_3$ s. As well as happened at the OES, the data show us again that the **DTC** is present only in some of the  $M_3$ s.

#### **Variability of the trigonid crest types at the EDJ**

The four basic types of trigonid expression at the OES contrast with the greater variability, with a wider spectrum of crests types and combinations, at the EDJ. As we can see in Table 6, the type A at the OES is the one showing higher variability at the EDJ. However, and despite this variability, all teeth present a general good correlation between the enamel and dentine surface in such a way that continuous MdTC at the OES tend to correspond with continuous MeTC or MdTC at the dentine and viceversa. Similarly, continuous DTC at the OES tend to correspond with 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 discontinuous DTC. **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. **Type C** at the OES (continuous MdTC and DTC) exhibits the co-expression of two continuous crests also at the EDJ, except in AT-100 (left  $M_3$ ) where the MeTC or MdTC is absent -type 3- and in AT-811 (right  $M_3$ ) where the DTC is discontinuous -type 14-. **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.

## DISCUSSION

### Variability of the trigonid crest types 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 a 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 crests at the EDJ.

Regarding the distal trigonid crest at the EDJ, Wu and Turner II did not find individuals expressing both a MdTC and DTC (Wu and Turner II, 1993); and Bailey et al. (Bailey et al., 2011) stated that they have not seen molars with a «true» distal trigonid crest (Bailey et al., 2011). Our study contradicts both statements since we have identified several cases of co-expression of MdTC and DTC on one hand, and we have also found cases of «true» distal trigonid crest in SH sample, although they are not very common (2 molars or 4.65%) and only M<sub>3</sub>s display it. Concerning a crest that connects middle and distal segments, Bailey et al. (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<sub>3</sub>s from SH sample (11.62%).

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 (64.51%) present a middle-middle crest («true» middle trigonid crest sensu Bailey et al., 2011) whereas the remaining 11 (35.48%) 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 according to Bailey et al. 2011 was exclusive of the Neanderthals.

In addition, among all the molar classes, the M<sub>3</sub>s 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 (Martínón-Torres et al., 2012), prevented in some cases an easy identification of the morphological features. Despite of this inconvenience, there is a general concordance in the expression of continuous crests at the OES and the EDJ, with only two M<sub>3</sub>s exceptions (AT-100 and AT-811).

### Taxonomical implications

According to Bailey (Bailey, 2002) and Martínón-Torres (Martínón-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 frequencies tend to be lower (Martín-Torres et al., 2012, 2008, 2007). 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 combination of traits (Bermúdez de Castro, 1986; Bermúdez de Castro et al., 1999; Martín-Torres et al., 2007; Martín-Torres et al., 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 ratifies the results of Bailey et al. (2011), whose data affirm that this type is also consistent in the Neanderthals and very rare in *H. sapiens*.

Future studies in larger samples are necessary to know whether these SH types are present in other hominin groups or they are particular to the SH group. If they are present in earlier hominins it would mean that SH group 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 that those types are not present in any other hominin group, they should be considered as derived (and maybe autapomorphic) 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; Martín-Torres et al., 2012).

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 (Fig. 4). Thus, if we analyze our sample and pay attention to 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 the SH molars is in concordance with the results presented by Bailey et al. (2011).

## CONCLUSIONS

In agreement with Bailey and colleagues (Bailey et al., 2011) and because the dentine exhibits greater variability and more different trigonid crest types than the enamel, it was necessary to use different scoring system than the traditional ones (Korenhof, 1982; Wu and Turner II, 1993) in order to characterize in a more pre-

cise manner the morphology of this sample. Also in accordance with Bailey et al. (2011), our analysis has revealed a higher variability of trigonid crest expressions at the EDJ compared to the OES.

However, and in general terms, our results broadly ratify the strong harmony of trait expression between the enamel (OES) and the dentine (EDJ) (Bailey et al., 2011; Skinner et al., 2008). Because of that, we may also point out that both the expression and the grade of development of the trigonid crest patterns at the enamel is mostly determined by the manifestation at the dentine. This fact is particularly relevant as it implies the possibility of predicting 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.

Based on the results of the 43 lower molars specimens analyzed from the Sima de los Huesos site, the complete lack of trigonid crest type B, type C and type D in SH  $M_1s$  and  $M_2s$ , could be an interesting feature to help classify isolated dental specimens, but we must contrast it with other fossils hominins. Additionally, we observe a greater variability of trigonid crest patterns in  $M_3s$  than in  $M_1s$  and  $M_2s$  for the overall molars sample.

In concordance with previous studies based on the OES morphology, our study ratifies that SH is characterized by displaying the type of trigonid crest patterns that have been classically considered as typical of *H. neanderthalensis* and significantly different from *H. sapiens* (Bailey, 2002; Bailey et al., 2011; Martínón-Torres et al., 2012). However, it has also shown some trigonid crest types that were present neither in the *H. neanderthalensis* sample nor in the *H. sapiens* sample. We think is desirable to analyze other Pleistocene hominins in order to have greater fossil record that allows us to get more taxonomic and phylogenetic information about these traits expression as well as to make possible evolutionary inferences about the expression of this trait in relation with other ancestral hominins.

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Table 1  
**List of molars analyzed in the present study with the number of the individual they are assigned to, sex and age at death estimated by death Bermúdez de Castro et al. (2004)**

Tooth	N	Individual	Sigla	Sex	Age
<b>PERMANENT RIGTH MOLARS (N)</b>					
<b>M<sub>1</sub> right</b>	10	II	AT-2	M	12.5-14.5
		III	AT-101	F	15-17
		X	AT-141	F	15-17
		XI	AT-272	F	13-15
		XIV	AT-2276	-	12.5-14.5
		XVIII	AT-943	M	9.5-11.5
		XX	AT-3175	M	12.5-14.5
		XXIV	AT-2438	-	12.5-14.5
		XXV	AT-3933	F	11-13
		XXVI	AT-561	F	16-18
<b>M<sub>2</sub> right</b>	7	II	AT-142	-	12,5-14,5
		III	AT-271	F	15-17
		XI	AT-1761	F	13-15
		XIV	AT-284	-	12,5-14,5
		XVIII	AT-1752	M	9,5-11,5
		XX	AT-3890	M	12,5-14,5
		XXVI	AT-1756	M	16-18
<b>M<sub>3</sub> right</b>	12	IV	AT-811	F	26-32
		XVIII	AT-2277	M	9,5-11,5
		XXIV	AT-2438	-	12,5-14,5
		XXV	AT-3943	F	11-13
		XXVI	AT-30	F	16-18
		-	AT-143	-	-
		-	AT-599	-	-
		-	AT-942	-	-
		-	AT-1468	-	-
		-	AT-1959	-	-
		-	AT-2777	-	-
		-	AT-3182	-	-

Tooth	N	Individual	Sigla	Sex	Age
<b>PERMANENT LEFT MOLARS (N)</b>					
<b>M<sub>1</sub> left</b>	12	III	AT-22	F	15-17
		IV	AT-14	F	26-32
		VI	AT-1759	F	16-18
		VII	AT-21	M	24-30
		X	AT-556	F	15-17
		XI	AT-286	F	13-15
		XIV	AT-1459	–	12,5-14,5
		XVIII	AT-829	M	9,5-11,5
		XIX	AT-576	F	16-18
		XX	AT-4318	M	12,5-14,5
		XXIV	AT-1458	–	12,5-14,5
		XXV	AT-3934	F	11-13
<b>M<sub>2</sub> left</b>	11	II	AT-3179	–	12,5-14,5
		III	AT-273	F	15-17
		X	AT-169	F	15-17
		XI	AT-557	F	13-15
		XIV	AT-2272	–	12,5-14,5
		XVIII	AT-941	M	9,5-11,5
		XX	AT-946	M	12,5-14,5
		XXIV	AT-2396	–	12,5-14,5
		XXV	AT-6579	F	11-13
		XXVI	AT-2270	F	16-18
		XXVII	AT-3176	M	20-26
<b>M<sub>3</sub> left</b>	10	IV	AT-100	F	26-32
		VII	AT-13	M	24-30
		XVIII	AT-2271	M	9,5-11,5
		XXIV	AT-2385	–	12,5-14,5
		XXV	AT-6580	F	11-13
		–	AT-598	–	–
		–	AT-1473	–	–
		–	AT-1945	–	–
		–	AT-2273	–	–
		–	AT-2760	–	–

Table 2  
**Typology and description of TC forms identified at the enamel surface of the SH sample**

<b>Type A</b>	Continuous MdTC with an absent or discontinuous DTC.
<b>Type B</b>	Continuous DTC with an absent or discontinuous MdTC.
<b>Type C</b>	Continuous MdTC and DTC.
<b>Type D</b>	Absent or discontinuous MdTC and DTC.

Table 3  
**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»**

TRIGONID CREST PATTERN AT ENAMEL				
	Total molar sample	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>
<b>MIDDLE TRIGONID CREST</b>	<b>93.0%</b> (40/43)	<b>100.0%</b> (14/14)	<b>100.0%</b> (11/11)	<b>83.3%</b> (15/18)
<b>DISTAL TRIGONID CREST</b>	<b>25.5%</b> (11/43)	<b>0.0%</b>	<b>0.0%</b>	<b>61.1%</b> (11/18)

Table 4

**Typology and description of TC forms identified at the dentine surface of the SH sample**

<b>Type 1</b>	Continuous MdTC with an absent or discontinuous DTC.
<b>Type 2</b>	Continuous MeTC with an absent or discontinuous DTC.
<b>Type 3</b>	Continuous DTC when at least one of the origins is the distal segment, with an absent or discontinuous MeTC or MdTC.
<b>Type 4</b>	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.
<b>Type 5</b>	Continuous MdTC and a continuous DTC arising from the middle segments.
<b>Type 6</b>	Continuous MdTC and a continuous DTC when at least one of the origins is the distal segment.
<b>Type 7</b>	Continuous MdTC and a discontinuous DTC when at least one of the origins is the distal segment.
<b>Type 8</b>	Continuous MdTC and a discontinuous DTC arising from the distal segments.
<b>Type 9</b>	Continuous MeTC and continuous DTC when at least one of the origins is the distal segment.
<b>Type 10</b>	Continuous MdTC, a discontinuous DTC when at least one of the origins is the distal segment, and a pronounced distal ridge on one side.
<b>Type 11</b>	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.
<b>Type 12</b>	Continuous MdTC, a discontinuous DTC arising from the middle segments and discontinuous DTC arising from the distal segments.
<b>Type 13</b>	Continuous MeTC, a discontinuous DTC arising from the middle segments and discontinuous DTC arising from the distal segments.
<b>Type 14</b>	Continuous MeTC, a discontinuous DTC when at least one of the origins is the distal segment, and a pronounced distal ridge on one side.

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»**

TRIGONID CREST PATTERN AT DENTINE				
	Total molar sample	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>
<b>MESIAL TRIGONID CREST</b>	<b>20.9% (9/43)</b>	<b>0.0%</b>	<b>27.2% (3/11)</b>	<b>33.3% (6/18)</b>
<b>MIDDLE TRIGONID CREST</b>	<b>72.0% (31/43)</b>	<b>100.0% (14/14)</b>	<b>72.7% (8/11)</b>	<b>50.0% (9/18)</b>
<b>DISTAL TRIGONID CREST</b>	<b>23.2% (10/43)</b>	<b>0.0%</b>	<b>0.0%</b>	<b>55.5% (10/18)</b>

Table 6

**Variability of the TC types found at the EDJ and their correspondence to the OES from the SH sample.**

ENAMEL (OES)	DENTINE (EDJ)
<b>Type A</b>	1 - 2 - 7 - 8 - 10 - 11 - 12 - 13 - 14
<b>Type B</b>	3
<b>Type C</b>	3 - 5 - 6 - 9 - 14
<b>Type D</b>	4

Figure 1  
**Definition and schemes (below) of some of the molar crown structures used in this study**

CARLSEN (1987)	SCOTT & TURNER (1997)	MARTINÓN ET AL. (2012)
Lobe	Lobe	Cusp
Accessory Lobe Segment (ALS)	Mesial Accessory Lobe (MAL)	Mesial Segment (MS)
Essential Lobe Segment (ELS)	Essential Accessory Lobe (EAL)	Essential Segment (ES)
Accessory Lobe Segment (ALS)	Distal Accessory Lobe (DAL)	Distal Segment (DS)
Essential Cusp (EC)	Cusp (C)	Cusp Tip (CT)

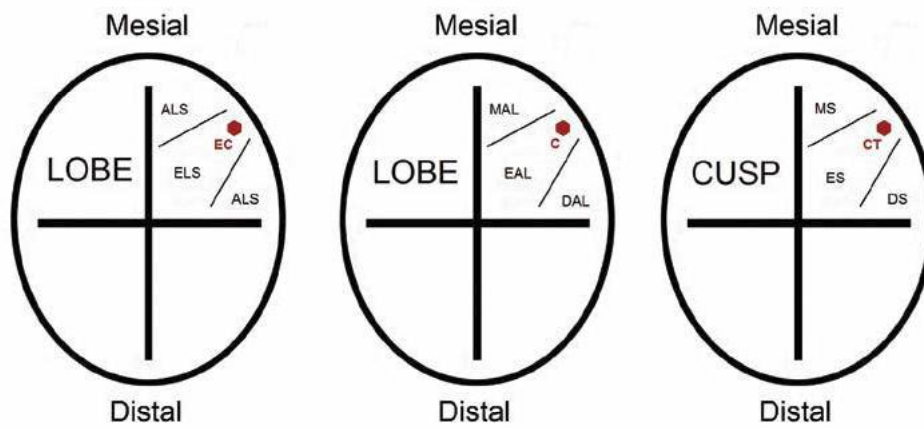


Figure 2  
**A: occlusal enamel surface illustrating a Middle Trigonid Crest (MdTC) and a Distal Trigonid Crest (DTC). B: occlusal dentine surface illustrating a Middle Trigonid Crest (MdTC) and a Distal Trigonid Crest (DTC). C: occlusal dentine surface where we can see a Mesial Trigonid Crest (MeTC). The green line from protoconid tip to metaconid tip defines the position of the crests**

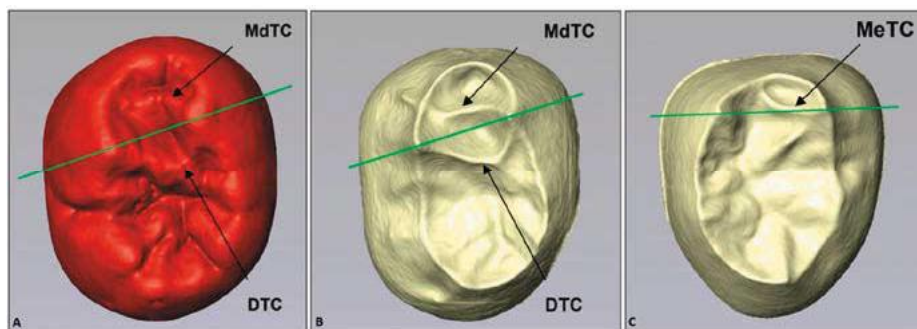


Figure 3

Occlusal surface schemes of the OES (upper left) (explanation in table 2) and EDJ (upper right) (explanation in table 4) 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. Red lines mean that the crest/ridges are present in the form they are depicted

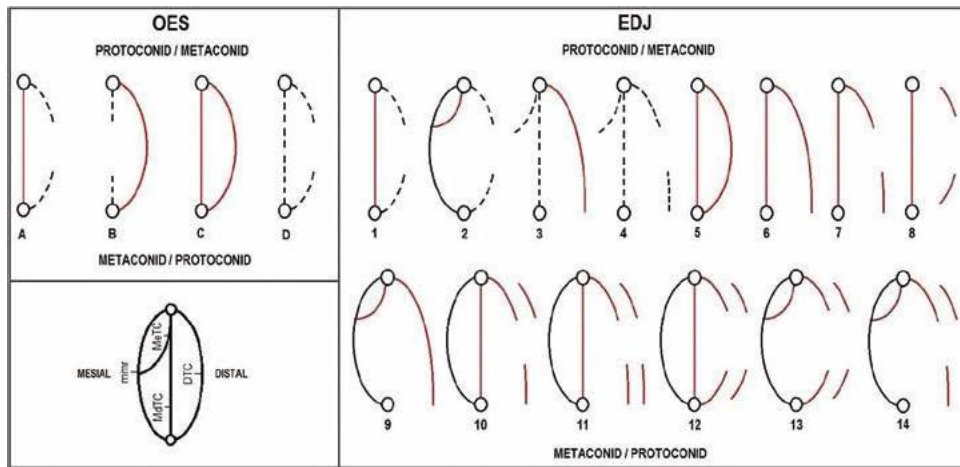
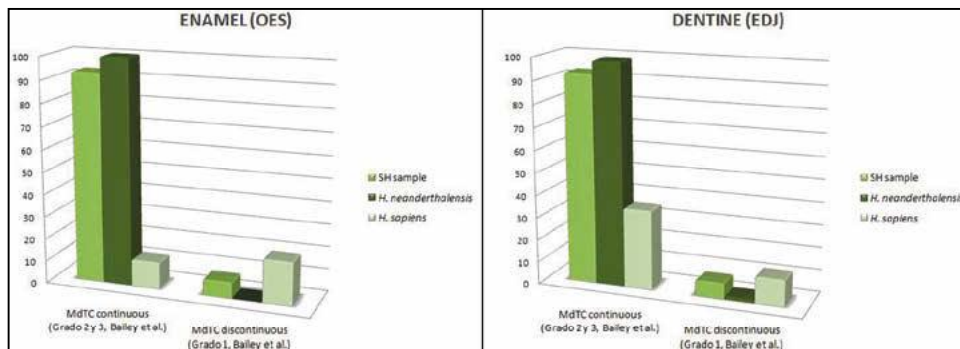


Figure 4

Illustrations of differences among specimens for grades of presence of middle trigonid crest (MdTC) at the OES and EDJ. Note that *H. neanderthalensis* and *H. sapiens* data have been taken from Bailey and colleagues (Bailey et al., 2011)











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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.

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R É S U M É

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*Homo neanderthalensis*  
*Homo sapiens*  
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 Configuration des crêtes du trigonide

La configuration de la crête du trigonide des molaires inférieures est caractéristique chez les hominins 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 hominins 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.

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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; Martínón-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 <sub>1</sub> (n)	M <sub>2</sub> (n)	M <sub>3</sub> (n)
<i>H. heidelbergensis</i>	Sima de los Huesos <sup>a</sup>	62	22	18	22
<i>H. neanderthalensis</i>	Engis <sup>b</sup>	1	1	–	–
	Gibraltar <sup>b</sup>	3	2	1	–
	Ehringsdorf <sup>c</sup>	1	1	–	–
	Abri Bourgeois-Delaunay <sup>c</sup>	1	1	–	–
	Regourdou <sup>c</sup>	6	2	2	2
	Abri Suard <sup>c</sup>	4	3	–	1
	Krapina <sup>c</sup>	20	7	6	7
	Hunas <sup>c</sup>	1	–	–	1
<i>H. sapiens</i>	Roc de Marsal <sup>c</sup>	2	2	–	–
	Equus Cave <sup>b</sup>	2	2	–	–
	Qafzeh <sup>b</sup>	8	4	4	–
	Lagar Velho <sup>c</sup>	1	1	–	–
	El Mirador <sup>a</sup>	9	3	3	3
	CENIEH <sup>a</sup>	12	4	7	1

<sup>a</sup> CENIEH micro-computed tomography data base.

<sup>b</sup> ESRF<sup>®</sup> data base.

<sup>c</sup> NESPOS<sup>®</sup> 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; Martínón-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<sup>2</sup> × 4 m<sup>2</sup> 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; Martínón-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; Martínón-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<sup>®</sup> and ESRF<sup>®</sup> 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; Martínón-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

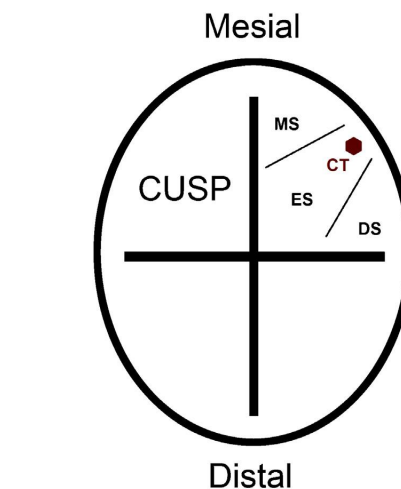


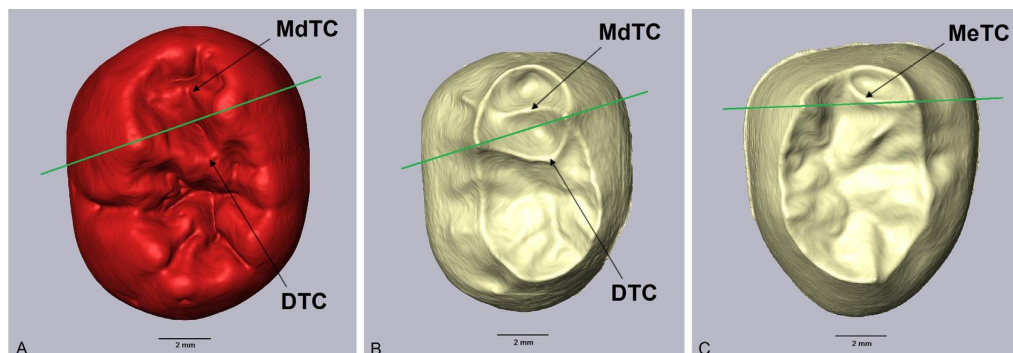
Fig. 1. Scheme of some of the molar crown structures used in this study. MS: mesial segment; ES: essential segment; DS: distal segment; CT: cusp tip.

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 cuspidé.

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.

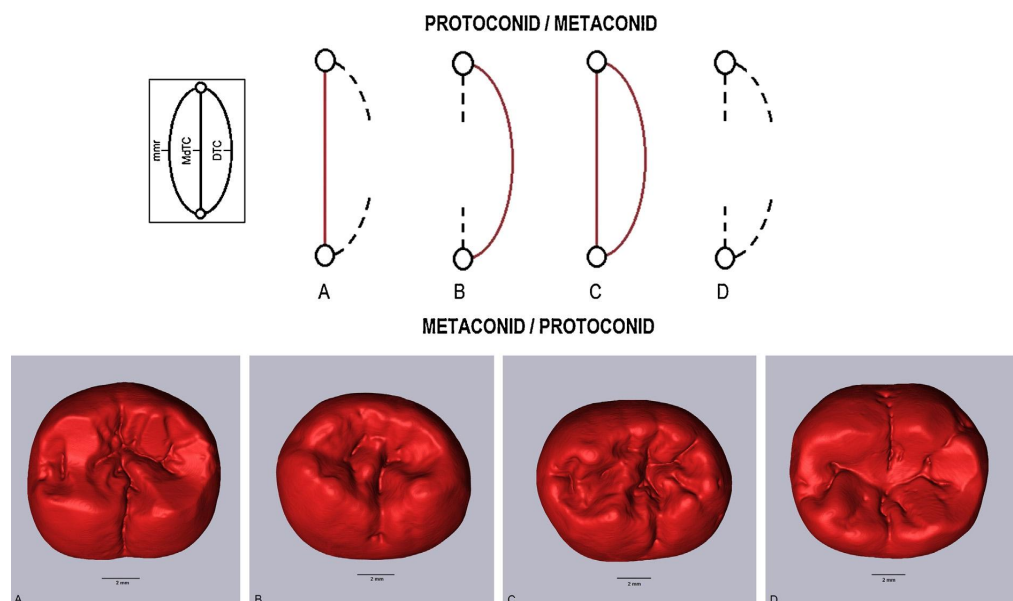
Finally, in recent studies, Skinner et al. (2008b) and Bailey et al. (2011), scored crests at the EDJ based on their origin and the relative position of one to another, defining a mesial, a middle and a distal trigonid crest. According to them, a mesial trigonid crest could occur between the mesial marginal 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; Martínón-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 cuspidés (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-2385) ; type C (AT-2271) ; type D (AT-943).

Based on [Korenhoj, 1982](#).

**Table 2**

Percentages and frequencies of the continuous middle (MdTC) and distal trigonid crest (DTC) at the OES (only one antimerer 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 <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>
Middle trigonid crest at OES				
SH	93.0% (40/43)	100.0% (14/14)	100.0% (11/11)	83.3% (15/18)
<i>H. neanderthalensis</i>	97.0% (33/34)	100.0% (16/16)	100.0% (8/8)	90.0% (9/10)
<i>H. sapiens</i>	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)
<i>H. neanderthalensis</i>	20.5% (7/34)	6.2% (1/16)	12.5% (1/8)	50.0% (5/10)
<i>H. sapiens</i>	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<sub>1</sub> and M<sub>2</sub> samples present a continuous MdTC. For the M<sub>3</sub>s, 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<sub>1</sub>s (50%) and M<sub>3</sub>s (50%), followed by M<sub>2</sub>s (25%). Regarding a **continuous DTC** at the OES, we observe that for the SH sample, these are only present in the M<sub>3</sub>s. Meanwhile, the Neanderthal sample is the only one that exhibits continuous DTC in all molar types, with an increase from M<sub>1</sub> to M<sub>3</sub>. 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<sub>1</sub>, M<sub>2</sub> and total molar sample. For the M<sub>3</sub>s, 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<sub>3</sub> 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<sup>2</sup> 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 <sub>1</sub>	–	0.00 <sup>a</sup>	0.34	–
M <sub>2</sub>	–	0.00 <sup>a</sup>	0.22	–
M <sub>3</sub>	0.62	0.15	0.56	0.02 <sup>a</sup>
Total	0.42	0.00 <sup>a</sup>	0.60	0.00 <sup>a</sup>
NEA				
M <sub>1</sub>		0.00 <sup>a</sup>		0.37
M <sub>2</sub>		0.00 <sup>a</sup>		0.20
M <sub>3</sub>		0.09		0.07
Total		0.00 <sup>a</sup>		0.01 <sup>a</sup>

OES: outer enamel surface; SH: Sima de los Huesos; DTC: distal trigonid crest; MdTC: middle and distal trigonid crest.

<sup>a</sup> 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<sub>1</sub> to the M<sub>3</sub>. *H. sapiens* are the only group with a discontinuous MeTC. For the SH sample we did not record any M<sub>1</sub> with a continuous MeTC. In general terms, the **continuous MdTC** decreases its expression from the M<sub>1</sub>s to the M<sub>3</sub>s. Overall, M<sub>1</sub>s 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<sub>1</sub>s and M<sub>2</sub>s. In particular, all the M<sub>2</sub>s from SH and 7 of 8 Neanderthal M<sub>2</sub>s 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<sub>1</sub>, M<sub>2</sub> and total molar sample. Regarding the DTC, SH shows higher frequencies of expression than *H. sapiens* for the M<sub>2</sub>, M<sub>3</sub> and the total molar sample. Thus, the frequencies of MdTC for the M<sub>3</sub>s and DTC for M<sub>1</sub>s 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<sub>1</sub>s, M<sub>2</sub>s and M<sub>3</sub>s

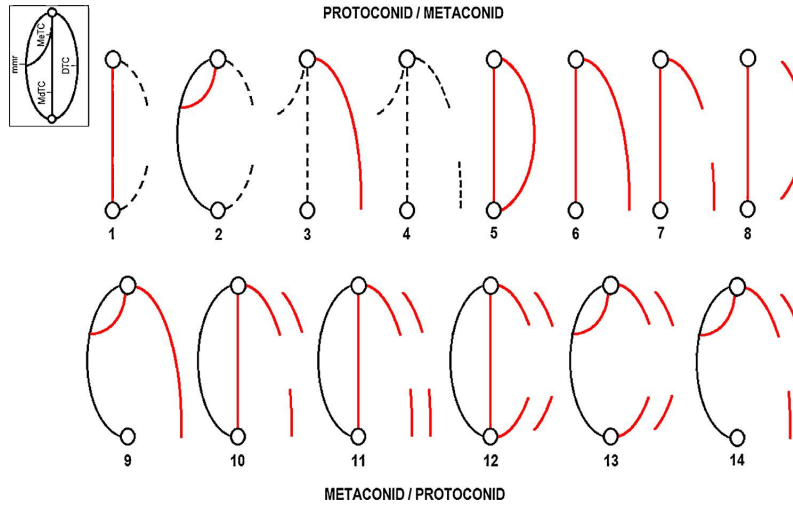
**Table 4**  
Typology and description of trigonid crest forms identified at the dentine surface of the SH sample.

**Tableau 4**  
Typologie et description des formes de crêtes du trigonide identifiées à la surface de la dentine de l'échantillon SH.

<b>Type 1</b>	Continuous MdTC with an absent or discontinuous DTC
<b>Type 2</b>	Continuous MeTC with an absent or discontinuous DTC
<b>Type 3</b>	Continuous DTC when at least one of the origins is the distal segment, with an absent or discontinuous MeTC or MdTC
<b>Type 4</b>	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
<b>Type 5</b>	Continuous MdTC and a continuous DTC arising from the middle segments
<b>Type 6</b>	Continuous MdTC and a continuous DTC when at least one of the origins is the distal segment
<b>Type 7</b>	Continuous MdTC and a discontinuous DTC when at least one of the origins is the distal segment
<b>Type 8</b>	Continuous MdTC and a discontinuous DTC arising from the distal segments
<b>Type 9</b>	Continuous MeTC and continuous DTC when at least one of the origins is the distal segment
<b>Type 10</b>	Continuous MdTC, a discontinuous DTC when at least one of the origins is the distal segment, and a pronounced distal ridge on one side
<b>Type 11</b>	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
<b>Type 12</b>	Continuous MdTC, a discontinuous DTC arising from the middle segments and discontinuous DTC arising from the distal segments
<b>Type 13</b>	Continuous MeTC, a discontinuous DTC arising from the middle segments and discontinuous DTC arising from the distal segments
<b>Type 14</b>	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**

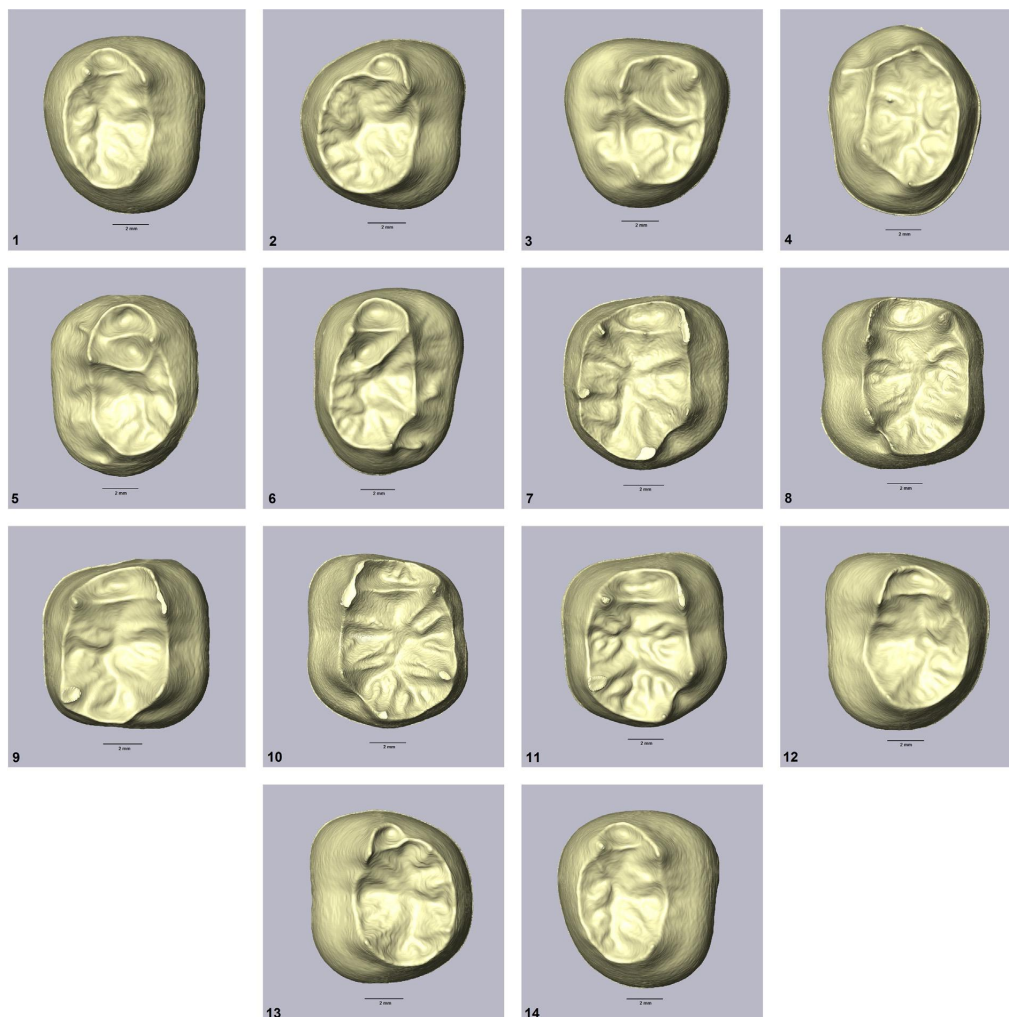
Frequencies and percentages of the continuous mesial (MeTC), middle (MdTC) and distal trigonid crest (DTC) at the EDJ (only one antimer included). We consider the trait is "present" when the crest is continuous. Otherwise we consider that the trait is "absent".

**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 <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>
<b>Mesial trigonid crest at EDJ</b>				
SH	20.9% (9/43)	0.0%	27.2% (3/11)	33.3% (6/18)
<i>H. neanderthalensis</i>	20.5% (7/34)	12.5% (2/16)	25.0% (2/8)	30.0% (3/10)
<i>H. sapiens</i>	7.14% (2/28)	8.3% (1/12)	0.0%	25.0% (1/4)
<b>Middle trigonid crest at EDJ</b>				
SH	72.0% (31/43)	100.0% (14/14)	72.7% (8/11)	50.0% (9/18)
<i>H. neanderthalensis</i>	76.4% (26/34)	87.5% (14/16)	75.0% (6/8)	60.0% (6/10)
<i>H. sapiens</i>	39.2% (11/28)	58.3% (7/12)	25.0% (3/12)	25.0% (1/4)
<b>Distal trigonid crest at EDJ</b>				
SH	23.2% (10/43)	0.0%	0.0%	55.5% (10/18)
<i>H. neanderthalensis</i>	14.7% (5/34)	6.2% (1/16)	12.5% (1/8)	30.0% (3/10)
<i>H. sapiens</i>	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<sup>2</sup> 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 <sub>1</sub>	0.17	0.27	0.17	0.00 <sup>a</sup>	0.38	0.09
M <sub>2</sub>	0.91	0.10	0.91	0.03 <sup>a</sup>	0.22	0.01 <sup>a</sup>
M <sub>3</sub>	0.85	0.74	0.61	0.08	0.07	0.00 <sup>a</sup>
Total	0.97	0.14	0.66	0.00 <sup>a</sup>	0.08	0.00 <sup>a</sup>
NEA						
M <sub>1</sub>		0.72		0.07		0.49
M <sub>2</sub>		0.14		0.05		0.06
M <sub>3</sub>		0.85		0.19		0.12
Total		0.19		0.00 <sup>a</sup>		0.02 <sup>a</sup>

DTC: distal trigonid crest; MdTC: middle and distal trigonid crest; MeTC: mesial trigonid crest; EDJ: enamel-dentine junction.

<sup>a</sup> 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<sub>1</sub> (Table 8), M<sub>2</sub> (Table 9) and M<sub>3</sub> (Table 10) samples using the individual count method. In the M<sub>1</sub>s, 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<sub>2</sub>s (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*

**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.

the maximum value at the OES is represented by **type D** (which in turn is absent in SH and Neanderthal M<sub>2</sub>s) and the lowest by **type A** (which in turn was the most frequent type in SH and *H. neanderthalensis* M<sub>2</sub>s). At the EDJ, the highest frequencies are for **types 11** and **13** for the SH M<sub>2</sub>s; **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<sub>3</sub> samples, there is a greater variability between the trigonid crest types on enamel and dentine than in M<sub>1</sub>s and M<sub>2</sub>s (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<sub>3</sub>s corresponds to **types 5** and **6** in Neanderthals corresponds to **type 2**, and in *H. sapiens* to **type 4**.

**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<sub>3</sub>s 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<sub>3</sub>s from SH sample (11.6%) and four molars from Krapina – one M<sub>1</sub>, one M<sub>2</sub> and two M<sub>3</sub>s – 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<sub>1</sub> 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<sub>1</sub> 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<sub>3</sub>s 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 Martínón-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<sub>2</sub> 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<sub>2</sub> 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<sub>3</sub> 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<sub>3</sub> 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

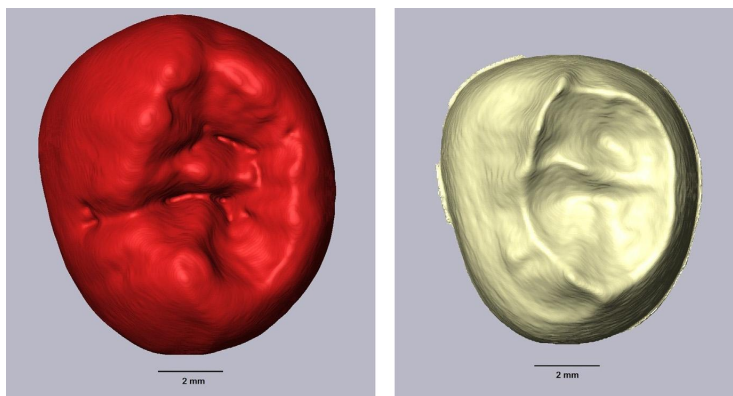
OES: outer enamel surface; EDJ: enamel-dentine junction; SH: Sima de los Huesos.

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

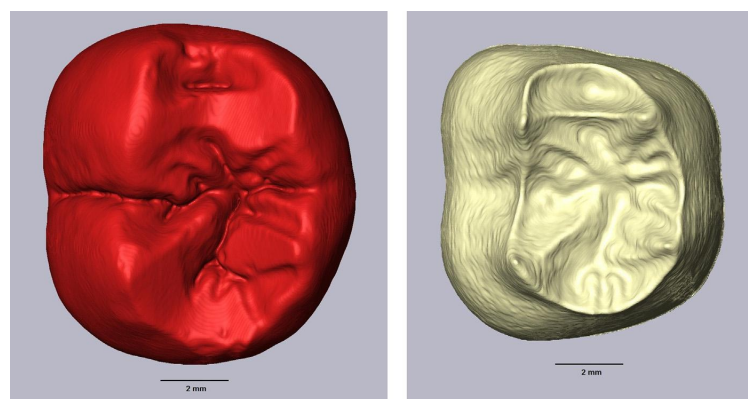
In our study, we have followed some traditional criteria from the ASUDAS (Turner et al., 1991; Wu and Turner, 1993) to score the trigonid crest at the OES (for more details see Terminological Considerations above), but we have also recorded the full variability expressed at the EDJ

to have a more precise knowledge morphological variation in the SH sample. According to Bailey et al. (2002a,b) and Martínón-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., Martínón-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<sub>3</sub> 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<sub>3</sub> (AT-2385). Reconstitution virtuelle de modèles de dentine et d’émail informatisés sur un registre microtomographique.



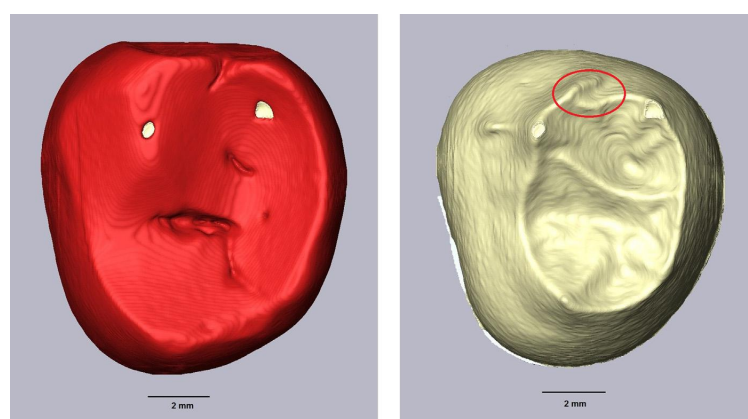
**Fig. 7.** (Color online.) Illustration of a “true” middle trigonid crest at enamel-dentine junction (EDJ) and outer enamel surface (OES) in an *M*<sub>2</sub> molar specimen (AT-946). Virtual reconstruction of dentine and enamel computer models based on micro-computed tomography.

**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*<sub>2</sub> (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; Martínón-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

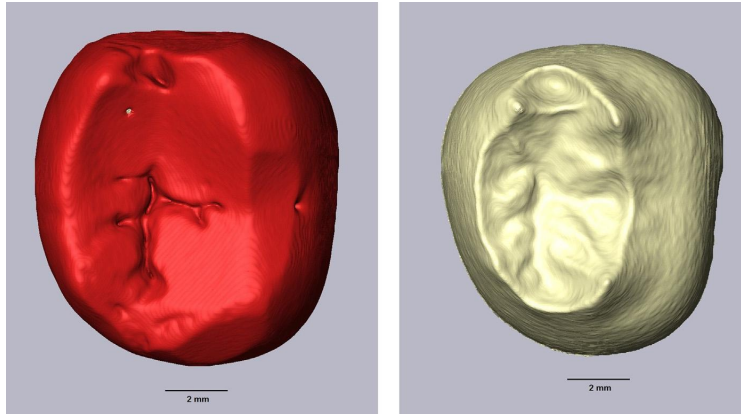
types that are expressed in the SH and *H. neanderthalensis* that are absent in the *H. sapiens* group (i.e., types 3, 5, 6, 9, 13 and 14). If analysis of larger and geographically diverse modern human samples confirms this difference, it may be of particular utility in the taxonomic assignment of isolated 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*<sub>3</sub> (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*<sub>3</sub> (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.



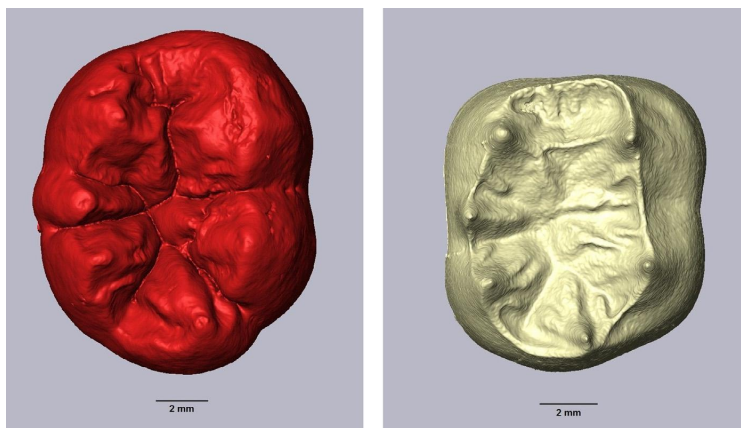
**Fig. 9.** (Color online.) Enamel and dentine surface of a  $M_3$  (AT-811) with lack of correspondence (see text for specific mention). Virtual reconstruction of dentine and enamel computer models on micro-computed tomography.

**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 crest 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.

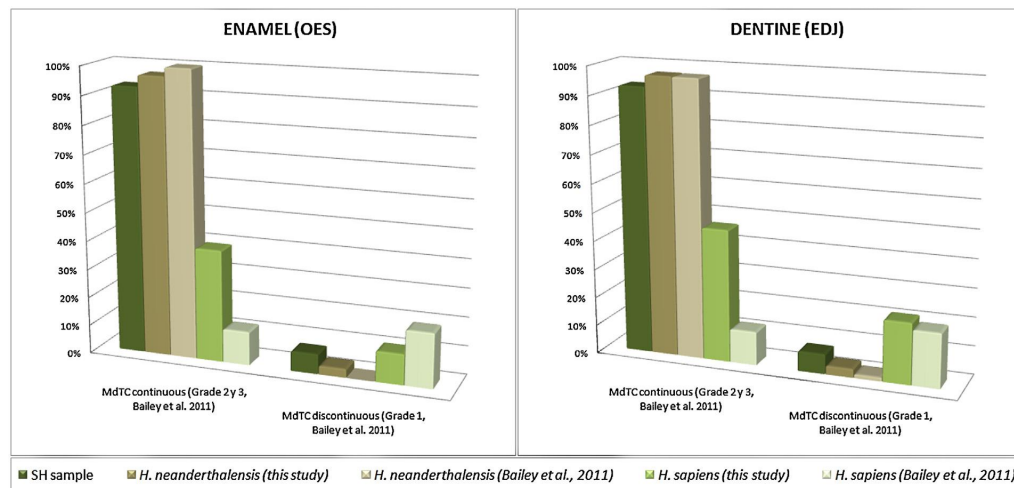
**Fig. 10.** (Couleur en ligne.) Surface de l'émail et de la dentine d'une  $M_1$  (EQ-H5) avec absence de correspondance (voir le texte pour plus de détails). Reconstruction virtuelle de modèles informatiques pour l'émail et la dentine à partir de données microtomographiques.

**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 continus ou discontinus.

	This study				Bailey's data					
	SH sample		<i>H. neanderthalensis</i>		<i>H. sapiens</i>		<i>H. neanderthalensis</i>		<i>H. sapiens</i>	
	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 autapomorphic) 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; Martínón-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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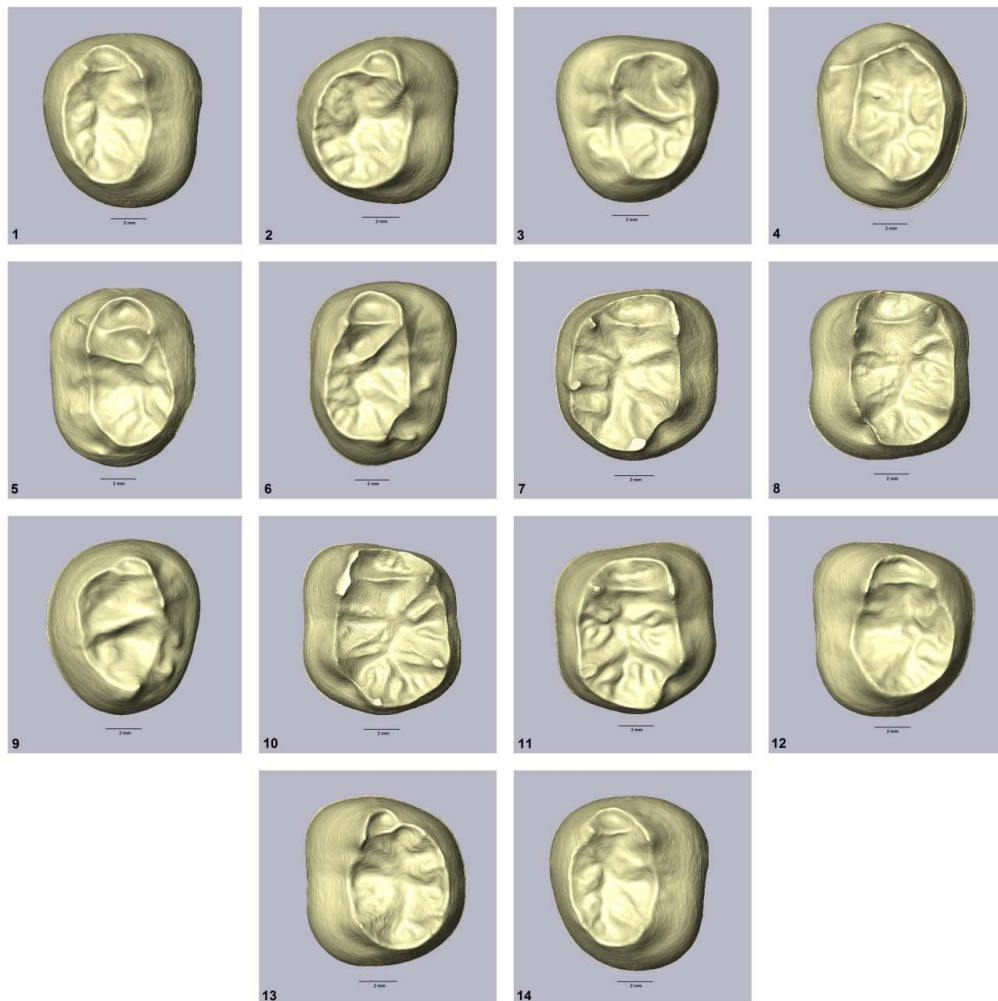
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**FE DE ERRATA / ERRATUM**

Mediante esta fe de errata manifestamos que en la Figura 5, el ejemplo de la dentina para el tipo 9 de los patrones de crestas del trigónido ha de ser modificado, siendo la imagen final la siguiente:

Through this erratum we want to clarify that in Figure 5, the example of type 9 for the trigonid crests patterns at the dentine has to be changed, being the final figure the following:









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## 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*

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### 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.

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### 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 Huevos (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.

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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.

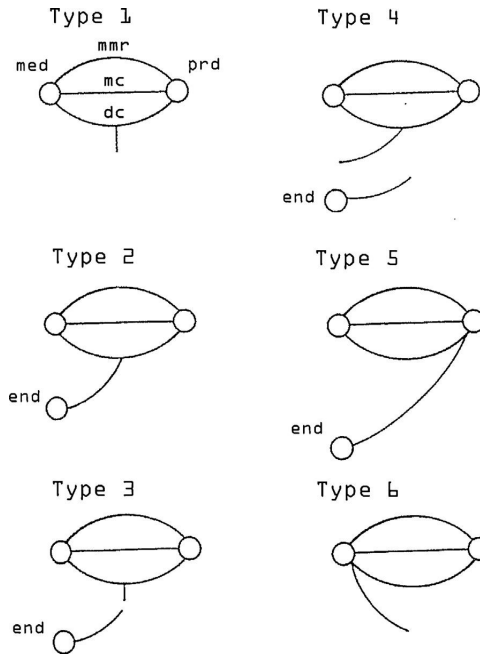


Fig. 1. Korenhof's types of talonid crest (modified from Korenhof, 1982; Fig. 24.8). Type 1. From the middle of the distal trigonid crest a small crest runs for some length in distal direction, but is not connected to any other distinct landmark. Type 2. From the middle of the distal trigonid crest an 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, mnr: 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 ; mnr : 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 intrapopulational 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<sub>2</sub>), because of their resemblance to the morphology of permanent molars. We have only included teeth with dental wear ≤ 5 (Molnar, 1971). Thus, the SH subsample consists of 63 out of 123 permanent molars and 1 out of 4 dm<sub>2</sub>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 μA and 512 × 512 to 4096 × 4096 image matrix. The resulting isometric voxel

size ranged from 18 μm<sup>3</sup> to 74 μm<sup>3</sup>. 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 antimerere	Total sample	Only one antimerere	Total sample	Only one antimerere
<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 antimerere [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 antimerere 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 antimerere (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 antimerere 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	P: 0.12	P: 0.76	–	P:0.89	P: 0.54	P:0.57	P: 0.28	P:0.55
SH vs. SAP	–	<b>P: 0.02</b> *	–	P:0.89	<b>P: 0.00</b> *	P: 0.92	<b>P: &lt;0.001</b> *	P: 0.55
NEA vs. SAP	P: 0.21	<b>P: 0.01</b> *	–	P:0.06	<b>P: 0.01</b> *	0.77	<b>P: &lt;0.001</b> *	<b>P:0.02</b>

\* 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	–	–	–	–
Total	22	19	22	63	19	10	11	40	14	14	4	32

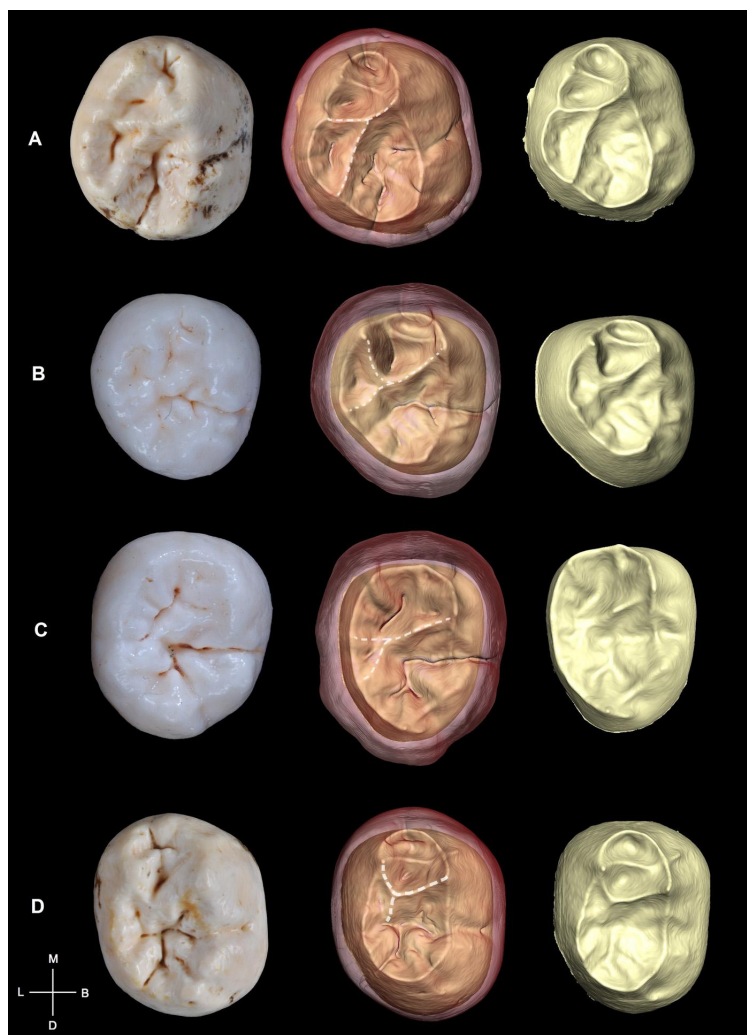
Of the four cases we scored a talonid crest in SH, two belong to the same individual (Individual XVIII) but the left molar expresses type 1 (AT-2271) whereas the right molar (AT-2277) expresses type 2. We think that AT-2271 (Fig. 2D) could be a case of a “truncated” type 2, where the strong reduction 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 antimere, and in AT-1959 (Fig. 2B) the talonid crest is absent in its antimere (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 Javanese 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



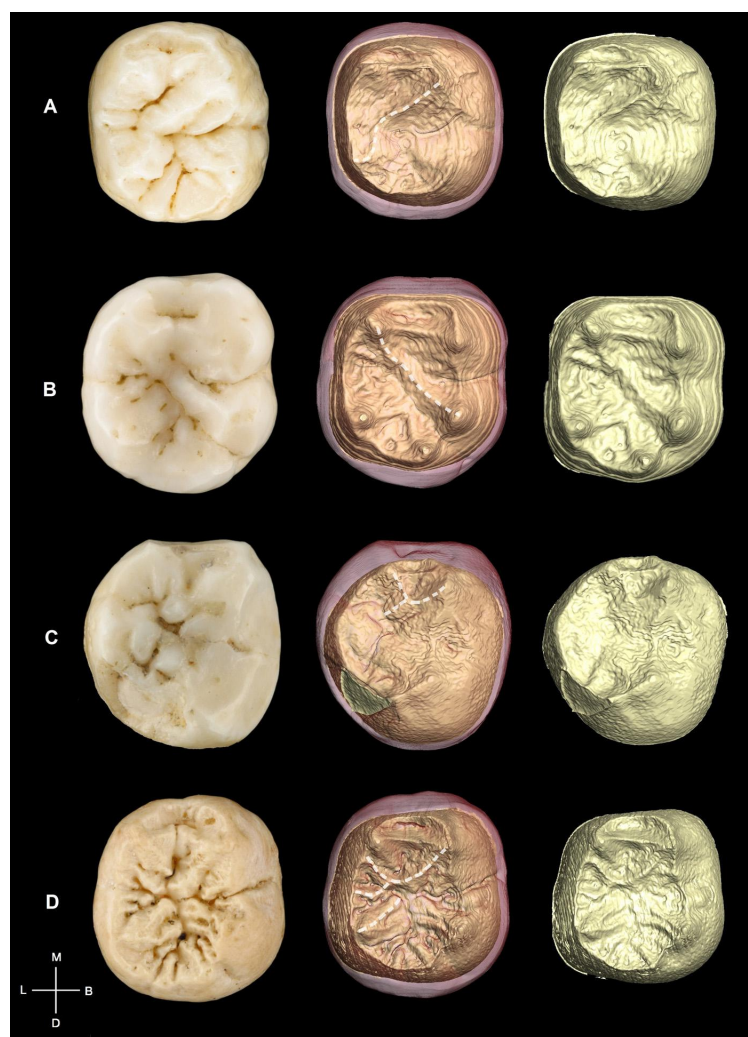
**Fig. 2.** (Color online) Talonid crest types of the SH permanent lower molar sample. (A) AT-2277 (right M<sub>3</sub>, type 2); (B) AT-1959 (right M<sub>3</sub>, type 2); (C) AT-2273 (left M<sub>3</sub>, type 2); (D) AT-2271 (left M<sub>3</sub>, type 1). C and D have been mirrored. Teeth not to scale.

**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*



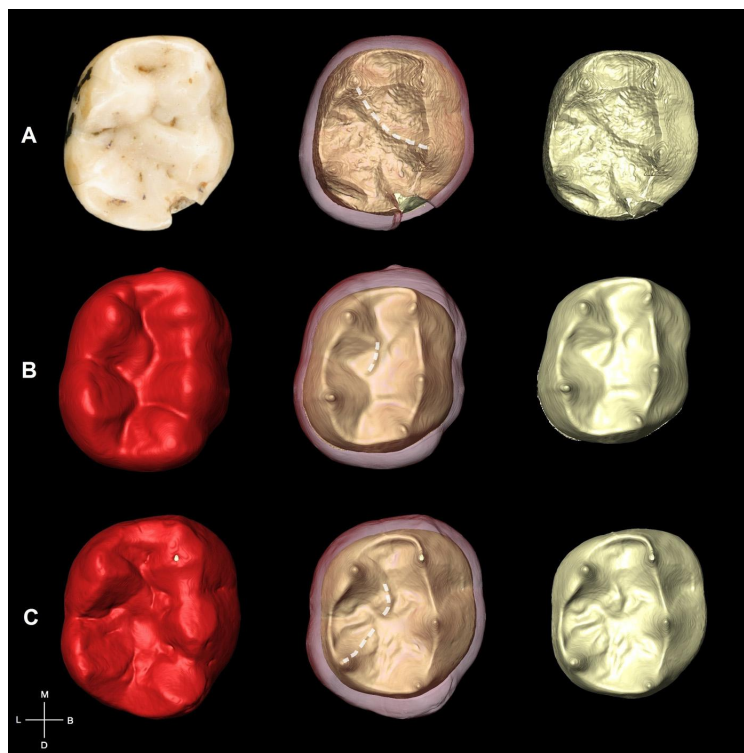
**Fig. 3.** (Color online) Examples of talonid crest types of the Neanderthal permanent lower molar sample. (A) D106 from Krapina (left M<sub>3</sub>, type 5); (B) D81 from Krapina (left M<sub>1</sub>, type 6); (C) D5 (left M<sub>3</sub>, type 1) and D7 (right M<sub>3</sub>, type 4). A, B and C specimens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

**Fig. 3.** (Couleur en ligne) Exemples de types de crête du talonide d'un échantillonage 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<sub>2</sub> 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<sub>2</sub>. (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<sub>2</sub>, 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<sub>2</sub> from SH.

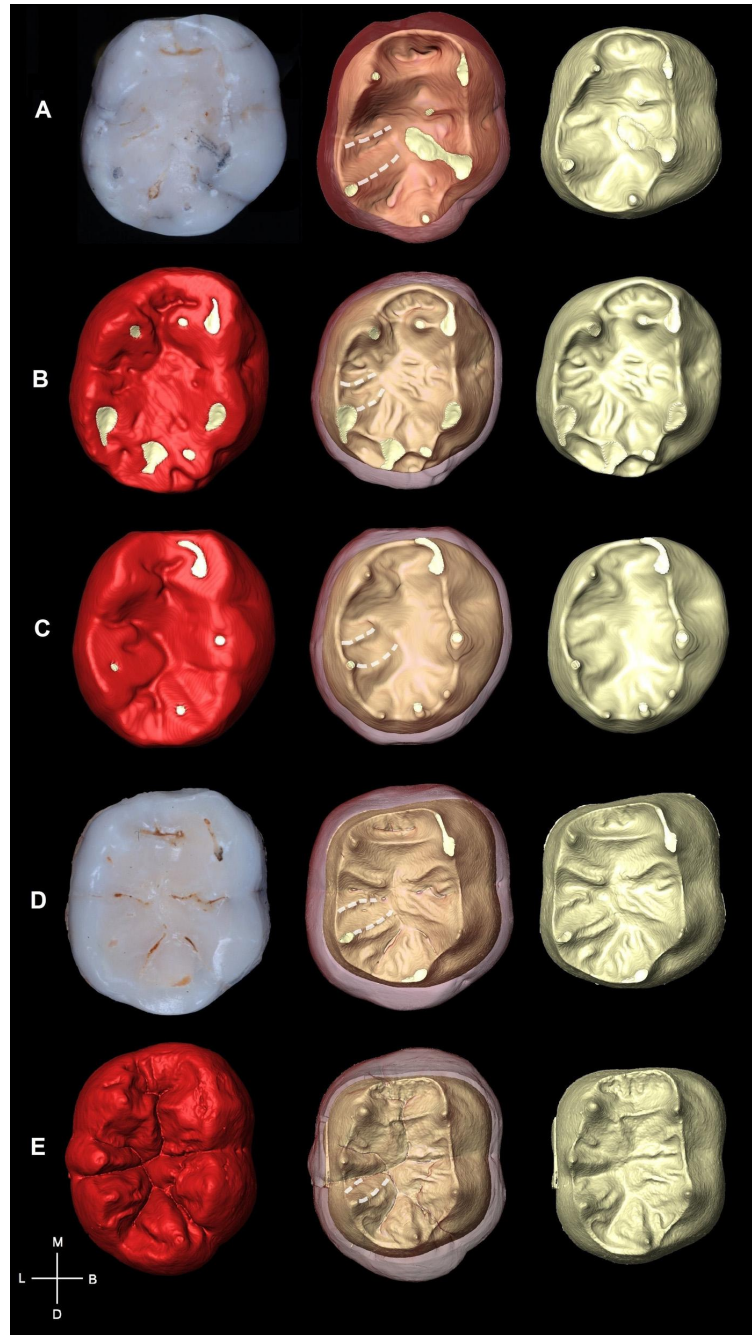
**4. Discussion**

In 1982, Korenhof published a “new landmark” on modern human dentitions, based on his study of the dm<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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; Zanolli, 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* (Martínón-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; Martínón-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; Martínón-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  $M_3s$  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 (Martínón-Torres et al., 2012) where the frequencies of distal trigonid crests in  $M_3s$  were particularly high (Martínón-Torres et al., 2012; Martínez de Pinillos et al., 2014). Our study reveals that most talonid crests in permanent molars are displayed by  $M_3s$ , 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; Martínón-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.

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## Characterization of the enamel-dentine junction of the hominin permanent lower molars from Arago (Tautavel, France).

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### Regarding to

The human fossils found in the Caune de l'Arago in Tautavel (southern France) are an important source of information to investigate human evolution in Europe during the Middle Pleistocene (de Lumley M.-A., 2015). To date, this site has yielded 148 human remains that according to the latest dates obtained for the Arago hominin-bearing layers (Falguères et al., 2015), are roughly contemporaneous with the hominin from Sima de los Huesos site (Arnold et al., 2014). Here we present for the first time the trigonid crest pattern exhibited at the outer enamel surface (OES) and enamel dentine junction (EDJ) of the Middle Pleistocene hominins from Arago by means of microcomputed tomography (microCT). Moreover, since this pattern is potentially useful for taxonomic and phylogenetic assignments (Bailey, 2002a, 2002b; Martínez de Pinillos et al., 2014; Martín-Torres et al., 2014), we also present a comparative study of this morphological trait among *H. antecessor*, the hominins from Sima de los Huesos site and several *H. neanderthalensis* and *H. sapiens* specimens. After analysing the trigonid crest expressions of the Early and the Middle Pleistocene populations of Europe, our results reveals that the Arago dental sample exhibit Neanderthal patterns but with a more primitive state concerning to the Sima de los Huesos hominins (Arsuaga et al., 2014; Bermúdez de Castro et al., 2003; de Lumley M.-A., 2015).

**Keywords:** Caune de l'Arago; trigonid crest patterns; Sima de los Huesos; *Homo antecessor*; *Homo neanderthalensis*; *Homo sapiens*.

## Introduction

Teeth are usually the most abundant and well preserved remains of the whole fossil record. In addition, dental morphological features have a high genetic component of expression, so teeth become a valuable source of traits with utility for taxonomic and phylogenetic studies (Hrdlička, 1923; Kaifu et al., 2005; Martínón-Torres et al., 2012, 2007; Turner, 1991). Among these traits, trigonid crest patterns bear a significant taxonomic signal, particularly for the identification of the Neanderthal lineage (Bailey, 2002a, 2002b; Bailey et al., 2011; Irish, 1998; Martínez de Pinillos et al., 2014; Martínón-Torres et al., 2014; Scott and Turner II, 1997). In this study we present for the first time, the characterization of the trigonid crest pattern at the dentine and enamel surfaces of the permanent lower molars of the hominins from la Caune de l'Arago in Tautavel (France).

Since 1964 to date, the Arago site has provided more than 140 human fossils associated with fauna remains and several Mode 2 lithic industries (de Lumley and Barsky, 2004). The whole assemblage was recovered from a 10 m. thick stratigraphical sequence (de Lumley et al., 2014). Recently, new chronological studies of la Caune de l'Arago have allowed a better understanding of the stratigraphical deposits (Falguères et al., 2015). All the human fossils come from 15 archaeostratigraphic units ranging from 550ka (unit Q at the base) to 400 ka (unit C at the top); the majority of the human remains come from, units F and G (de Lumley M.-A., 2015). The samples included in this study belong to Middle (unit F and G) and Upper (unit C) Stratigraphical Complex with an age of 450 to 350 ka (de Lumley M.-A., 2015), meaning the contemporaneity with the hominins from Sima de los Huesos (SH) dated to  $427\pm 12$  ka (Arnold et al., 2014). Therefore, Arago is together with the Atapuerca-Sima de los Huesos locality, one of the largest and best documented samples to investigate human evolution in Europe during the Middle Pleistocene.

The hominin fossils from la Caune de l'Arago have been classically attributed to *H. heidelbergensis* (Gómez-Robles et al., 2008; Martínón-Torres et al., 2012) understood as a chronospecies of the Neanderthal lineage (e.g., Arsuaga et al., 1997) or as the last common ancestor of both Neanderthals and modern humans (Stringer, 2012). Recently, de Lumley M.-A.,

(2015) related the Arago specimens with *H. erectus* from Africa and Asia, and proposed its assignment to *H. erectus tautavelensis*. Previous studies of the Arago remains identified primitive features but also some apomorphies relating them to Neanderthals (Arsuaga et al., 2014; Bermúdez de Castro et al., 2003; Gómez-Robles et al., 2015, 2008, 2007). Interestingly, the majority of researchers agree that Arago sample seems to be less derived than other contemporaneous population like SH. In particular, Bermúdez de Castro et al. (2003) defined the Arago teeth as “intermediate” between the Early Pleistocene population from Gran Dolina-TD6 (*H. antecessor*) and the Middle Pleistocene population from the SH site, suggesting a scenario of discontinuity between the Early and the Middle Pleistocene lineages in Europe. The Middle Pleistocene populations from Europe would not be the result of an in-situ evolution of the Early Pleistocene hominins but would represent the dispersal into Europe of a new group. In this context, Arago could be the result of a hybridization between the European residents with the new immigrants. Later studies on dentition ratified that Arago hominins were in general less derived than the Sima de los Huesos collection (Gómez-Robles et al., 2015, 2008, 2007; Martínón-Torres et al., 2012). Thus, a further comparison of the Arago hominins to the Early and Middle Pleistocene populations is crucial to understand its relationship and/or contribution to the origin of the Neanderthal species.

With this aim, we propose to analyse the trigonid crest pattern in the Arago lower molar sample and compare it to a wide hominin sample that include the Early and Middle Pleistocene hominins found in Atapuerca, as well as large sample of *H. neanderthalensis* and *H. sapiens*. In particular, the trigonid crest pattern is useful to characterise the Neanderthal species (Bailey, 2002a; Irish, 1998; Martínez de Pinillos et al., 2014; Martínón-Torres et al., 2014; Scott and Turner II, 1997), so it will be especially useful to assess the degree of neanderthalization of the Arago teeth with regard to SH. This study will contribute with new data to the understanding of the evolutionary scenario of Europe from the Early to the Middle Pleistocene transition.

## **Material**

To date, the complete Arago fossil sample comprises 148 human remains consisting of different post-cranial fragments, 5 mandibles and 123 teeth. The complete molar sample consists of six

specimens, four right and two left. The type of fossilization of the A-69 (right M<sub>2</sub>) prevents the proper segmentation of the dental tissues and thus, we will analyse five out of the six lower molars from the Middle Pleistocene stratigraphic levels (see Table 1).

Table 1. List of the Arago lower permanent molars included in the study with the inventory number, the stratigraphic level and the chronology (the OIS and chronology has been taken from de Lumley M.-A., (2015) and Falguères et al., (2015)).

Inventory number	Specimen	Side	Stratigraphic Units	OIS / Chronology
A-40	M <sub>1</sub>	Right	Unit C	OIS 10 / 350-400 ka
A-68	M <sub>2</sub>	Right	Unit C	OIS 10 / 350-400 ka
A-10	M <sub>2</sub>	Right	Unit F	OIS 12 / 392 ± 43 ka
A-32	M <sub>2</sub>	Left	Unit F	OIS 12 / 392 ± 43 ka
A-106	M <sub>3</sub>	Left	Unit G	OIS 12 / 438 ± 31 ka

The comparative sample (Table 2) comprises molars from the Early Pleistocene hominins from Gran Dolina-TD6 (*Homo antecessor*), the Middle Pleistocene population of SH, and a number of specimens of *Homo neanderthalensis* and *Homo sapiens*. The comparative sample belonging to *H. antecessor*, SH, *H. sapiens* from El Mirador site (Calcolithic and Bronze Ages) and the contemporary *H. sapiens* sample was scanned at the National Research Centre on Human Evolution (CENIEH) (Burgos, Spain) and at the Multidisciplinary Laboratory of the ‘Abdus Salam’ International Centre for Theoretical Physics (ICTP) (Trieste, Italy). The microCT of Neanderthals and *H. sapiens* specimens were obtained from NESPOS<sup>®</sup> and ESRF<sup>®</sup> databases.

Table 2. Study sample of lower permanent molars. We write in brackets the number of the sample size including only one antimer per individual.

SITES	SPECIES	N TOTAL	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>
Arago <sup>1</sup>	-	5	1	3(2)	1
Sima de los Huesos <sup>1</sup>	-	63 (43)	22 (14)	19 (11)	22 (15)
TD6 <sup>1</sup>	<i>Homo antecessor</i>	8	3	3	2
Engis <sup>3</sup>	<i>Homo neanderthalensis</i>	1	1	-	-
Gibraltar <sup>3</sup>		3 (2)	2 (1)	1	-
Ehringsdorf <sup>4</sup>		1	1	-	-
Abri Bourgeois-Delaunay <sup>4</sup>		1	1	-	-
Regourdou <sup>4</sup>		6 (3)	2 (1)	2 (1)	2 (1)
Abri Suard <sup>4</sup>		4	3	-	1
Krapina <sup>4</sup>		21	7	7	7
Hunas <sup>4</sup>		1	-	-	1
Roc de Marsal <sup>4</sup>		2 (1)	2 (1)	-	-
Equus Cave <sup>3</sup>	<i>Homo sapiens</i>	2	2	-	-
Qafzeh <sup>3</sup>		8 (4)	4 (2)	4 (2)	-
Lagar Velho <sup>4</sup>		1	1	-	-
El Mirador <sup>1</sup>		20 (17)	8 (6)	7 (6)	5
Contemporary sample <sup>1-2</sup>		55 (52)	16 (15)	26 (24)	13

<sup>1</sup> CENIEH microCT data base / <sup>2</sup> ICTP microCT data base / <sup>3</sup> ESRF<sup>®</sup> data base / <sup>4</sup> NESPOS<sup>®</sup> data base



## Methodology and scoring procedures

In this study we have used virtual three-dimensional reconstructions to compare the enamel and dentine surfaces of all the specimens analysed. We have excluded all teeth partially broken or those with a wear degree higher than 5 in Molnar's standards (Molnar, 1971). The teeth were scanned at high (18 $\mu$ m) and medium (36 $\mu$ m) resolution with the Scanco Medical Micro-CT80 system and the GE Phoenix v/tome/x housed at the CENIEH in Burgos (Spain) and with the microCT X-ray ICTP-ELETTRA located at the Multidisciplinary Laboratory of the ICTP of Trieste (Italy). Scans were performed at energies that ranged from 70 to 120kV depending on the sample and with an intensity of scanning of 110-140 $\mu$ A. Most of the teeth were located in a maximum scan length of 140mm from the source point, with a maximum scan size diameter of 75.8mm, and with image matrix from 512 x 512 to 1024 x 1024 pixels.

The scanned images were imported into the Amira 5.4 or Amira 6.0 software (Visage Imaging, Inc.) and after the volume rendering we oriented the tooth in anatomical position. Later, the cervical plane was done following (Olejniczak et al., 2008a, 2008b, 2008c) and both enamel and dentine tissues were segmented using the histogram value. Finally, the volume was done semi-automatically with manual corrections and no filters.

For the comparison of the trigonid crests expression at the outer enamel surfaces (OES) we used the Korenhof's scoring system (Korenhof, 1982). We scored the trait as present if the crest was continuous and, absent if it was absent or discontinuous. Based on this system, we defined four types of trigonid crests patterns at the OES. **Type A**: continuous MdTC and 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. For the characterization of the EDJ we used the scoring system described in Martínez de Pinillos et al., (2014) which differentiates 14 types of trigonid crests patterns depending on the combination of mesial/middle and distal trigonid crests expressions (see Fig. 1 and Table 3).

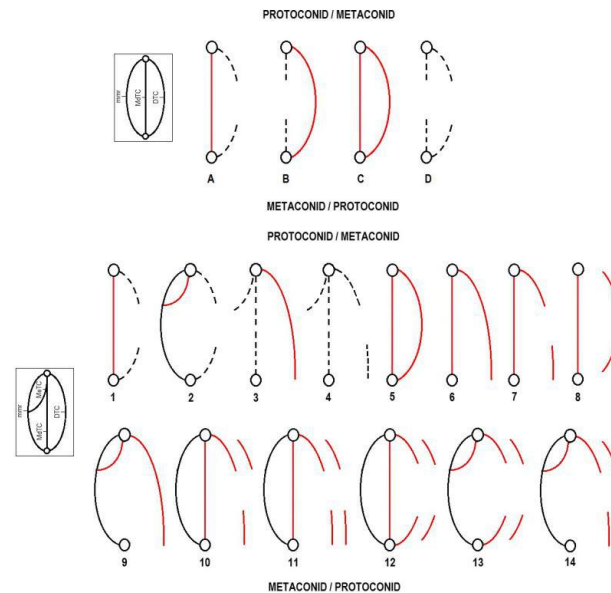


Fig. 1. Top: representation of the four basic types of trigonid crests on enamel surface identified in our study (based on Korenhof, 1982). View is towards the occlusal surface at the OES including the tips of the cusps (open circles) of the protoconid and metaconid (mmr: mesial marginal ridge). Explanation in the text. Bottom: illustration of all types of trigonid crests on dentine surface identified in our study following Martínez de Pinillos et al., (2014). Explanation in Table 3. View is towards the occlusal surface of the EDJ including the tips of the dentine horn (open 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.

Table 3. Description of the different trigonid crest types at the dentine surface used to classify the overall sample.

<b>Type 1</b>	Continuous MdTC with an absent or discontinuous DTC.
<b>Type 2</b>	Continuous MeTC with an absent or discontinuous DTC.
<b>Type 3</b>	Continuous DTC when at least one of the origins is the distal segment, with an absent or discontinuous MeTC or MdTC.
<b>Type 4</b>	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.
<b>Type 5</b>	Continuous MdTC and a continuous DTC arising from the middle segments.
<b>Type 6</b>	Continuous MdTC and a continuous DTC when at least one of the origins is the distal segment.
<b>Type 7</b>	Continuous MdTC and a discontinuous DTC when at least one of the origins is the distal segment.
<b>Type 8</b>	Continuous MdTC and a discontinuous DTC arising from the distal segments.
<b>Type 9</b>	Continuous MeTC and continuous DTC when at least one of the origins is the distal segment.
<b>Type 10</b>	Continuous MdTC, a discontinuous DTC when at least one of the origins is the distal segment, and a pronounced distal ridge on one side.
<b>Type 11</b>	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.
<b>Type 12</b>	Continuous MdTC, a discontinuous DTC arising from the middle segments and discontinuous DTC arising from the distal segments.
<b>Type 13</b>	Continuous MeTC, a discontinuous DTC arising from the middle segments and discontinuous DTC arising from the distal segments.
<b>Type 14</b>	Continuous MeTC, a discontinuous DTC when at least one of the origins is the distal segment, and a pronounced distal ridge on one side.

Although all teeth were analyzed, for the statistical comparison we have used the unilateral count method to avoid redundancy of the underlying genetic information (Turner, 1987). In case of asymmetry the tooth with the highest degree of expression for this pattern was selected, since it is potentially expressing the full genetic signal. Both sexes were pooled together as sexual dimorphism has little effect on dental morphology (Turner, 1991).

**Results**

*Outer enamel surface (OES)*

The continuous MdTC at the OES is represented by type A and C (see Figure 1). Four out of five (one M<sub>1</sub> and three M<sub>2</sub>s) Arago molars exhibit a continuous MdTC, being the M<sub>3</sub> the only one that does not exhibit this pattern (see Table 4 and Figure 2). If we use the unilateral count method (see Table 5 and Figure 3), similar high frequencies of continuous MdTC were obtained for SH and Neanderthal samples and in contrast to lower percentages in TD6 and *H. sapiens*.

Table 4. Trigonid crest types at the OES and EDJ of the overall Arago sample.

Inventory number	Teeth	OES	EDJ
A-40	M <sub>1</sub>	A	10
A-68	M <sub>2</sub>	A	12
A-10	M <sub>2</sub>	A	12
A-32	M <sub>2</sub>	A	12
A-106	M <sub>3</sub>	D	4

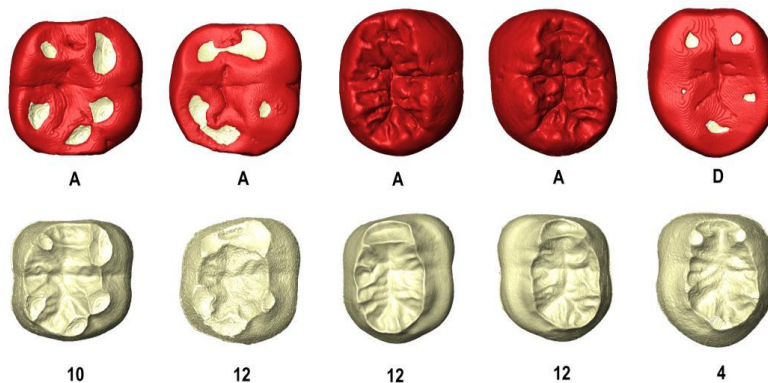


Fig. 2. Virtual reconstruction of the enamel (upper) and dentine (lower) surfaces for the Arago molars with their correspondent trigonid crest type. From left to right: Arago 40 (LRM<sub>1</sub>), Arago 68 (LRM<sub>2</sub>), Arago 10 (LRM<sub>2</sub>), Arago 32 (LLM<sub>2</sub>), and Arago 106 (LLM<sub>3</sub>).



Table 5. Frequency of expression of trigonid crests and their percentages on both enamel (OES) and dentine (EDJ) for the M<sub>1</sub>, M<sub>2</sub> and M<sub>3</sub> permanent molars analyzed of Arago, *H. antecessor* (TD6), Sima de los Huesos (SH), *H. neanderthalensis* (NEA) and *H. sapiens* (SAP). Only one antimer is included.

OES TYPES	M <sub>1</sub>					M <sub>2</sub>					M <sub>3</sub>				
	ARAGO	TD6	SH	NEA	SAP	ARAGO	TD6	SH	NEA	SAP	ARAGO	TD6	SH	NEA	SAP
A	1 (100%)	1 (33.33%)	14 (100%)	15 (93.75%)	8 (30.76%)	2 (100%)	2 (66.66%)	11 (100%)	7 (77.77%)	7 (21.87%)	-	1 (50%)	4 (26.66%)	4 (40%)	7 (38.88%)
B	-	-	-	-	1 (3.84%)	-	-	-	1 (11.11%)	-	-	-	1 (6.66%)	-	1 (5.55%)
C	-	-	-	1 (6.25%)	-	-	-	-	1 (11.11%)	-	-	-	9 (60%)	5 (50%)	-
D	-	2 (66.66%)	-	-	17 (65.38%)	-	1 (33.33%)	-	-	25 (78.12%)	1 (100%)	1 (50%)	1 (6.66%)	1 (10%)	10 (55.55%)
<b>Total</b>	<b>1</b>	<b>3</b>	<b>14</b>	<b>16</b>	<b>26</b>	<b>2</b>	<b>3</b>	<b>11</b>	<b>9</b>	<b>32</b>	<b>1</b>	<b>2</b>	<b>15</b>	<b>10</b>	<b>18</b>
<b>EDJ TYPES</b>	<b>n / %</b>	<b>n / %</b>	<b>n / %</b>	<b>n / %</b>	<b>n / %</b>	<b>n / %</b>	<b>n / %</b>	<b>n / %</b>	<b>n / %</b>	<b>n / %</b>	<b>n / %</b>	<b>n / %</b>	<b>n / %</b>	<b>n / %</b>	<b>n / %</b>
1	-	-	-	-	2 (7.69%)	-	-	2 (18.18%)	-	3 (9.37%)	-	-	-	-	3 (16.66%)
2	-	-	-	-	2 (7.69%)	-	-	-	-	2 (6.25%)	-	-	1 (6.66%)	3 (30%)	3 (16.66%)
3	-	-	-	-	1 (3.84%)	-	-	-	1 (11.11%)	1 (3.12%)	-	-	1 (6.66%)	-	1 (5.55%)
4	-	2 (66.66%)	-	-	16 (61.53%)	-	3 (100%)	-	-	23 (71.87%)	1 (100%)	1 (50%)	1 (6.66%)	1 (10%)	10 (55.55%)
5	-	-	-	-	-	-	-	-	-	-	-	-	3 (20%)	1 (10%)	-
6	-	-	-	1 (6.25%)	-	-	-	-	1 (11.11%)	-	-	-	3 (20%)	2 (20%)	-
7	-	-	2 (14.28%)	1 (6.25%)	1 (3.84%)	-	-	-	1 (11.11%)	-	-	-	-	1 (10%)	-
8	-	-	4 (28.57%)	1 (6.25%)	2 (7.69%)	-	-	-	-	2 (6.25%)	-	-	2 (13.33%)	-	-
9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10	1 (100%)	1 (33.33%)	4 (28.57%)	5 (31.25%)	-	-	-	1 (9.09%)	2 (22.22%)	1 (3.12%)	-	1 (50%)	-	1 (10%)	-
11	-	-	3 (21.42%)	2 (12.50%)	1 (3.84%)	2 (100%)	-	3 (27.27%)	-	-	-	-	-	-	-
12	-	-	1 (7.14%)	3 (18.75%)	1 (3.84%)	-	-	2 (18.18%)	2 (22.22%)	-	-	-	-	1 (10%)	-
13	-	-	-	1 (6.25%)	-	-	-	3 (27.27%)	-	-	-	-	-	-	-
14	-	-	-	2 (12.50%)	-	-	-	-	2 (22.22%)	-	-	-	2 (13.33%)	-	-
<b>Total</b>	<b>1</b>	<b>3</b>	<b>14</b>	<b>16</b>	<b>26</b>	<b>2</b>	<b>3</b>	<b>11</b>	<b>9</b>	<b>32</b>	<b>1</b>	<b>2</b>	<b>15</b>	<b>10</b>	<b>18</b>

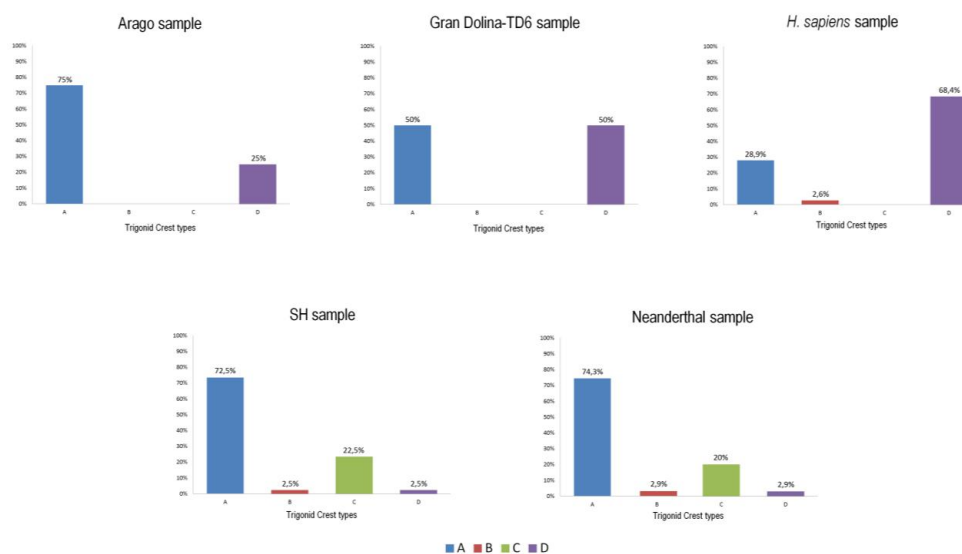


Fig. 3. Bar charts showing the percentages for the different trigonid crest types at the outer enamel surfaces (OES) of each hominin group analyzed.

The continuous DTC at the OES is represented by type B and C (see Figure 1). A continuous DTC was not recorded in any of the Arago molars (see Table 4 and Figure 2). Regarding the percentages (see Table 5 and Figure 3), none of the TD6 and only a 2,6% of the *H. sapiens* samples exhibit this pattern. However, higher frequencies of continuous DTC was present in the Neanderthal sample (increasing its frequency from M<sub>1</sub>s to M<sub>3</sub>) and in the SH sample (exclusively in the M<sub>3</sub>s). Type C is exclusive of the SH and Neanderthal groups.

#### Enamel dentine junction (EDJ)

Depending on the sample, we recorded different types of trigonid crest at the EDJ (Tables 3, 5 and Figure 4). As happened at the OES, at the EDJ four out of the five (one M<sub>1</sub> and three M<sub>2</sub>s) Arago molars present continuous MdTC. Of these, the M<sub>1</sub> presents type 10 and the M<sub>2</sub>s present type 12. The M<sub>3</sub> displays a type 4 (discontinuous MdTC and DTC) (Table 4 and Figure 2). If we take into account just one antimere (Table 5 and Figure 4), type 4 is the most common in *H. antecessor* (two M<sub>1</sub>s, three M<sub>2</sub>s and one M<sub>3</sub>) and *H. sapiens* (seventeen M<sub>1</sub>s, twenty three M<sub>2</sub>s and ten M<sub>3</sub>s). In SH sample type 11 is the commonest, displayed by six molars (three M<sub>1</sub>s and three M<sub>2</sub>s). Type 10 is the commonest in Neanderthals, recorded in eight molars (five M<sub>1</sub>s, two M<sub>2</sub>s and one M<sub>3</sub>).

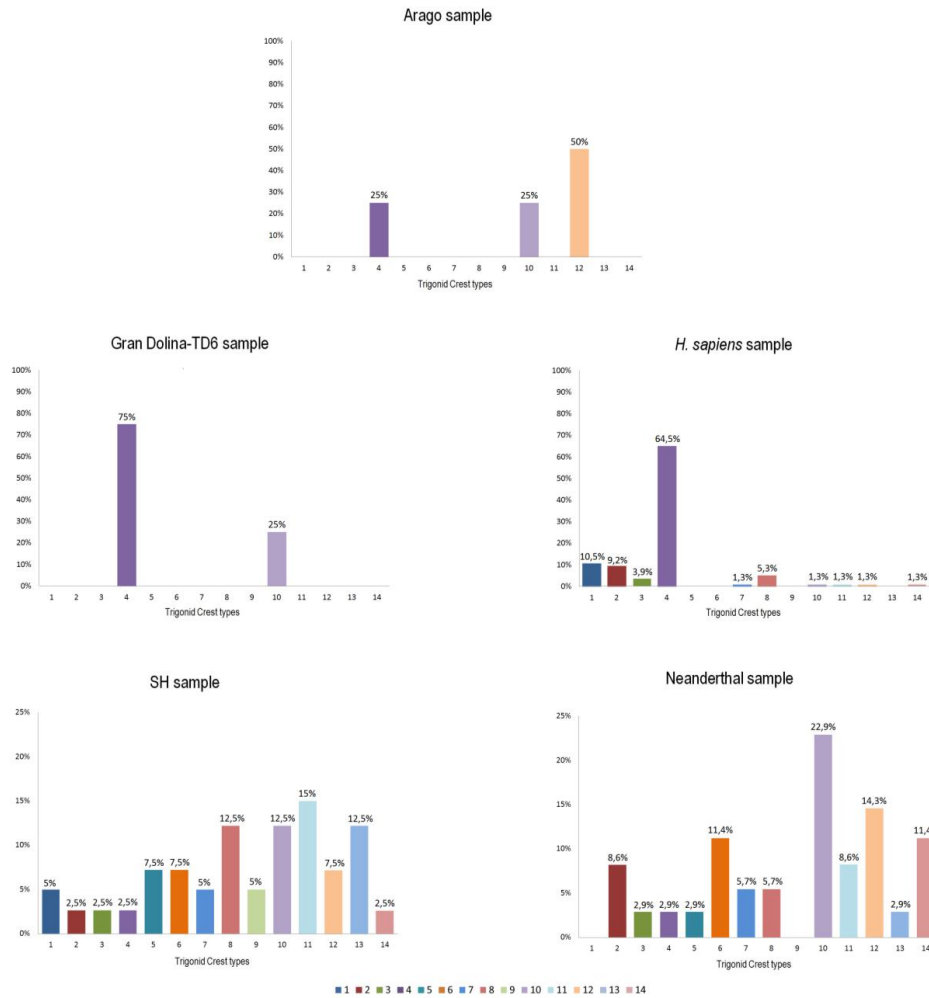


Fig. 4. Bar charts showing the percentages for the different trigonid crest types at the enamel dentine junction (EDJ) of each hominin group analyzed. Note that the scale of the Y-axis between the SH and Neanderthal graphs and the rest is different in order to make it visually more clear.

The continuous MeTC at the EDJ is represented by type 2, 9, 13 and 14 (see Figure 1). A continuous MeTC is absent in the Arago sample (see Table 4 and Figure 2). In table 5 and Figure 4, we can observe that TD6 sample does not exhibit a continuous MeTC and *H. sapiens* presents this pattern (type 2 and 14) in eight molars, two M<sub>1S</sub>, two M<sub>2S</sub> and four M<sub>3S</sub>. In SH the continuous MeTC is present in three M<sub>2S</sub> (type 13) and six M<sub>3S</sub> (type 2, 9, 13 and 14). The Neanderthal sample shows this pattern in all molars (three M<sub>1S</sub> with type 13 and 14, two M<sub>2S</sub> with type 14 and three M<sub>3S</sub> with type 2) increasing the percentages from M<sub>1S</sub> (18.75%) to M<sub>2S</sub> (22.2%) to M<sub>3S</sub> (30%).

Correspondence of trigonid crest expression between the OES and EDJ

Despite the great variability of the trigonid crests types expressed at the dentine, there is a good correspondence between the OES and the EDJ in that continuous crests at the OES tend to correspond to EDJ types that include continuous crest. Of all samples, Arago is the only one that exhibits a total correlation between the enamel and dentine surfaces. In *H. antecessor* two M<sub>2S</sub> (ATD6-5 and ATD6-113) that present type A at the OES show a type 4 at the EDJ. SH sample contains mismatches in two M<sub>3S</sub> (AT-100 and AT-811), with a type C at the enamel and a type 3 and 14 at the dentine, respectively. The exceptions in the Neanderthal sample are three M<sub>3S</sub> (Regourdou 1, Krapina D4 and Krapina D106) that exhibit type C at the OES and type 2 at the EDJ. Finally, *H. sapiens* is the group who exhibits most discrepancies among all the samples (three M<sub>1S</sub>, three M<sub>2S</sub> and one M<sub>3</sub>). For the M<sub>1S</sub>, one specimen from the contemporary *H. sapiens* sample displays a type A at the OES and a type 4 at the EDJ, and EQ-H5 and MIR4 P22 205 exhibit a type D at the OES and a type 11 and 2 at the EDJ, respectively. For the M<sub>2S</sub>, Qafzeh 10 shows a type A at the enamel and a type 4 at the dentine, and two specimens from the contemporary *H. sapiens* sample present a type D at the OES and type 1 and 3 at the EDJ. The M<sub>3</sub> (MIR202-T34) shows a type A at the enamel and a type 4 at the dentine.

**Discussion and concluding remarks**

Given the taxonomic and phylogenetic information contained in the trigonid crests (Bailey, 2002a, 2002b; Irish, 1998; Scott and Turner II, 1997; Zubov, 1992a, 1992b), in this study we have analyzed this expression in the European Pleistocene populations in order to explore their phylogenetic affinities. Four out of the five Arago molars express the typical Neanderthal feature, i.e., a continuous middle trigonid crest. This pattern is the most frequent in our SH and *H. neanderthalensis* samples. The Arago sample differs from the SH and Neanderthal groups in that the variability of expression is lower. The type B at the OES - which corresponds with type 3 at the EDJ- and type C -which is a type 5, 6 and 9 at the EDJ- are absent. This absence would support a previous statement about the possibility that some trigonid crest types at the EDJ (type 9) may be exclusive of the SH population (Martínez de Pinillos et al., 2014) and evince the highly derived state of SH population (Arsuaga et al., 2014; Gómez-Robles et al., 2008, 2007; Gómez-Robles and Polly, 2012; Martínón-Torres et al., 2012). However, we should be cautious since the lower variability of the Arago group



may be an artefact of the small sample size and not representative of the real variability of the original population. Interestingly, the continuous MdTC is absent in the M<sub>3</sub> (A-106), despite this is the tooth class that typically bears the highest percentages of continuous middle and, particularly, distal trigonid crests in the SH and Neanderthal groups (Bailey et al., 2011; Martínez de Pinillos et al., 2014; Martín-Torres et al., 2014). In this aspect, the pattern of expression of trigonid crests in Arago would support previous statements about the Neanderthal affinities of the Arago sample, but also to a less derived status with regard to the SH population (Arsuaga et al., 2014; Bermúdez de Castro et al., 2003; de Lumley M.-A., 2015).

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## Brief Communication: Virtual Reconstruction of the Early Pleistocene Mandible ATD6-96 from Gran Dolina-TD6-2 (Sierra De Atapuerca, Spain)

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**KEY WORDS** mandible; virtual reconstruction; *Homo antecessor*; Sierra de Atapuerca

### ABSTRACT

**Objectives:** In this report, we present a further study of the late Early Pleistocene ATD6-96 human mandible, recovered from the TD6-2 level of the Gran Dolina cave site (Sierra de Atapuerca, northern Spain) and attributed to *Homo antecessor*.

**Methods:** ATD6-96 consists of a left half of a gracile mandible of an adult individual with the premolars and molars in place that is broken at the level of the lateral incisor-canine septum. The present analysis is based on a virtual reconstruction of the whole mandible by means of computed tomography (CT). We have reconstructed the symphysis using information from a modern human sample, as well as from a wide sample composed of several *Homo* specimens.

**Results:** This research has allowed us to record new variables with taxonomic and phylogenetic interest. We have estimated the length/width index of the alveolar arcade, as well as the percentage of the arcade length with regard to the total length. The latter confirms that ATD6-96 shares with all African and Asian *Homo* species a primitive structural pattern, as it was established in previous studies. In contrast, the length/width index of the alveolar arcade in the *H. antecessor* specimen is close to the mean values of Neandertals and the Atapuerca-Sima de los Huecos hominins.

**Conclusions:** *H. antecessor* is derived regarding the shape of the mandibular alveolar arcade within the genus *Homo* and points to an early divergence from contemporaneous African populations. Our results also ratify the affinities of *H. antecessor* with Neandertals, although the precise relationship with this lineage needs further research. *Am J Phys Anthropol* 159:729–736, 2016. © 2015 Wiley Periodicals, Inc.

### INTRODUCTION

Three-dimensional (3D) virtual imaging has become an essential tool in palaeoanthropological studies. It is common that fossils are recovered from the sites with some preservation damage such as postdepositional breakages, distortion due to sediment pressure, or some degree of incompleteness. Due to the aid of 3D virtual imaging techniques, we can now reconstruct damaged specimens and obtain new type of data on old and new fossil findings (e.g., Ponce de León and Zollikofer, 1999; Manzi et al., 2001; Sémal et al., 2005; Zollikofer et al., 2005; Guipert et al., 2007; Mafart et al., 2007; Sylvester et al., 2008; Gunz et al., 2009; Berge and Goullaras, 2010; Bermúdez de Castro et al., 2010; Vialet et al., 2010; Spoor et al., 2015).

In this report, we aim to present new variables of taxonomic interest from the mandible ATD6-96, recovered in 2003 from the TD6-2 level of the Gran Dolina cave in Sierra de Atapuerca, Northern Spain. Although this mandible has been already the subject of previous studies (Carbonell et al., 2005; Bermúdez de Castro et al.,

2014) there were some variables that could not be assessed due to its degree of incompleteness. In this study, we performed a virtual reconstruction of the

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missing parts of the mandible by means of computed tomography (CT) and we obtained new information that is relevant, not only about this specimen in particular, but also about the evolutionary meaning of the Gran Dolina-TD6 hominin assemblage. These hominins represent one of the oldest European humans (*Homo antecessor*, Bermúdez de Castro et al., 1997) and display a particular combination of cranial and postcranial features that may be crucial for understanding the first settlement of Europe.

## MATERIALS

### The TD6 level

The Gran Dolina cave site (TD) fills up a large cavity about 27 m deep and with a maximum width of 17 m. The stratigraphic section of the site was cut and exposed by the construction of a railway trench. Gil and Hoyos (1987) divided this section from bottom to top into eleven levels: TD1–TD11. However, the stratigraphy of the Gran Dolina site is under continuous refinement. There is a vertical cut of the section in progress (e.g., Bermúdez de Castro et al., 2008). In addition, a wide pit about 10 m deep, excavated below the present level of the ancient railway, is currently under study. Parés and Pérez-González (1995, 1999) observed a polarity reversal between TD7 and T8, interpreted as the Matuyama/Brunhes boundary, meaning that levels TD8–TD11 were deposited during the Middle Pleistocene, whereas levels TD7–TD1 were attributed to the Early Pleistocene. The combination of paleomagnetic data and US-ESR ages suggests an age range between 0.78 and 0.86 Ma (million years ago) for TD6-2 (Falgüeres et al., 1999). Thermoluminescence (TL) ages on samples taken one meter below the Brunhes/Matuyama boundary (0.78 Ma) give an age of  $0.96 \pm 0.12$  Ma for TD6 (Berger et al., 2008), which may correspond to MIS 25. The last systematic dating of the Gran Dolina sequence has been made by Moreno (2011) using the ESR dating method on optically bleached quartz. Moreno analysed six samples for TD6 and TD7, obtaining an age range of 0.80–0.88 Ma for these levels, which is consistent with the biostratigraphic and paleomagnetic analyses and suggest that the TD6 human assemblage was likely deposited during the MIS 21.

### The mandible ATD6-96

The specimen ATD6-96 was recovered in 2003 during the excavation of a small area of the TD6-2 level, near the test pit digged during the 1994–1997 field seasons. ATD6-96 is a left half of a gracile mandible of an adult individual with the premolars and molars in place. ATD6-96 presents a perimortem fracture at the level of the lateral incisor-canine septum and from this point the whole right side is missing. It also presents some minor cracks between the corpus and the ramus, at the region of the gonial angle and the neck of condyle that have not altered the original morphology. A noticeable elevation at the basal border suggests the birth of the genial apophysis. The third molar (M3) is fully erupted and shows a minimal wear facet at the mesial marginal ridge. During the restoration process of the ATD6-96 specimen (López-Polín et al., 2008), the corpus and ramus were separated, and the roots of the M3 could be observed directly. These roots are at stage RC of tooth formation (Moorrees et al., 1963). Given the small size of



Fig. 1. Lateral view of ATD6-96.

ATD6-96 (Fig. 1) we consider that this specimen probably belonged to a female individual (Carbonell et al., 2005).

## METHODS

The methodology applied for the study of ATD6-96 includes the virtual reconstruction of the mandible by mirroring the preserved portions and by estimating the width of the missing symphysis. Once the whole mandible was virtually reconstructed we recorded some variables with taxonomic interest related with the shape and measurements of the mandibular arcade.

The specimen ATD6-96 was scanned with a Tomographic system (Tomograph YXILON Compact Yxlon International, X-Ray GmbH) housed at the University of Burgos, using the following settings: voltage 130 kV, amperage 4 mA, and resultant voxel size of  $0.109 \text{ mm} \times 0.109 \text{ mm} \times 0.20 \text{ mm}$ . The resulting images were imported into Amira (Visage Imaging) software to obtain the 3D volume of the mandibular left side. Following, a second reconstruction was performed by mirroring the original stack of images (left hemimandible) to obtain the right hemimandible and create the 3D volume. Moreover, a cast of the right and left sides of ATD6-69 was produced (Scanner 3D Nextengine housed at the University of Burgos) to assist in the digital reconstruction.

As the canine alveolus is not complete due to a postdepositional breakage it was necessary to mirror the remaining half. The reconstructed 3D volume was then aligned and placed resulting in an entire alveolar rim. The same process was performed on the right side.

Next, both the left and right hemimandibles were rotated on the "x, y, and z" planes until the anatomical position was reached, that is, that the wear plane of the buccal cusps of the P4 and M1 is positioned approximately in the same plane and perpendicular to the vertical axis.

Once the two hemimandibles are orientated we still have to spatially align one respect to the other. For this purpose it is necessary to reconstruct the symphyseal region. To achieve this goal we defined two landmarks: 1, the middle point of the internal side (IS) of the interdental septum between the permanent canine (C) and the permanent lateral incisor (I2), 2, the middle point of the external side (ES) of the interdental septum between the C and I2.

Then, we obtain the variables IS-IS and ES-ES with a Limit<sup>®</sup> digital caliper. IS-IS is defined as the distance between the middle innermost point of the interdental septum between the C and the I2 on the right side, and the same point on the left side. ES-ES is defined as the distance between the middle outermost point of the interdental septum between the C and the I2, on the right side, and the same point on the left side, respectively. These points are easy to determine and their identification is straightforward. The most important consideration concerning these landmarks is that they are not related to the morphology of the symphysis. The morphology of this part of the mandible is highly variable in hominins and highly derived in modern humans. Consequently, we need to reconstruct the missing part of ATD6-96 employing only size information. The IS-IS and ES-ES variables are a reference to obtain the width of the symphysis, and they are independent of the morphological features (e.g., mental trigone, mental fossae, etc.), of this part of the mandible.

In order to confirm the reliability of these landmarks, the IS-IS and ES-ES variables were independently obtained by two of us (MM-M and CG-C) in the same modern human mandibular sample. In both cases the variables followed a normal distribution (Kolmogorov-Smirnov test;  $P > 0.05$ ). Homogeneity of the variances is also accomplished (Levene test,  $P > 95\%$ ). The ANOVA analysis gives a  $P$  value of 0.607 for the ES-ES variable and a  $P$  value of 0.502 for the IS-IS variable. In summary, no significant differences (95% of signification level) were observed between the measurements obtained by MM-M and CG-C. Using the formula  $[(m1-m2)/m2] \times 100$ , where  $m1$  and  $m2$  are the measurements obtained by each observer, the interobserver average error was 3.0% for the IS-IS variable and 4.4% for the ES-ES variable.

Furthermore, in order to analyse the goodness of these measurements we carried out a linear regression analysis of these two variables (IS-IS and ES-ES) measured in a modern human sample ( $N = 30$ ). The analysis was performed with  $R$  statistical language and its graphical user interface  $R$  Commander. The distribution of the data fits a linear regression ( $P$  value =  $6.16 \times 10^{-6}$ ,  $R^2 = 0.52$ ). The equation and their confidence intervals (95%) are:

$$\text{IS-IS} = 4.39 + 0.61 \times \text{ES-ES}$$

$$95\% \text{ Lower IS-IS} = -0.05 + 0.39 \times \text{ES-ES}$$

$$95\% \text{ Upper IS-IS} = 8.84 + 0.83 \times \text{ES-ES}$$

Given a mean value of 19.8 for the ES-ES (independent variable), the 95% confidence interval for IS-IS is 16.1–16.8 (mean value: 16.5).

The values indicate that it exists a good correlation between these two landmarks/anatomical features, so we can confidently use them to “anchor” one hemimandible with regard to the other and to estimate the width of the symphysis and the spatial relationship of the hemimandibles.

In order to estimate the width of the symphyseal region in ATD6-96 we have followed different approaches. The first approach is based on the symphyseal width of a modern sample. We employed a sample of 30 modern human mandibles of unknown sex from the San José cemetery of Burgos, housed at the Laboratory of Human Evolution (University of Burgos). Using the mean values, as well as

the 95% confidence interval of the mean values of the modern population (see above) could be a reasonable approach to our reconstruction, since ATD6-96 is a small specimen. However, we realize that by using a modern population (or any other hominin population) we fall into circular reasoning. Ideally, we would need a large number of mandibles from the same Early Pleistocene *H. antecessor* population to have a high interval of confidence in the reconstruction. For this reason, in a second approach, we recorded the IS-IS and ES-ES variables in a selected sample of mandibles belonging to different *Homo* paleodemes (species). The specimens studied were originals (Dmanisi, Tighenif, Arago, and Atapuerca-Sima de los Huesos) and first generation casts. Four of these specimens (D211, D2735, KNM ER-820, and KNM-WT 15000) have a U-shaped alveolar arcade. Each reconstruction requires a correct orientation of the mandibles and it is a manual time-consuming task. As expected, using the measurements of some large hominins specimens in the reconstruction resulted in symphysis with a large width.

Finally, once the mandible has been reconstructed we recorded a series of mandibular measurements with taxonomic value to assess the phylogenetic affinity of this specimen in relation to others of the fossil record (see Table 3 of this article and Rosas and Bermúdez de Castro, 1998; Gabounia et al. 2002). Following Rosas and Bermúdez de Castro (1998) we obtained the width (defined as the M3-M3 distance) and the length (the distance between the infradentale (ID) and the distal surface of the M3) of the mandible. The ID is taken at the middle point of the ES-ES distance. With these measurements we obtained the length/width index. Moreover, we also calculated the total length of the mandible (L11) and the total length of the alveolar arcade (L7) (Gabounia et al., 2002). The maximum length of the alveolar arcade of ATD6-96 virtual reconstruction was taken with the specimen placed in the same anatomical position as the rest of the mandibles, that is, with the wear plane of the P4 and the M1 positioned in the same plane and perpendicular to the vertical axis. The maximum length is the perpendicular between the ID and the line joining the more distal points of the right and left condyles. The L7/L11 represents the percentage of the alveolar arcade with regard to the total length of the mandible.

## RESULTS

Table 1 shows the descriptive statistics for the IS-IS and ES-ES measurements and for the IS-IS/ES-ES relationship of the modern human sample from the San José cemetery. In Table 2 we give the IS-IS and ES-ES measurements obtained in the *Homo* sample. It is interesting to note that the relationship between IS-IS/ES-ES in this sample is between the range of variation of the 30 human modern specimens from the San José cemetery (Table 1), so it seems a relatively constant index regardless taxonomic assignment of the specimen employed as a reference for the reconstruction. Therefore, although we could have used a larger *Homo* sample, it seems reasonable to expect that the results would be the same.

Using the mean values of the IS-IS and ES-ES measurements obtained in the modern human sample and in some *Homo* specimens, we obtained a certain number of virtual reconstructions for the ATD6-96 mandible. This



way our reconstructions is not taxonomically biased a priori and we break a possible circular reasoning.

Using the mean values of the modern human sample (Table 2) we obtain the reconstruction showed in Figure 2, in which the length (ID–M3) is 62.5 and the width (M3–M3) is 73.6. The length/width index is 84.9. When

we make the reconstruction using the IS–IS and ES–ES values obtained in different *Homo* specimens we get similar values for the length (range 63.2–64.3) and a range between 71.1 and 81.2 for the width (Table 3 and Fig. 3).

In all cases, including the 95% confidence interval for the modern sample, we have obtained a length/width index below 90, with a range of 79.2–89.3 (Table 3 and Fig. 4). In general, the larger is the *Homo* specimen used in the reconstruction the lower the length/width index. Given the small size of ATD6-96, we expect that the most appropriate values are the IS–IS and ES–ES obtained in the modern human sample (mean values). These values give a length/width index of 84.9.

The length/width index obtained in the modern human sample is similar to that of Neandertals and the Atapuerca-Sima de los Huesos hominins, and lower than that obtained in other European and Asian Middle Pleistocene hominins and *H. sapiens* (see Fig. 4 and Table 3 of Rosas and Bermúdez de Castro, 1998). A value of 84.9 means that the alveolar arcade of ATD6-96 was parabolic and therefore, derived regarding the *Homo* U-shaped primitive condition. In order to further test how reliable is this shape, we explore how the two hemimandibles should rotate in order to obtain a U-shaped arcade. If we take as a fixed value the mean of the IS–IS distance obtained in a modern sample, the ES–ES distance should increase up to 24.0 mm to get a U-shape. As we can see in Table 2, this ES–ES value is similar to that of the larger specimens of the *Homo* sample (e.g., Tighenif 2 and 3, Mauer, etc.), so it does not look reasonable for a mandible as small as ATD6-96. In contrast, if we rotate the hemimandibles to obtain a parabolic arcade using the same IS–IS distance, the ES–ES distance decreases to more reasonable values, between 20.0 and 22.0 mm or even less.

Using all the reconstructions obtained using the modern sample, as well as the different hominins, we have estimated the L7 and L11 variables. In average, the length of the alveolar arcade represents about the 54%

TABLE 1. Descriptive statistics for the IS–IS<sup>a</sup> and ES–ES<sup>a</sup> measurements of the modern human sample from the San Jose cemetery

	N	X	SD	Range
IS–IS	30	16.48	1.20	14.27–19.84
ES–ES	30	19.73	1.49	17.43–22.86
IS–IS/ES–ES	30	83.66	4.54	75.80–92.50

<sup>a</sup>IS–IS and ES–ES: see text for a definition of these measurements.

TABLE 2. Value for the IS–IS and ES–ES measurements in some *Homo* specimens

	IS–IS	ES–ES	IS–IS/ES–ES
D 211	17.38	21.54	80.68
D 2735	20.44	22.28	91.74
KNM-ER 820	18.07	22.55	80.13
KNM-WT 15000	20.86	24.37	85.59
Tighenif 2	20.74	24.76	83.76
Tighenif 3	21.49	25.9	82.97
Mauer	18.88	22.00	85.80
Arago 2	20.87	26.20	79.65
Atapuerca-SH IV <sup>1</sup>	16.4	20.76	78.99
Atapuerca-SH XII	20.19	23.34	86.50
Atapuerca-SH XV	18.43	23.43	78.65
Atapuerca-SH XIX	19.70	24.25	81.23
Atapuerca-SH XXII	17.29	21.20	81.55
Atapuerca-SH XXVIII	19.15	23.75	80.63
Zafarraya	17.80	20.25	87.90

1. Atapuerca, Sima de los Huesos site. In Roman numbers: individual.

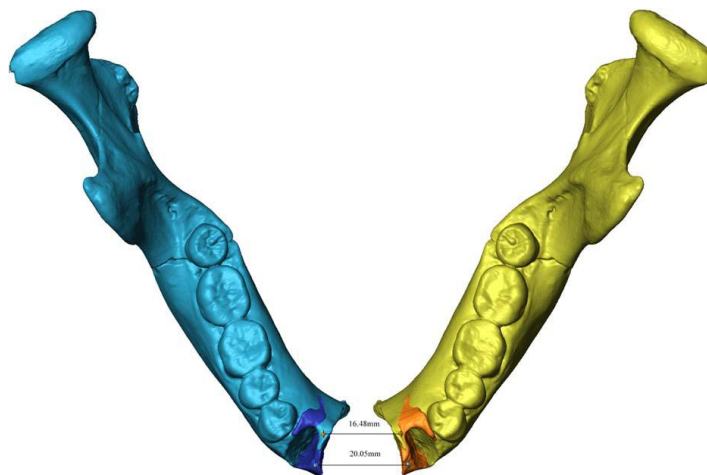


Fig. 2. Digital reconstruction of ATD6-96 using the mean values obtained in the modern: ES–ES = 19.7 mm and IS–IS = 16.5 mm. The original is the left side (yellow). Note that for technical limitations a value of 20.05 instead of 19.7 was obtained in the reconstruction; see text for further details.

VIRTUAL RECONSTRUCTION OF ATD6-96 MANDIBLE

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of the total length of the mandible (range 53.5–54.7), aligning ATD6-96 with specimens like Bañolas or Montmaurin, and clearly surpassing the values of Neanderthals, Mauer, and Arago 2 (Table 4).

DISCUSSION

In this study we performed a virtual reconstruction of the Early Pleistocene mandible ATD6-96 recovered from the TD6-2 level of the Gran Dolina site, in Sierra de Atapuerca.

TABLE 3. Values of the bimolar M3–M3 distance (width) and infradental–M3 (length), and length/width index obtained using different reconstructions from a modern human sample and some hominins

	Bimolar M3–M3 distance	Infradental–M3	Length/width index
Modern sample (mean value)	73.6	62.5	84.9
Modern sample 95% lower IS–IS	73.6	62.6	85.1
Modern sample 95% upper IS–IS	73.0	62.9	86.1
D 211	74.0	63.5	85.8
D 2735	78.3	63.5	81.1
KNM-ER 820	74.4	63.6	85.5
KNM-WT 15000	80.4	63.9	79.5
Tighenif 2	80.2	64.2	80.1
Tighenif 3	81.2	64.3	79.2
Mauer	75.9	63.7	83.9
Arago 2	80.4	63.9	79.5
Atapuerca-SH IV <sup>1</sup>	71.1	63.2	88.9
Atapuerca-SH XII	74.8	64.0	85.5
Atapuerca-SH XV	72.4	63.5	87.7
Atapuerca-SH XIX	73.5	64.0	87.1
Atapuerca-SH XXII	71.1	63.5	89.3
Atapuerca-SH XXVIII	72.7	64.0	88.0
Zafarraya	74.7	63.5	85.1

1. Atapuerca, Sima de los Huesos site. In Roman numerals: individual.

This reconstruction allowed us to obtain some measurements, which are useful for estimating some indices with taxonomic utility signal.

The shape of the alveolar arcade is related to the overall architecture of the skull. In a study of the Dmanisi mandible D211, Rosas and Bermúdez de Castro (1998) obtained a value of 110.2 for the length/width index of the alveolar arcade of this specimen. This value is similar to that recorded in some *A. afarensis* specimens, OH 13, KNM-ER 1805, KNM-ER 992, KNM-BK 8518, KNM-BK 67, and one specimen from Zhoukoudian (ZHD H1). Other Asian *H. erectus*, like Lantian and ZHD G1 show index values close to 100.0. Similarly, we estimate that a value above 100 for this index could be obtained for the recent reconstruction of OH 7 (Spoor et al., 2015). Furthermore, whereas it is not possible to obtain this index in the immature individual KNM-WT 15000, this specimen exhibits a clear U-shaped mandibular dental arcade. In other words, mandibles with an index about 100 or above this value display a narrow and broadly U-shaped arcade, and this can be considered as the primitive condition for the *Homo* clade. In contrast, the Middle and Early Pleistocene mandibles show values of the index less than 100 (Rosas and Bermúdez de Castro, 1998), displaying a parabolic alveolar arcade and a much wider M3 bimolar width than the archaic *Homo* mandibles. In ATD6-96 this variable would be slightly above 70.0 like in the majority of the European Pleistocene specimens. The estimated index of the alveolar arcade in ATD6-96 is close to the mean values of Neanderthals and the Atapuerca-SH hominins. Therefore, we can conclude that *H. antecessor* is derived for the *Homo* clade regarding the shape of the mandibular alveolar arcade.

Concerning the total length of ATD6-96, it is interesting to note that this specimen is the smallest of the large sample studied by Gabounia et al. (2002) (Table 4 and Fig. 5). This could support the assignment of ATD6-96 to a female individual. Previous studies pointed out that ATD6-96 exhibits a primitive structural pattern

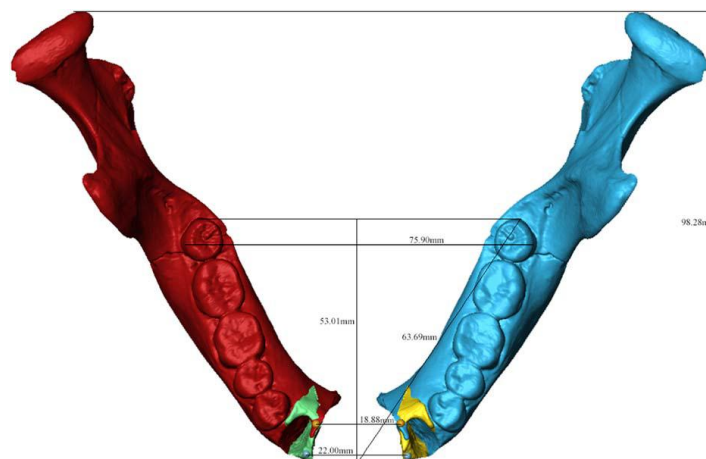
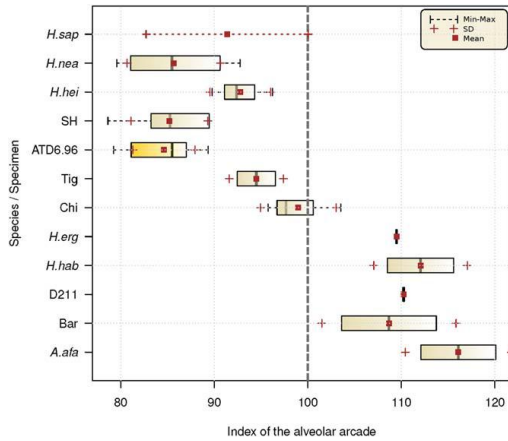


Fig. 3. Digital reconstruction of ATD6-96 using the mean values obtained in the Mauer specimen: IS–IS = 18.9 mm; ES–ES: 22.00; Infradental–M3: 63.69 mm; M3 (buccal)–M3 (buccal): 75.90 mm; L7: 53.01 mm and L11: 98.28 (see text for further details). The original is the left side (red).



**Fig. 4.** Index of the alveolar arcade measured on different species and specimens. A vertical dashed gray line is marked in the value of 100, which means that both lineal measures used to obtain the index are equal. All the species/specimen raw data, including their sample sizes, were obtained from Rosas and Bermúdez de Castro (1998). ATD6-96 is represented by the values of the indexes obtained by reconstructing the mandible using 18 different models; see text for further details. Note that none of the indexes of *Homo antecessor* falls beyond 100. *A. afa*: *Australopithecus afarensis*; Bar: Baringo; D211: Dmanisi mandible; *H. hab*: *Homo habilis*; *H. erg*: *Homo ergaster*; Chi: China; Tig: Tighenif; ATD6-96: *Homo antecessor* mandible; SH: Sima de los Huesos; *H. hei*: *Homo heidelbergensis*; *H. nea*: *Homo neanderthalensis*; *H. sap*: *Homo sapiens*; see Table 3 of Rosas and Bermúdez de Castro (1988) to check the specimens included in each sample.

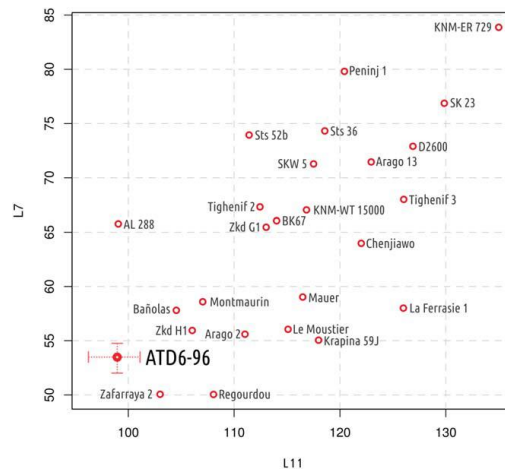
shared with all African and Asian *Homo* species, defined by features such as the position of the mental foramen, the lateral prominence, and the mylohyoid line in relation to the alveolar margin at M3 level, as well as the relief of the pterygoid fossa or the intersection between the mandibular notch and the condyle (Carbonell et al., 2005). The percentage of the alveolar arcade obtained in our reconstruction can be also considered within this primitive *Homo* structural pattern. In fact, for this feature, ATD6-96 is placed with several African and Eurasian Early and Middle Pleistocene *Homo* specimens, between the high percentages obtained for *Australopithecus* and *Paranthropus* and the low percentages of the Neanderthals (see Fig. 3 of Gabounia et al., 2002). In these hominins mid-facial prognathism is responsible for the relative short dental arcade with regard to the total length of the mandible. In contrast, ATD6-96 is derived concerning other features such as the oblique inclination of the retromolar area, the partial covering of the M3 by the ramus, or the absence of alveolar prominence (Carbonell et al., 2005).

Our results have provided an index of the alveolar arcade that is similar to the mean values obtained in Neanderthals and the SH hominins. This result is not fully surprising, given that *H. antecessor* shares other features with Neanderthals and the SH hominins (Arsuaga et al., 1999; Carretero et al., 1999; Gómez-Robles et al., 2007; Bermúdez de Castro et al., 2012). Furthermore, we also noticed a large medial pterygoid

**TABLE 4.** Measurements of the mandible in a large hominin sample<sup>1</sup>

Specimen	Total length (L11)	Length of the alveolar arcade (L7)	L7/L11 × 100
ATD6-96 (mean value) <sup>2</sup>	98.9	53.5	54.1
AL 288	99.0	65.8	66.5
Sts 52b	111.4	73.9	66.3
Sts 36	118.6	74.3	62.6
SK 23	129.9	77.9	59.9
SKW5	117.5	71.3	60.7
Peninj	120.4	79.8	66.3
KNM-ER 729	135.0	83.9	62.1
KNM-WT 15000	116.8	67.0	57.4
BK 67	114.0	66.1	58.0
D 2600	126.9	72.9	57.4
Tighenif 2	112.4	67.3	59.9
Tighenif 3	126.0	68.0	53.9
Chenjiawo	122.0	64.0	52.4
Zhoukoudian H1	106.0	56.0	52.8
Zhoukoudian G1	113.0	65.5	57.9
Mauer	116.5	59.0	50.6
Arago 2	111.0	55.6	50.1
Arago 13	122.9	71.5	58.2
Montmaurin	107.0	58.6	54.7
Zafarraya 2	103.0	50.1	48.6
Le Moustier	115.1	56.1	48.7
Krapina 59J	118.0	55.0	46.6
La Ferrassie	126.0	58.1	46.1
Regourdou	108.0	50.1	46.4
Banolas	104.5	57.8	55.3

1. Data obtained from Gabounia et al. (2002).
2. These values represent the average measurements of L7 and L11 obtained from the eighteen reconstructions made in this research.



**Fig. 5.** Total mandibular length (L11) plotted against the total length of the alveolar arcade (L7). Gabounia et al. (2002) obtained these measurements for the sample of fossil specimens included in this figure. The average of L7 for the eighteen reconstructions of ATD6-96 was also plotted against the average of L11 obtained in these reconstructions. Minimum and maximum ranges for L7 and L11 are represented as vertical and horizontal dashed lines. Note the small size of ATD6-96 in relation to other fossil specimens.

tubercle present in ATD6-96, a feature that is highly frequent in Neandertals (89%) and the Atapuerca-Sima de los Huesos (SH) hominins (55%) (Bermúdez de Castro et al., 2014).

As we concluded in previous studies, all these features cannot be considered as Neandertal autapomorphies, but traits which may have appeared much earlier than previously considered, in an Early Pleistocene hominin population. Considering these results and the fact that the mandibular body of the *H. antecessor* mandibles is low and narrow (Rosas and Bermúdez de Castro, 1999; Carbonell et al., 2005; Bermúdez de Castro et al., 2008) we consider that these hominins clearly diverged from other African Early Pleistocene hominins. In contrast, the TD6 hominins exhibits clear affinities with Pleistocene Eurasian hominins and show a particular and intriguing mosaic of features (Bermúdez de Castro et al., 2015).

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## Comparative analysis of the trigonid crests patterns in *Homo antecessor* molars at the enamel and dentine surfaces



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### ABSTRACT

As the Atapuerca fossil samples are the most representative remains to understand the evolution of the genus *Homo* in Europe during the Early and Middle Pleistocene, the study of their dentition is becoming increasingly important. Based on these findings, recent studies have helped to refine the evolutionary hypotheses about the settlement of Europe proposing a less linear settlement of the continent with several migrations and/or interbreeding of these groups. Here, we deal with the affinities between the Early and the Middle Pleistocene populations of Europe by studying the dental morphology of these groups with microtomography (microCT). The aim with this report is to present for the first time the trigonid crest pattern exhibited by the Early Pleistocene hominins from Gran Dolina-TD6 assigned to *Homo antecessor* species. For this purpose, and knowing that the molar trigonid crest pattern bears a significant taxonomic and phylogenetic value, we also present a comparative study of this trait at the outer enamel surface (OES) and enamel dentine junction (EDJ) of *H. antecessor*, Sima de los Huesos (SH), *Homo neanderthalensis* and *Homo sapiens*. Further morphological comparisons among them will help to provide new and valuable information to investigate the evolutionary scenario of the first European settlement. Our study ratifies the similarities between SH and *H. neanderthalensis* in the expression of a continuous mid-trigonid crests at the enamel and dentine surfaces. However, this feature cannot be considered a Neanderthal apomorphy since it can be also found in lower frequencies in the Gran Dolina hominins. Thus, *H. antecessor* would be phenetically closer to *H. sapiens* who would have preserved a primitive pattern.

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### 1. Introduction

One of the most recent and debated issues in paleoanthropology focuses on the nature of the first human settlement in Europe (MacDonald et al., 2012; Bermúdez de Castro and Martínón-Torres, 2013; Bermúdez de Castro et al., 2013; Mosquera et al., 2013; Parés et al., 2013; Toro-Moyano et al., 2013; Muttoni et al., 2015). In 1994, about ninety human fossil remains were recovered from the *Aurora*

*Stratum*, an Early Pleistocene level of the b section of Gran Dolina-TD6 site in Sierra de Atapuerca (Carbonell et al., 1995, 1999). The unique combination of primitive and derived features concerning the *Homo* clade, allowed the naming of a new *Homo* species, *Homo antecessor* (Bermúdez de Castro et al., 1997). Regarding the age of the TD6 sedimentary deposit, Moreno (2011) obtained an age range of 0.80–0.88 Ma for six samples analysed from TD6 and TD7, which is consistent with the paleomagnetic and biostratigraphic studies and suggest that the human accumulation was deposited during MIS 21.

The site consists of a cave completely filled with sediments which have been divided in 11 stratigraphic levels. To date, TD6 stratum has provided more than 150 human remains (Carbonell et al., 1995; Bermúdez de Castro et al., 1997, 1999, 2008, 2012; Pablos et al., 2012) corresponding to a minimum of eleven

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individuals (Bermúdez de Castro et al., 2006), mainly characterized by the combination of plesiomorphic and apomorphic traits. The combination of a clearly primitive dentition (Bermúdez de Castro et al., 1999b; Martínón-Torres, 2006; Gómez-Robles et al., 2008) and a modern face (Arsuaga et al., 1999; Freidline et al., 2013; Lacruz et al., 2013; Bermúdez de Castro and Martínón-Torres, 2014), together with the study of new African and Eurasian human remains (Manzi et al., 2001; Bermúdez de Castro et al., 2011; Liu et al., 2013; Toro-Moyano et al., 2013; Arsuaga et al., 2014; Xing et al., 2014a, b), have helped to reinforce the distinct taxonomic status for the TD6 hominins with regard to Early Pleistocene hominins from Africa and Asia (Zanolli et al., 2014; Zanolli, C., 2015) and from the Middle Pleistocene hominins from Europe (Martínón-Torres et al., 2011; MacDonald et al., 2012; Bermúdez de Castro and Martínón-Torres, 2013; Martínón-Torres et al., 2013; Meyer et al., 2014).

Initially, *H. antecessor* was proposed as the last common ancestor between *Homo sapiens* and *Homo neanderthalensis* based on the expression of several apomorphies shared among them (Bermúdez de Castro et al., 1997; Martínez and Arsuaga, 1997). This scenario was challenged in 2003 with the dental comparison between the increased TD6 and Sima de los Huesos (SH) collection (Bermúdez de Castro et al., 2003), and recently discussed in Martínón-Torres et al. (2012), Gómez-Robles et al. (2013), Bermúdez de Castro and Martínón-Torres (2014), Bermúdez de Castro et al. (2015a) among others. Without denying the phylogenetic link, these studies point to the possibility of a population discontinuity between *H. antecessor* and the Middle Pleistocene populations which would have replaced or absorbed the first European populations. The unique combination of primitive and derived features that *H. antecessor* shared with SH, Neanderthals and *H. sapiens* samples, suggests the possibility that they all may have shared a common ancestor which could have evolved in Africa or Western Asia (Bermúdez de Castro and Martínón-Torres, 2014; Bermúdez de Castro et al., 2015a, b). Thus, the hominin fossils from Gran Dolina-TD6 could represent a side branch originated in the cladogenesis of an ancestral Early Pleistocene population. Each new branch would exhibit a combination of features inherited from the ancestral population together with other traits that would be unique to this cladogenetic event (Bermúdez de Castro and Martínón-Torres, 2014; Bermúdez de Castro et al., 2015a, b). Moreover, the study of two new mandibles recovered from Gran Dolina-TD6 revealed that *H. antecessor* shared some features with *Homo erectus* from China and Java (Martínez, 1995; Arsuaga et al., 1997, 1999; Carbonell et al., 2005; Bermúdez de Castro et al., 2008), as it was also suggested with the dental evidence (Martínón-Torres et al., 2006, 2007). These similarities could imply that the relationship between the Asian and the European fossils is closer than that with the African samples (Martínón-Torres et al., 2007). In this context, an increased hypodigm from Asia as well as from TD6 level would be crucial to test this hypothesis and, in particular, the phylogenetic position of *H. antecessor*.

Teeth are considered an important and reliable source of morphological characters for phylogenetic analysis due to the well preserved genetic component in their expression (Hrdlička, 1923; Turner et al., 1991; Kaifu et al., 2005; Martínón-Torres et al., 2007, 2012). In this study we will provide new data of interest to understand the possible evolutionary scenario of Europe during the Early to the Middle Pleistocene transition. Our aim is to investigate the affinities between extant and extinct human population taxa within the hominin clade (Irish, 1993; Irish and Guatelli-Steinberg, 2003; Skinner, M.M. et al., 2008). For this purpose, and knowing that the expression of trigonid crest pattern can bear an important taxonomic and phylogenetic signal (Scott and Turner II, 1997; Irish, 1998; Bailey, 2002; Bailey et al., 2011), we present for the first time

the trigonid crest pattern at the outer enamel surface (OES) and enamel dentine junction (EDJ) of *H. antecessor* and we compare it to SH, *H. neanderthalensis* and *H. sapiens*.

2. Materials and methods

2.1. Gran Dolina-TD6 and comparative sample

To date, the TD6 level of Gran Dolina has provided more than 150 hominin fossils that include cranial, postcranial and dental remains (see Bermúdez de Castro et al., 2015b for the latest assessment). The dental sample consists of 53 specimens (7 deciduous and 46 permanent) that have been scanned at the CENIEH premises. The number of TD6 hominin permanent molars is 18, 9 of which are lower molars. Since one of the specimens is broken, our final study sample consists of 8 lower molars (see Table 1).

Table 1

List of the TD6 lower permanent molars included in the study, with the inventory number and the hominin they belong to.

Hominin	Inventory number	Specimen	Side
I	ATD6-5	M <sub>1</sub> , M <sub>2</sub> , M <sub>3</sub>	Right
V	ATD6-94	M <sub>1</sub>	Right
VII	ATD6-113	M <sub>2</sub> , M <sub>3</sub>	Left
VIII	ATD6-112	M <sub>1</sub>	Right
-	ATD6-144	M <sub>2</sub>	Right

Concerning the comparative sample, we have included in this study several molars that belong to SH, *H. neanderthalensis* and *H. sapiens*. As we can see in Table 2, we have used the NESPOS<sup>®</sup> and ESRF<sup>®</sup> databases to get the microCT images of the overall Neanderthal sample and some of the *H. sapiens* specimens. The rest of the analyzed sample -*H. antecessor* (Gran Dolina-TD6), SH, *H. sapiens* from the Calcolithic and Bronze Age (El Mirador) and the contemporary *H. sapiens* sample - was scanned at the CENIEH. We have excluded from the study all teeth partially broken or those with a wear degree higher than 5 in Molnar's standard (Molnar, 1971).

Table 2

Study sample of lower permanent molars. We write in brackets the number of the sample size including only one antimer per individual.

Species	Origin	N total	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>
<i>H. antecessor</i>	TD6 <sup>a</sup>	8	3	3	2
<i>H. heidelbergensis</i>	Sima de los Huesos <sup>a</sup>	63 (43)	22 (14)	19 (11)	22 (18)
<i>H. neanderthalensis</i>	Engis <sup>b</sup>	1	1	-	-
	Gibraltar <sup>b</sup>	3 (2)	2 (1)	-	1
	Ehringsdorf <sup>c</sup>	1	1	-	-
	Abri	1	1	-	-
	Bourgeois-Delaunay <sup>c</sup>	6 (3)	2 (1)	2 (1)	2 (1)
	Regourdou <sup>c</sup>	4	3	-	1
	Krapina <sup>c</sup>	21	7	7	7
<i>H. sapiens</i>	Hunas <sup>c</sup>	1	-	-	1
	Roc de Marsal <sup>c</sup>	2 (1)	2 (1)	-	-
	Equus Cave <sup>b</sup>	2	2	-	-
	Qafzeh <sup>b</sup>	8 (4)	4 (2)	4 (2)	-
	Lagar Velho <sup>c</sup>	1	1	-	-
	El Mirador <sup>a</sup>	14	6	5	3
	CENIEH <sup>a</sup>	12	4	7	1

<sup>a</sup> CENIEH microCT data base.

<sup>b</sup> ESRF<sup>®</sup> data base.

<sup>c</sup> NESPOS<sup>®</sup> data base.

2.2. Micro-computed tomography analysis and surface generation

Virtual three-dimensional reconstructions of the OES and EDJ of the teeth analyzed in this study are based on a high-resolution micro-CT carried out with the Scanco Medical Micro-CT80 system set at the CENIEH research center.

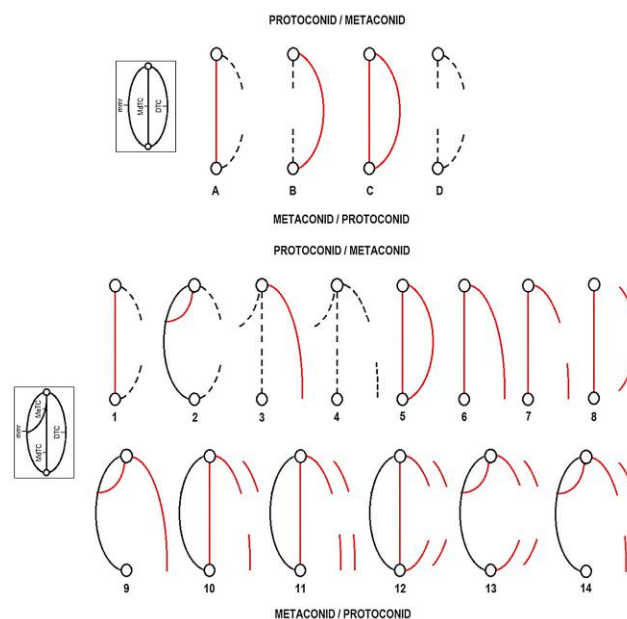
Scans were performed at energies of 70 kV and intensity of scanning of 114  $\mu$ A. Teeth are located in a maximum scan length of 140 mm from the source point, with a maximum scan size diameter of 75.8 mm, and with image matrix from 512 x 512 to 1024 x 1024 pixels. The sampletime of one projection is 800.000 $\mu$ s and the microCT takes nearly 500 parallel projections for each 180°. Pixel dimensions and slices spacing of the resultant images ranged between 18 and 36 microns ( $\mu$ m).

The scanned images were imported into the Amira 5.3.3 (Visage Imaging, Inc.) and after the volume rendering we oriented the tooth in anatomical position. Later, the cervical plane was done following Olejniczak et al. (2008a, b, c) and both enamel and dentine tissues were segmented using the histogram value. We have only included those teeth with a contrast good enough between enamel and dentine to allow a precise segmentation of both tissues. Finally, the

volume was done semi-automatically with manual corrections and no filters.

2.3. Scoring procedures and morphological analysis

In this study, we have used the scoring system described in Martínez de Pinillos et al. (2014) for both enamel and dentine surfaces. Following traditional scoring systems for the trigonid crests expression (Korenhof, 1982; Scott and Turner II, 1997), at the OES we only identify the presence/absence of a middle trigonid crest (MdTC) and a distal trigonid crest (DTC), meaning “presence” when the crest is continuous and “absence” when there is no crest or if it is discontinuous. Based on their pattern of expression we can recognize four basic types (see Fig. 1 top): **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. For the trigonid crests classification at the EDJ, we have also used the 14 typologies identified in Martínez de Pinillos et al. (2014) (see Fig. 1 bottom and Table 3).



**Fig. 1.** Top: representation of the four basic types of trigonid crests on enamel surface identified in our study (based on Korenhof, 1982). View is towards the occlusal surface at the OES including the tips of the cusps (open circles) of the protoconid and metaconid (mmr: mesial marginal ridge). Explanation in the text. Bottom: illustration of all types of trigonid crests on dentine surface identified in our study following Martínez de Pinillos et al., 2014. Explanation in Table 2. View is towards the occlusal surface of the EDJ including the tips of the dentine horn (open 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.

**Table 3**  
Description of the different trigonid crest types at the dentine surface used to classify the overall sample.

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.

Due to the fact that the dental morphological features are barely affected by sexual dimorphism (Turner et al., 1991), both sexes were analyzed together. Although both antimeres were analyzed, we used 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, since we consider that represents the underlying genetic load.

**3. Results**

**3.1. Trigonid crest types at the OES**

When calculating the frequencies of expression and percentages of the continuous MdTC and DTC at the OES, only one antimeres has been included. Thus, in Table 4 we can observe that regarding the continuous MdTC (type A or C) in M<sub>1s</sub>, TD6 and *H. sapiens* samples present less than the 50% for this pattern, while the total SH and *H. neanderthalensis* samples (100%) exhibit this type of crest. Regarding the M<sub>2s</sub>, once again the totality of the SH and Neanderthal samples present a continuous MdTC, whereas in TD6 is a 66.6% and in *H. sapiens* a 21.4%. For the M<sub>3s</sub>, this pattern is present for at least half of the TD6 (50%) and *H. sapiens* (50%) sample analyzed, while for SH and *H. neanderthalensis* samples the percentages are higher, a 83.3% and a 90% respectively. Concerning the expression of a continuous DTC at the OES, TD6 and *H. sapiens* samples do not present any molar with this pattern, and SH sample presents this type of crest exclusively in the M<sub>3s</sub> (61.1%). The Neanderthal sample is the only one that exhibits continuous DTC in all molar types, and the frequencies increase distally: 6.2% in M<sub>1s</sub>, 11.1% in M<sub>2s</sub> and 50% in M<sub>3s</sub>.

In Fig. 2, we see different pie charts representing the frequencies of the pattern of expression for the total molar samples for each hominin sample at the OES. TD6 and *H. sapiens* are similar, and they only exhibit Types A and D, although the Type A is more frequent in *H. antecessor* (50%) than in *H. sapiens* (33%), whereas SH and Neanderthals would present similar percentages for all types, except for the unique expression of Type B (5% in SH).

**3.2. Trigonid crest types at the EDJ**

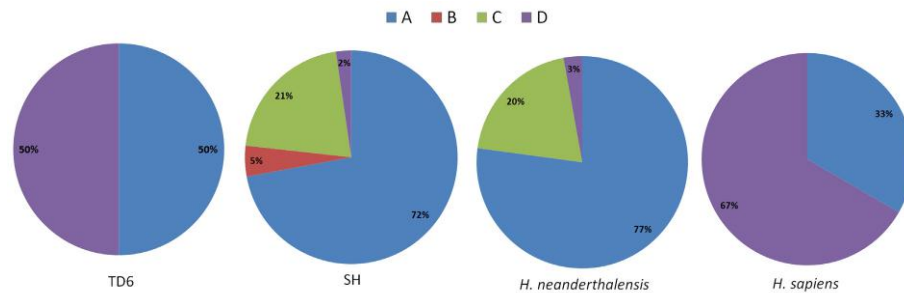
In Table 5 we see that in the TD6 sample there are not continuous mesial trigonid crests (MeTC), while this crest is present in variable percentages in the rest of the groups, except for the M<sub>1s</sub> of SH and the M<sub>2s</sub> of *H. sapiens*. On the other hand the highest percentages of a continuous MeTC for SH (33.3%), Neanderthals (30%) and *H. sapiens* (25%) are present in M<sub>3s</sub>. Regarding the expression of a continuous MdTC, TD6 sample presents this type of crest in the M<sub>1s</sub> (33.3%) and the M<sub>3s</sub> (50%) whereas there are no examples of this crest in the M<sub>2s</sub>. For SH and Neanderthals, we can observe that the frequencies decrease distally in both samples, with a 100% in M<sub>1s</sub>, 72.7% in M<sub>2s</sub> and 50% in M<sub>3s</sub> for SH, and a 87.5% in M<sub>1s</sub>, 75% in M<sub>2s</sub> and 60% in M<sub>3s</sub> for *H. neanderthalensis*. With regard to *H. sapiens*, more than the half of the M<sub>1s</sub> (58.3%) present this type of crest, whereas in the M<sub>2s</sub> and M<sub>3s</sub> samples the frequency of this type is only 25%. Concerning the expression of a continuous DTC, this pattern was absent in the TD6 and *H. sapiens* samples. However, it is present in the M<sub>1s</sub> (6.2%), M<sub>2s</sub> (12.5%) and M<sub>3s</sub> (30%) of *H. neanderthalensis*, and only in the M<sub>3s</sub> (55.5%) of the SH sample.

**Table 4**  
Percentages and frequencies of the continuous middle (MdTC) and distal trigonid crest (DTC) at the OES (only one antimeres included). We consider the trait is "present" when the crest is continuous. Otherwise we consider that the trait is "absent".

	Total molar sample	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>
<b>Middle trigonid crest at OES</b>				
TD6	50.0% (4/8)	33.3% (1/3)	66.6% (2/3)	50.0% (1/2)
SH	93.0% (40/43)	100.0% (14/14)	100.0% (11/11)	83.3% (15/18)
<i>H. neanderthalensis</i>	97.1% (34/35)	100.0% (16/16)	100.0% (9/9)	90.0% (9/10)
<i>H. sapiens</i>	33.3% (11/33)	40.0% (6/15)	21.4% (3/14)	50.0% (2/4)
<b>Distal trigonid crest at OES</b>				
TD6	0.0%	0.0%	0.0%	0.0%
SH	25.5% (11/43)	0.0%	0.0%	61.1% (11/18)
<i>H. neanderthalensis</i>	20.0% (7/35)	6.2% (1/16)	11.1% (1/9)	50.0% (5/10)
<i>H. sapiens</i>	0.0%	0.0%	0.0%	0.0%

**Table 5**  
Frequencies and percentages of the continuous mesial (MeTC), middle (MdTC) and distal trigonid crest (DTC) at the EDJ (only one antimer included). We consider the trait is "present" when the crest is continuous. Otherwise we consider that the trait is "absent".

	Total molar sample	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>
<b>Mesial trigonid crest at EDJ</b>				
TD6	0.0%	0.0%	0.0%	0.0%
SH	20.9% (9/43)	0.0%	27.2% (3/11)	33.3% (6/18)
<i>H. neanderthalensis</i>	20.0% (7/35)	12.5% (2/16)	22.2% (2/9)	30.0% (3/10)
<i>H. sapiens</i>	6.06% (2/33)	6.6% (1/15)	0.0%	25.0% (1/4)
<b>Middle trigonid crest at EDJ</b>				
TD6	25.0% (2/8)	33.3% (1/3)	0.0%	50.0% (1/2)
SH	72.0% (31/43)	100.0% (14/14)	72.7% (8/11)	50.0% (9/18)
<i>H. neanderthalensis</i>	76.4% (26/35)	87.5% (14/16)	75.0% (6/9)	60.0% (6/10)
<i>H. sapiens</i>	39.2% (11/33)	58.3% (7/15)	25.0% (3/14)	25.0% (1/4)
<b>Distal trigonid crest at EDJ</b>				
TD6	0.0%	0.0%	0.0%	0.0%
SH	23.2% (10/43)	0.0%	0.0%	55.5% (10/18)
<i>H. neanderthalensis</i>	14.7% (5/35)	6.2% (1/16)	12.5% (1/9)	30.0% (3/10)
<i>H. sapiens</i>	0.0%	0.0%	0.0%	0.0%



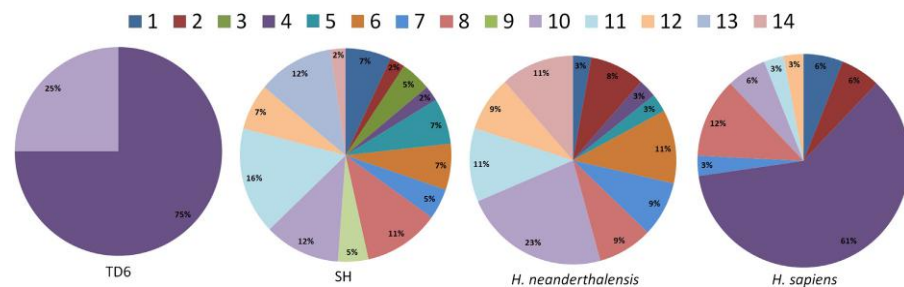
**Fig. 2.** Pie charts showing the percentages of the different types of trigonid crest at the outer enamel surface (OES) for the total molar samples (only one antimer included) of each hominin group analyzed.

In Fig. 3 we can observe that for the total molar sample, TD6 sample displays two types of trigonid crests at the EDJ: type 4 (75%) and type 10 (25%). However, it is interesting to note that only in one out of the 6 M with type 4 the crest is fully absent (grade 0 according to Bailey et al., 2011), whereas the rest display a discontinuous crest (or grade 1 according to Bailey et al., 2011). By contrast, SH exhibits the largest variability of the overall hominin samples, with the highest percentage on type 11 (16%) and the lowest on type 2, 4 and 14 (2%). *H. neanderthalensis* presents also a great variability and is characterized by a 23% for type 10 and a 3%

for type 1, 4 and 5. Finally, *H. sapiens* sample is characterized for the largest percentage in type 4 (61%) and the small percentage in types 7, 11 and 12 (3%).

3.3. Variability of the trigonid crest types and frequencies of expression by tooth class

In previous studies (Martín-Torres et al., 2014; Martínez de Pinillos et al., 2014), we have shown that despite a higher variability of the different types of trigonid expression presented at the



**Fig. 3.** Pie charts showing the percentages of the different types of trigonid crest at the enamel dentine junction (EDJ) for the total molar samples (only one antimer included) of each hominin group analyzed.

EDJ, all teeth usually exhibit a good correlation between the enamel and dentine surfaces in terms of absence/presence of continuous crests in both surfaces. Thus, we can observe that except for ATD6-5 (right M<sub>2</sub>), ATD6-113 (left M<sub>2</sub>) and Qafzeh 10 (left M<sub>2</sub>), all teeth that present a continuous MdTC with absent or discontinuous DTC (type A) at the enamel surface, present a continuous MeTC/MdTC with a discontinuous DTC at the EDJ. Overall, teeth with a trigonid crest type B at the OES show an absent or discontinuous MeTC/MdTC and a continuous DTC at the EDJ. Concerning the teeth with continuous MdTC and DTC (type C) at the enamel, there is a complete correspondence with the dentine surface except for five exceptions: 2 M<sub>3</sub>s of SH (AT-100 and AT-811) and 3 specimens from *H. neanderthalensis* (Regourdou 1, Krapina D4 and Krapina D106). The absent or discontinuous MdTC and DTC (type D) at the OES, corresponds to the dentine surface with an absent or discontinuous MeTC/MdTC and DTC in all cases except for two M<sub>1</sub>s from *H. sapiens* (EQ-H5 and MIR4 P22 205).

Table 6 shows the frequency of trigonid crest expression at the OES and EDJ by tooth class using the individual count method. Thus, at the OES we can observe that for the M<sub>1</sub>s, the highest frequency of expression corresponds to type D for TD6 (66.66%) and *H. sapiens* (60%) samples, and type A for SH (100%) and Neanderthals (93.75%). Concerning the M<sub>2</sub>s, the highest percentage for TD6 (66.66%), SH (100%) and Neanderthals (88.88%) is represented by type A, whereas *H. sapiens* exhibits a 78.75% of type D. Regarding the M<sub>3</sub>s, we can observe that TD6 and *H. sapiens* present a 50% for type A and the other 50% for type D, while SH exhibits all types of crests with the highest percentage for type C (50%), followed by type A (33.33%), B (11.11%) and D (5.56%). *H. neanderthalensis* is characterized by type C (50%), type A (40%) and type D (10%).

exhibits a 50% for type 4 and a 50% for type 10, whereas in *H. neanderthalensis* the highest frequencies correspond to type 2 (30%), and in SH sample to type 5 (16.66%) and 6 (16.66%).

4. Discussion

In this paper, we have explored the diversity and the phenetic affinities among different hominin groups regarding the expression of trigonid crest patterns. As we have already shown in previous studies (Martín-Torres et al., 2014; Martínez de Pinillos et al., 2014), although there is a wider spectrum of trigonid crest types at the EDJ than at the OES, there is a general good concordance -with only few exceptions-between both surfaces. Interestingly, if we consider only those molars that exhibit a mismatch between the trigonid crest pattern at the OES and EDJ, we observe that in TD6, SH and Neanderthal samples the OES would overestimate the frequency of a continuous trigonid crest at the EDJ (i.e. for TD6 a type A at the OES is a type 4 at the EDJ, for Neanderthals a type C at the OES is a type 2 at the EDJ, and for SH a type C at the OES is a type 3 and 14 at the EDJ). However in the *H. sapiens* sample, only in 1 out of 3 discrepancies the OES would overestimate the expression of a continuous crest at the EDJ (i.e. a type A at the OES is a type 4 at the EDJ) whereas the other two discrepancies would underestimate the frequencies of continuous crests at the EDJ (i.e. a type D at the OES is a type 2 and 11 at the EDJ).

Our results together with other studies (Arsuaga et al., 1999; Bermúdez de Castro et al., 1999a; Lacruz et al., 2013) would mean that, regarding the trigonid crests patterns, there are more phenetic affinities between TD6 and *H. sapiens*, and between SH and *H.*

Table 6 Frequency of expression of trigonid crests and their percentages on both enamel and dentine for the M<sub>1</sub>, M<sub>2</sub> and M<sub>3</sub> permanent molars analyzed of *H. antecessor* (TD6), *H. heidelbergensis* (SH), *H. neanderthalensis* (NEA) and *H. sapiens* (SAP).

OES TYPES	M <sub>1</sub>				M <sub>2</sub>				M <sub>3</sub>			
	TD6	SH	NEA	SAP	TD6	SH	NEA	SAP	TD6	SH	NEA	SAP
	n/%	n/%	n/%	n/%	n/%	n/%	n/%	n/%	n/%	n/%	n/%	n/%
A	1 (33.33%)	14 (100%)	15 (93.75%)	6 (40%)	2 (66.66%)	11 (100%)	8 (88.88%)	3 (21.42%)	1 (50%)	6 (33.33%)	4 (40%)	2 (50%)
B	0	0	0	0	0	0	0	0	0	2 (11.11%)	0	0
C	0	0	1 (6.25%)	0	0	0	1 (11.11%)	0	0	9 (50%)	5 (50%)	0
D	2 (66.66%)	0	0	9 (60%)	1 (33.33%)	0	0	11 (78.57%)	1 (50%)	1 (5.56%)	1 (10%)	2 (50%)
<b>Total</b>	<b>3</b>	<b>14</b>	<b>16</b>	<b>15</b>	<b>3</b>	<b>11</b>	<b>9</b>	<b>14</b>	<b>2</b>	<b>18</b>	<b>10</b>	<b>4</b>
EDJ TYPES	n/%	n/%	n/%	n/%	n/%	n/%	n/%	n/%	n/%	n/%	n/%	n/%
1	0	1 (7.14%)	0	1 (6.66%)	0	2 (18.18%)	1 (11.11%)	0	0	0	0	1 (25%)
2	0	0	0	1 (6.66%)	0	0	0	0	0	1 (5.55%)	3 (30%)	1 (25%)
3	0	0	0	0	0	0	0	0	0	2 (11.11%)	0	0
4	2 (66.66%)	0	0	7 (46.66%)	3 (100%)	0	0	11 (78.57%)	1 (50%)	1 (5.55%)	1 (10%)	2 (50%)
5	0	0	0	0	0	0	0	0	0	3 (16.66%)	1 (10%)	0
6	0	0	1 (6.25%)	0	0	0	1 (11.11%)	0	0	3 (16.66%)	2 (20%)	0
7	0	2 (14.28%)	1 (6.25%)	1 (6.66%)	0	0	2 (22.22%)	0	0	0	0	0
8	0	4 (28.57%)	1 (6.25%)	2 (13.33%)	0	0	1 (11.11%)	2 (14.28%)	0	1 (5.55%)	1 (10%)	0
9	0	0	0	0	0	0	0	0	0	2 (11.11%)	0	0
10	1 (33.33%)	3 (21.42%)	5 (31.25%)	1 (6.66%)	0	1 (9.09%)	2 (22.22%)	1 (7.14%)	1 (50%)	1 (5.55%)	1 (10%)	0
11	0	3 (21.42%)	3 (18.75%)	1 (6.66%)	0	3 (27.27%)	0	0	0	1 (5.55%)	1 (10%)	0
12	0	1 (7.14%)	3 (18.75%)	1 (6.66%)	0	2 (18.18%)	0	0	0	0	0	0
13	0	0	0	0	0	3 (27.27%)	0	0	0	2 (11.11%)	0	0
14	0	0	2 (12.50%)	0	0	0	2 (22.22%)	0	0	1 (5.55%)	0	0
<b>Total</b>	<b>3</b>	<b>14</b>	<b>16</b>	<b>15</b>	<b>3</b>	<b>11</b>	<b>9</b>	<b>14</b>	<b>2</b>	<b>18</b>	<b>10</b>	<b>4</b>

At the EDJ, and considering that this surface shows more variability than the enamel one, type 4 is the most common trigonid crest pattern for the total *H. sapiens* sample and for the TD6 M<sub>1</sub>s (66.66%) and M<sub>2</sub>s (100%). In SH, the most frequent type in M<sub>1</sub>s is type 8, and in Neanderthals it corresponds to type 10. Regarding the M<sub>2</sub> samples, the most frequent types in SH are type 11 and type 13 whereas in Neanderthals are type 7, 10 and 14. Regarding M<sub>3</sub>s, TD6

*neanderthalensis* respectively. Within the latter, it is worthy to mention the case of Hunas M<sub>3</sub>. This tooth seems to departure from the typical Neanderthal pattern by not showing a continuous trigonid crest. This would be in accordance with the warning that Kupczik and Hublin (2010) made about the taxonomic assignment of this specimen and calls for reassessment of this sample in the future.

Regarding the SH sample, it is important to remark that the types 3, 9 and 13 are exclusively present in the SH population and have not been found in the other three groups. For this reason, to date, these types of trigonid crests could be potentially considered as autapomorphic characters for the SH hominin samples, which would confirm the more derived state of this population with regard to *H. neanderthalensis* (Gómez-Robles et al., 2007, 2008; Gómez-Robles and Polly, 2012; Martín-Torres et al., 2012). However, future analysis of larger Eurasian Pleistocene samples will allow us to assess if this pattern is indeed exclusive to the SH group and to elucidate its evolutionary meaning.

Following other studies about other skeletal parts (Arsuaga et al., 1999; Carretero et al., 1999; Carbonell et al., 2005; Martín-Torres et al., 2006, 2007; Gómez-Robles et al., 2007; Bermúdez de Castro et al., 2012; Pablos et al., 2012; Lacruz et al., 2013) this study ratifies that in the dentition *H. antecessor* presents a mosaic of primitive and derived features, and that these features are polymorphic in nature. Most plesiomorphic features in TD6 regarding the *Homo* clade are found in the dentition (i.e. increasing size sequence for premolars and molars, asymmetry of the P<sub>3</sub> crown, abundant enamel crenulations, 5-cusped dryopithecus molars) (Bermúdez de Castro et al., 1999b; Bermúdez de Castro and Martín-Torres, 2013). However, TD6 hominins also present some derived dental traits that are exclusively shared with *H. neanderthalensis* such as the shape of lower second premolars and the upper first molar (Martín-Torres et al., 2006; Gómez-Robles et al., 2007). Regarding the presence/absence of a continuous mid-trigonid crest, *H. antecessor* (Fig. 4) would be closer to *H. sapiens* in presenting lower frequencies for this feature and in contrast with the high percentages in SH and *H. neanderthalensis*. In addition, *H. antecessor* does not display any of the types at the EDJ

(types 3, 9 and 13) that according to Martínez de Pinillos et al. (2014) are exclusive to the SH sample. Our study ratifies that the expression of a continuous mid-trigonid crest at both the OES and the EDJ is not a Neanderthal apomorphy but a symplesiomorphy that appeared in an ancestral population during the Early Pleistocene and became the typical Neanderthal condition by increasing its frequency in this lineage. This assumption is reinforced with the analysis of the left M<sub>1</sub>/M<sub>2</sub> from the Early Pleistocene African site of Mulhuli-Amo, Buia (1 ma) (Zanolli et al., 2014) that reveals the expression of a well developed continuous mid-trigonid crest (type 8 in Martínez de Pinillos et al., 2014). Moreover and according to Zanolli and Mazurier (2013) the number of molars from the early-Middle Pleistocene site of Tighenif, Algeria (700 kyr) with a continuous mid-trigonid crest at the EDJ (57.14%) is higher than the number of molars without it (42.85%). The absence of a continuous mid-trigonid crest in the specimens from late Early–early Middle Pleistocene site of Sangiran Dome (Central Java, Indonesia) (Zanolli, C., 2015) and from the Middle Pleistocene site of Hexian (Eastern China) (Xing, S. et al., 2014b), ratifies that the expression of a continuous trigonid crest pattern is more typical of the European Middle Pleistocene population and Neanderthals. However, in the lower right third molar (PA 1500) from the early-Late Pleistocene site of Xujiayao (Northern China) (Xing, S. et al., 2014a) while there is no mid-trigonid crest, a continuous distal trigonid crest is present (type 3 according to Martínez de Pinillos et al., 2014). This uncommon feature appears in the Middle Pleistocene fossils from SH (23.2%), Neanderthals (14.7%) and rarely in *H. sapiens* (2.98% according to Bailey et al., 2011), while there is no molar from Gran Dolina-TD6 with this pattern. More studies of ancient and late hominins from Asia are needed to better understand the morphological variability of the *H. erectus* species.

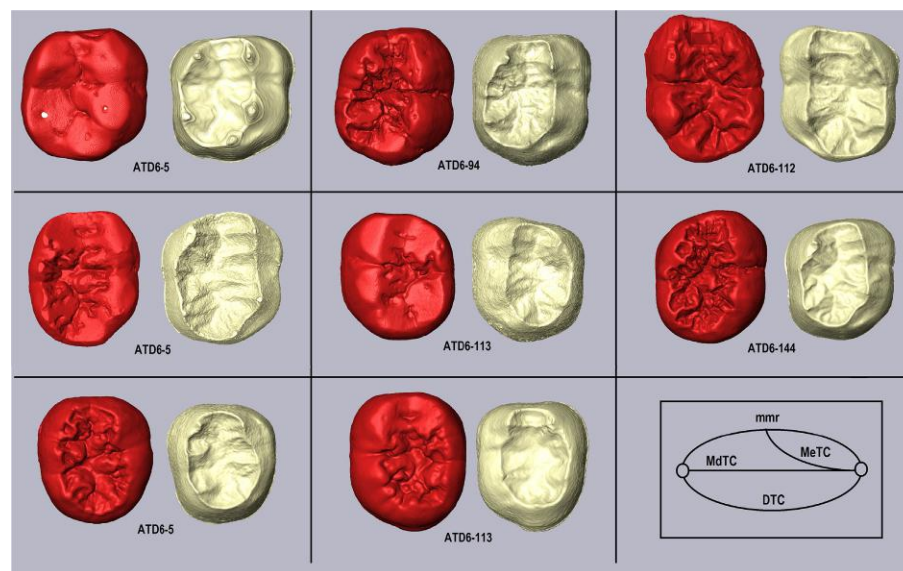


Fig. 4. Virtual reconstruction of the enamel and dentine surfaces for the TD6 M<sub>15</sub> (upper), M<sub>25</sub> (middle) and M<sub>35</sub> with schematic representation of the types of trigonid crests (lower), showing presence or absence of a continuous trigonid crests. Note that for our study we have considered that the trait "trigonid crest" is present only when the crest is continuous. However, we consider that the trait is absent if there is a total lack of a crest (grade 0 according to Bailey et al., 2011; see M<sub>2</sub> ATD6-5) or if the crest is discontinuous (grade 1 according to Bailey et al., 2011; see M<sub>2</sub> ATD6-144).

Overall, our results would be consistent with *H. antecessor* being close to the node of divergence between *H. neanderthalensis* and *H. sapiens* (Bermúdez de Castro and Martínón-Torres, 2013; Gómez-Robles et al., 2013).

Martínón-Torres et al. (2007a) defined an Eurasian dental pattern that was already present in the *H. antecessor* hominins, so far only found in the westernmost area of the European continent. Since then, further studies have investigated the feasibility of this scenario (Dennell et al., 2011; Martínón-Torres et al., 2011; Bermúdez de Castro and Martínón-Torres, 2013). Bermúdez de Castro and Martínón-Torres (2013) suggested the existence of an Eurasian clade, from where different hominin populations dispersed into Europe during the late Early and Middle Pleistocene. This clade would already express in different percentages a continuous mid-trigonid crest at both the enamel and the dentine surface, a feature that would later become the typical condition in *H. neanderthalensis*. This crest type seems to be present also in some Early and early Middle Pleistocene populations from Africa (Zanoli and Mazurier, 2013; Zanoli et al., 2014) although no other traits of the Eurasian dental pattern have been found in this continent.

Undoubtedly, additional comparative analysis of Eurasian and African Early Pleistocene hominins are necessary to test this hypothesis and thus to place *H. antecessor* in the phylogenetic tree.

### 5. Conclusions

Our results together with those obtained in previous studies reinforce the mosaic of primitive and derived features found in *H. antecessor* and that would be compatible with its phylogenetic position close to the node of divergence of *H. sapiens* and *H. neanderthalensis*. However, its location in the westernmost part of Europe suggests that TD6 hominins may represent an European branch of a cladogenetic event that occurred in a geographically more parsimonious area for the origin of both *H. sapiens* and *H. neanderthalensis*. *H. antecessor* might be one of the different migrations that dispersed from Asia or Africa into Europe during the Pleistocene. However, the access to a wider excavation area of the Gran Dolina-TD6 level in a near future will undoubtedly allow us to improve our understanding of this Early Pleistocene population variability.

Moreover and in concordance with previous research based on the dental morphology, the present study also confirms that SH population displays the typically Neanderthal trigonid crest pattern and, in some cases, it is even more derived as it displays some combinations that, to date, are exclusive to this group (Gómez-Robles et al., 2007, 2008, 2012; Martínón-Torres et al., 2012, 2014; Martínez de Pinillos et al., 2014). Future studies on other European Pleistocene hominins will allow a more precise evaluation of the variability of expression of this feature and to make phylogenetic and taxonomic inferences in relation with other ancestral hominins.

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### Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.quaint.2015.08.050>

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journal homepage: [www.elsevier.com/locate/quaint](http://www.elsevier.com/locate/quaint)*Homo antecessor*: The state of the art eighteen years later

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## ABSTRACT

It is eighteen years since the human fossils recovered from the TD6 level of the Gran Dolina cave site, in Sierra de Atapuerca (Burgos, northern Spain) were assigned to a new hominin species, *Homo antecessor*. This review summarizes the main results obtained from the study of these fossils during this period. The increase of the African and Eurasian fossil record, as well as the application of new methodological approaches, has led to competing interpretations about its hypothetical phylogenetic position and possible evolutionary scenarios. At present, we can argue that this species is defined by a unique mosaic of primitive traits for the *Homo* clade, a certain number of derived features present in modern humans, a significant suite of derived features shared with Neandertals and their ancestors in the European Middle Pleistocene (in particular with the Atapuerca-Sima de los Huesos hominins), and some derived features shared with the Chinese Middle Pleistocene hominins. From this evidence, we suggest that a speciation event could have occurred in Africa/Western Eurasia, originating a new *Homo* clade. *Homo antecessor*, most probably dated to the MIS 21, could be a side branch of this clade placed at the westernmost region of the Eurasian continent.

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## 1. Introduction

During the 1994 and 1995 field seasons, an assemblage of near ninety human fossil remains and about 150 Mode 1 artifacts were recovered from the so-called Aurora stratum of the TD6 lithostratigraphic unit (LU) of the Gran Dolina cave site in Burgos (Fig. 1), northern Spain (Carbonell et al., 1995, 1999). These findings occurred during the excavation of an archaeological test pit of about six square meters, made in order to evaluate the potential of the site. The first paleomagnetic studies revealed the presence of the Matuyama/Bruhnes reversal at the top of the TD7 LU, about 117 cm (cm) above the Aurora stratum (Parés and Pérez-González, 1995, 1999). The study of these human fossils evinced a unique combination of primitive and derived features regarding the *Homo* clade,

and we proposed a new *Homo* species, *H. antecessor* (Bermúdez de Castro et al., 1997).

It has been nearly 18 years since this proposal. In this period, another sixty human fossils were obtained in TD6 from a small area near the test pit made during the nineties of the twentieth century. During this excavation, the stratigraphic sequence of TD6 was refined (see Bermúdez de Castro et al., 2008a,b and Figs. 2 and 3) and new additional geochronological information is available from the Gran Dolina site (see below). Furthermore, new studies have been made from the TD6 human fossils. These studies, the finding of new African and Eurasian human remains (e.g. Abbate et al., 1998; Manzi et al., 2001; Asfaw et al., 2002; Gabunia et al., 2002; Macchiarelli et al., 2004; Lumley and Lordkipandize, 2006; Carbonell et al., 2008; Kappelman et al., 2008; Carretero et al., 2009; Krause et al., 2010; Viallet et al., 2010; Bermúdez de Castro et al., 2011; Roksandic et al., 2011; Liu et al., 2013; Toro-Moyano et al., 2013; Arsuaga et al., 2014; Xing et al., 2014, 2015) as well as the reinterpretation of specimens recovered in the past (e.g. Manzi et al., 2003; Mounier et al., 2009; Manzi et al., 2010; Stringer, 2012; Liu et al., 2013) have offered a considerable amount of information to reconsider our first proposal and to look for alternative and

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Fig. 1. The Gran Dolina cave site is about 27 m deep. The lower two thirds of the sequence belong to the Lower Pleistocene. A test pit made between 1993 and 1999, as well as a vertical cut of the entire sequence allowed to found the human fossils from the TD6 level (see arrow and Fig. 2).

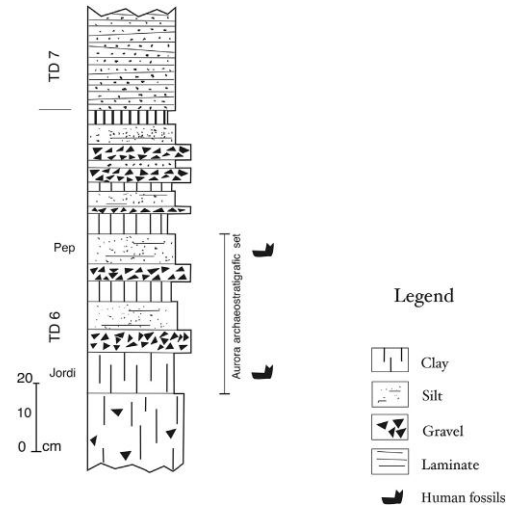


Fig. 2. Upper sequence of the lithostratigraphic unit TD6 from the Gran Dolina cave infilling (Matuyama Chron), which includes the “Aurora archaeostratigraphic set” (AAS), also known as TD6-2. All the human fossils of the *H. antecessor* hypodigm have been recovered from this section of the unit TD6. The AAS is not well defined as a sequence of different layers on the test pit performed in the 1994–1996. Thus, the AAS corresponds to what was named “Aurora stratum” during the first excavations (Carbonell et al., 1995). Modified from Bermúdez de Castro et al., 2008a).

possibly complementary hypotheses (e.g. Bermúdez de Castro et al., 2003; Martínón-Torres et al., 2007; Bermúdez de Castro et al., 2008a,b; Endicott et al., 2010; Martínón-Torres et al., 2011; McDonald et al., 2012; Bermúdez de Castro and Martínón-Torres, 2013).

In this review, we present a summary of the main results presented so far about the TD6 hypodigm, as well as the different interpretations made on the meaning of these hominins in the context of the African and Eurasian human evolution. It is important to note that a certain number of new analyses of the TD6 hominins are in progress, which undoubtedly will offer additional information to test our hypothesis. Furthermore, in a near future the present Atapuerca Research Team will have access to a wide area of the different thin sublevels forming the Aurora archaeostratigraphic set (also named TD6-2). This will be an opportunity to increase our knowledge of this hominin population, who lived in Western Europe during the late Early Pleistocene.

2. The TD6 level

The Gran Dolina cave site (TD) fills up a large cavity about 27 m deep and with a maximum width of 17 m (see Fig. 3 in Bermúdez de Castro et al., 2013). The stratigraphic section of the site was cut and exposed by the construction of a railway trench. Gil and Hoyos

(1987) divided this section from bottom to top into eleven levels: TD1 to TD11. However, the stratigraphy of the Gran Dolina site is under continuous refinement. There is a vertical cut of the section in progress, (e.g. Bermúdez de Castro et al., 2008a). In addition, we are currently studying a wide pit about 10 m deep excavated below the present level of the ancient railway (see Fig. 1). Parés and Pérez-González (1995, 1999) observed a polarity reversal between TD7 and T8, interpreted as the Matuyama/Brunhes boundary, meaning that levels TD8–TD11 were deposited during the Middle Pleistocene, whereas levels TD7–TD1 were attributed to the Early Pleistocene. This finding is consistent with the change in the fossil record of large- and micromammals, with a transition in TD6-2 (Faunal Unit 4), TD7–TD8 (Faunal Unit 5) and drastic change in TD9–TD11 (Faunal Unit 6) (Cuenca-Bescós and García, 2007; Cuenca-Bescós et al., 2010). Pollen analysis of TD6 (García-Antón, 1989) suggests a Mediterranean climate for this level, whereas the study of the amphibian and squamate reptile fossil record (Blain et al., 2009) of TD6-2 also suggests a slightly warmer temperature than today in Burgos.

The combination of paleomagnetic data and US–ESR ages suggest a range between 0.78 and 0.86 Ma (million years ago) for TD6-2 (Falgüeres et al., 1999). Thermoluminescence (TL) ages (Berger et al., 2008) on samples taken 1 m below the Brunhes/Matuyama boundary (0.78 Ma) give an age of  $0.96 \pm 0.12$  Ma for TD6, which may correspond to MIS 25. The last systematic dating of the Gran Dolina sequence has been made by Moreno (2011) using the ESR dating method on optically bleached quartz. This author analysed six samples for TD6 and TD7, obtaining an age range of 0.80–0.88 Ma for these levels, which is consistent with the biostratigraphic and paleomagnetic analyses and suggest that the human assemblage was deposited during MIS 21.

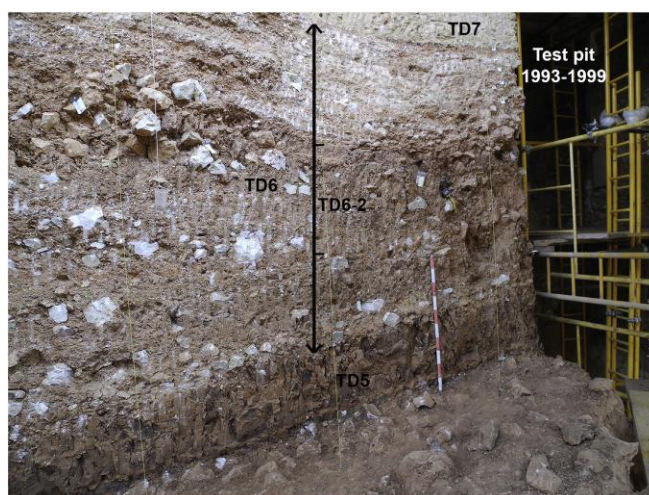


Fig. 3. Vertical cut of the Gran Dolina site, pointing the position of the TD7, TD6, and TD5 levels. The scaffold is placed in the hollow left by the test pit made between 1993 and 1999.

3. Materials and methods

3.1. The TD6 human remains

The human remains from TD6b are in good preservation, although the majority of them are fragmentary due to clear events of cannibalism (Fernández-Jalvo et al., 1999; Carbonell et al., 2010). Nevertheless, we recorded and analyse a number of cranial and postcranial features, mainly from the teeth, the mandibles and the face. Postcranial remains are also numerous and represent different anatomical elements, including nearly twenty-five hand and foot remains.

In this synthetic review we provide an overview of the information obtained from the study of the different cranial, and postcranial features observed in *H. antecessor*, carried out by Arsuaga et al. (1999), Carretero et al. (1999), Lorenzo et al. (1999), Rosas et al. (1999), Carbonell et al. (2005), Bermúdez de Castro et al. (2008a,b), Bermúdez de Castro et al. (2012) and Pablos et al. (2012). Concerning teeth, their crown and root morphology have been analysed in previous studies (Bermúdez de Castro et al., 1997; Bermúdez de Castro et al., 1999; Bermúdez de Castro et al., 2003; Carbonell et al., 2005; Bermúdez de Castro et al., 2008a,b; Martínón-Torres et al., 2006, 2007; Gómez-Robles et al., 2007, 2008, 2011, 2011, 2012).

3.2. Minimum number of individuals (MNI)

In previous studies we assessed the possible minimum number of individuals (MNI) currently represented in the TD6 hypodigm (e.g. Bermúdez de Castro et al., 2006). However, due to the considerable fragmentation of the hominin remains, this aspect remains difficult. Furthermore, the six sublevels (generally less than 10 cm) identified during the last excavations (Bermúdez de Castro et al., 2008a,b) are condensed near the wall of the cave, where the test pit was made during the nineties. Then, it was not possible to state the precise provenance of each of the human remains found in the test pit in correlation with the six levels, which were deposited in at least two different time events. Although we suspect that the MNI is higher than the estimation presented in Table 1, in this paper we prefer to be conservative and to avoid speculations with the association of some isolated permanent and deciduous specimens. The present TD6 hypodigm includes four isolated deciduous teeth, two permanent Incisive germs and two permanent complete lower incisors, some of which could represent additional immature or adult individuals. Summarizing, and considering that we have excavated only a small area of the TD6 level, our conclusions on the MNI are preliminary, except for the remarkable presence of a high percentage of immature individuals in the TD6 hypodigm (75%). The age at death of the individuals presented in Table 1 is only an indicative approach. We have used modern human standards with the aim of determining the MNI, but we are aware that this model may not apply for this Early Pleistocene population.

Table 1  
List of the individuals represented in the TD6 hominin hypodigm.

Hominin	Inventory number	Specimen	Age at death <sup>a</sup>
H1	ATD6-1	Left lower C	13.5–14.5
	ATD6-2	Left I <sub>2</sub>	
	ATD6-3	Right P <sub>3</sub>	
	ATD6-4	Right P <sub>4</sub>	
	ATD6-5	Right mandible fragment with M <sub>1</sub> –M <sub>3</sub> in-situ	
	ATD6-6	Fragment of crown of right lower C	
	ATD6-7	Right P <sub>3</sub>	
	ATD6-8	Right P <sub>4</sub>	
	ATD6-9	Left P <sub>4</sub>	

Table 1 (continued)

Hominin	Inventory number	Specimen	Age at death <sup>a</sup>
	ATD6-10	Right M <sup>1</sup>	
	ATD6-11	Left M <sup>1</sup>	
	ATD6-12	Right M <sup>2</sup>	
H2	ATD6-14	Left maxillary fragment, with dc–dm <sup>1</sup> in-situ	3.5–4.0
H3	ATD6-69	Maxilla and left zygomatic bone, including: left P <sup>3</sup> , M <sup>1</sup> , and unerupted M <sup>2</sup> , and right I <sup>2</sup> –M <sup>1</sup>	10.0–11.0
H4	ATD6-125	Right P <sub>4</sub>	13.5–14.5
H5	ATD6-94	Right M <sub>1</sub>	about 6.0
	ATD6-103	Right M <sup>1</sup>	
H6	ATD6-96	Left half mandible, including P <sub>3</sub> –M <sub>3</sub> in-situ	About 17.0
H7	ATD6-113	Fragment of the left half of a mandible including M <sub>2</sub> and M <sub>3</sub> in-situ.	About 17.0
H8	ATD6-112	Right part of the mandibular corpus, from the symphysis to the crypt of the M <sub>2</sub>	3.5–3.9

<sup>a</sup> In years, and according to modern human patterns of dental development (see Bermúdez de Castro et al., 1999).

4. Results of the main studies performed in the TD6 human fossils

In Tables 2, 3, and 4 we present the state (primitive or derived) of the main features identified so far in the TD6 hypodigm. The state of these features is evaluated in relation to the *Homo* clade.

associated anterior flexion of the maxillary surface near the nasal aperture. This last feature suggests that nose was projecting in ATD6-69. Arsuaga et al. (1999) conclude that the derived sapiens-like midfacial topography of ATD6-69 is not present in early *Homo* (i.e. *H. habilis*, *H. rudolfensis*) and *H. ergaster* (or African *H. erectus*). Interestingly, ATD6-69 shows a modern human pattern of dental

Table 2

Derived features shared by *H. antecessor* with modern humans.

- Face: – coronal orientation of the infraorbital surface, inferoposterior slope of this surface (with the canine fossa), anterior flexion in the maxillary surface and arcing of the zygomatico-alveolar crest, a projecting nose, and a zigomaxillary tubercle.
- Face: – modern (*H. sapiens*) growth remodelling pattern.
- Skull: – convex superior border of the temporal squama.
- Maxilla: – anterior position and almost vertical trajectory of the incisive canal.

Table 3

Primitive features of *H. antecessor* regarding the *Homo* clade.

- Lower premolars: – complex occlusal and root morphology, asymmetry of the crown, large talonid, and presence of cingulum.
- Permanent upper and lower molars: M<sub>2</sub> > M<sub>1</sub>.
- Permanent upper second molar: four well developed cusps.
- Permanent molars: complex occlusal enamel crenulation pattern.
- Mandible:
  - position of the mental foramen.
  - position of the lateral prominence.
  - position of the mylohyoid line in relation to alveolar margin at M<sub>3</sub> level.
  - trajectory of the mylohyoid line in relation to alveolar margin.
  - relief of the pterygoid fossa.
  - intersection between mandibular notch and condyle.
- Radius: absolutely and relatively long radial neck.

Table 4

Derived features shared by *H. antecessor* with Neandertals and Middle Pleistocene Atapuerca-SH hominins.

- Mandible: presence of the medial pterygoid tubercle.
- Mastoid region: small and minimally projecting mastoid process and the anteriorly obliterated digastric groove.
- Permanent lateral upper incisors: marked shovel shaped (Eurasian pattern).
- Permanent lower fourth premolars: reduced occlusal polygon.
- Permanent upper first molar: rhomboidal and compressed occlusal polygon and a skewed external outline with a bulging protrusion of the hypocone.
- Clavicle: – absolutely very long (maximum length), relatively slender (low robusticity index), pronounced shaft curvature, and relatively small epiphyses.
- Humerus: – large olecranon fossa and very thin medial and lateral pillars.
- Talus: – relatively narrower trochlea (only shared with Neandertals).

The finding that the TD6 hominins exhibit a sapiens-like midfacial morphology was surprising (Bermúdez de Castro et al., 1997; see Table 2). Arsuaga et al. (1999) made the first detailed study of the midface of the immature specimen ATD6-69 (H3). These authors described this specimen as having a coronal orientation of the infraorbital surface, an inferoposterior slope of this surface (with the development of a canine fossa), arcing of the zygomatico-alveolar crest, a forward position of the nasal aperture, and

development (Bermúdez de Castro et al., 1999b). Lacruz et al., (2013) have showed close similarities between ATD6-69 and *H. sapiens* regarding the facial growth remodeling pattern. This pattern is totally different from the presumed primitive pattern of the *Homo* clade, observed in the specimen KNM-WT 15000. Another subadult specimen, ATD6-38, which is similar in size and shape to ATD6-69, also presents canine fossa (Arsuaga et al., 1999). Furthermore, the adult specimen ATD6-58, represented by a left

large zygomaxillary fragment, exhibits a remarkable canine fossa, as well as a great zygomaxillary tubercle placed in a maxillary position, that projects out about 3.3 mm (Arsuaga et al., 1999). Finally, an adult small zygomaxillary fragment (ATD6-19) also shows a zygomaxillary tubercle in the same position, which projects out about 2.0 mm (Arsuaga et al., 1999). These authors suggest that the zygomaxillary tubercle may be present in the Zhoukoudian maxilla II. Thus, the Zhoukoudian and the TD6 hominins would represent the unique presence of this facial feature prior to the Late Pleistocene (Arsuaga et al., 1999). Furthermore, Vialet et al. (2010) have identified a facial pattern in the Chinese Middle Pleistocene specimens, Yunxian II and Nankin 1, that is similar to that presented by modern humans. Regarding all these results and since the African origin of our species seems to be undisputed for the majority of paleoanthropologists, the presence of a modern-like human face in *H. antecessor* has been the subject of interest of some other researchers (e.g., Freidline et al., 2013). The latter made an interesting theoretical ontogenetic study of the ATD6-69 face by means of 3D geometric morphometric analyses, with reference data mainly from Neandertals and modern humans. Freidline et al. (2013) concluded that ATD6-69 exhibits a modern-like human midfacial morphology, although their analyses placed ATD6-69 near the margin of modern human variation and intermediate between the modern humans and Middle Pleistocene human samples. According to these authors, the face of this individual would not have been significantly altered in the course of the subsequent development.

Finally, and concerning the skull features, the TD6 hominins share with Neandertals and modern humans a convex superior border of the temporal squama, as well as an anterior position of the incisive canal, which is nearly vertical (Arsuaga et al., 1999). These authors also concluded that the TD6 hominins show a small and minimally projecting mastoid process and the anteriorly obliterated digastric groove, a feature shared with Neandertals (Table 4).

Some of the mandibular features are primitive regarding the *Homo* clade (Table 3). However, in ATD6-96 and ATD6-113 the M3 is only partially covered by the ramus, the retromolar area is oblique, the relief of the masseteric fossa is shallow, and the posterior subalveolar fossa is moderately hollowed. In these mandibles, as well as in ATD6-5 there is no alveolar prominence and the angle of inclination of the mylohyoid groove is clearly lesser than 50°. In all these features, the *H. antecessor* mandibles are derived in relation to the earliest African *Homo* mandibles, as well as in relation to the earliest Javanese *H. erectus*. Furthermore, the small height and breadth of the *H. antecessor* mandibles contrast with the large dimensions of most African *Homo* specimens (except KNM-ER 1501 and OH 13), as well as with those of Sangiran 5, 8, 9, Hexian, Tighenif 1, 2, and 3, Sidi Abderrahman, and Arago 13. Moreover, the height of TD6 mandibles is lower than in the European Middle Pleistocene hominins and the Neandertals (see Table 2 in Rosas and Bermúdez de Castro, 1999). In this respect, *H. antecessor* is clearly derived, sharing their gracility with most Chinese Middle Pleistocene hominins (Carbonell et al., 2005). The mandible ATD6-96 exhibits a hypertrophied medial pterygoid tubercle (Carbonell et al., 2005; Bermúdez de Castro et al., 2012), a feature that has been included in the list of Neandertal apomorphies (Rak et al., 1994; Weaver, 2009).

Concerning teeth, the *H. antecessor* permanent lower and upper canines are derived regarding the *Homo* clade (see Martínón-Torres et al., 2008). However, they retain a vestigium of a cingulum and present conspicuous essential ridges, unlike European Middle Pleistocene hominins and *H. neanderthalensis*. The two *H. antecessor* P<sup>3</sup>s (ATD6-7 and ATD6-69) show an incipient derived morphology regarding the *Homo* clade. These teeth show a relatively reduced lingual cusp and a nearly symmetric shape, although

not as pronounced as in the Middle and Late Pleistocene hominins (Gómez-Robles et al., 2011). The P<sup>4</sup> in *H. antecessor* (ATD6-8, ATD6-9, and ATD6-69) is more derived than the P<sup>3</sup>, similar to that of Asian *H. erectus*, *H. neanderthalensis* and Atapuerca-SH hominins, but primitive regarding *H. sapiens*. The buccal surface of upper premolars show also a vestigium of a cingulum and several longitudinal grooves that resemble that of other Early and Middle Pleistocene fossils from Asia (except for Panxian Dadong, see Liu et al., 2013) and Africa but not from Europe (Martínón-Torres et al., 2011; Xing et al., 2014, 2015). Both the crown and root of the P<sub>3</sub> are remarkably primitive (Bermúdez de Castro et al., 1999; Gómez-Robles et al., 2008) and different from the European Middle Pleistocene hominins, Neandertals and *H. sapiens*. Although the *H. antecessor* P<sub>4s</sub> (ATD6-4 and ATD6-96) exhibit a primitive morphology, with an elongated, subrectangular outline and a mesially displaced metaconid, they also show a reduced occlusal polygon. *H. antecessor* shares this feature with *H. neanderthalensis* and the European Middle Pleistocene hominins (Martínón-Torres et al., 2006; see Table 4). The permanent upper first molars (ATD6-18, ATD6-69, and ATD6-103) share their conformation with Neandertals and some (but not all, e.g. Arago) European Middle Pleistocene hominins (but see Martínón-Torres et al., 2013 for differences in cusp proportions). This morphology includes a rhomboidal and compressed occlusal polygon and a skewed external outline with a bulging protrusion of the hypocone (Gómez-Robles et al., 2007). The reduced occlusal polygon of the P<sub>4</sub> in *H. antecessor* is another feature shared with *H. neanderthalensis* and the European Middle Pleistocene hominins (Martínón-Torres et al., 2006). In addition, upper lateral incisors from TD6 display a triangular shovel shape, with pronounced labial convexity (Martínón-Torres et al., 2007). This feature is part of the Eurasian dental pattern (Martínón-Torres et al., 2007) shared with Asian and European Early and Middle Pleistocene hominins and Neandertals (Table 4). Finally, and although the primitive M<sub>2</sub> > M<sub>1</sub> is the standard in both the maxillary and mandibular molar series, the strong size reduction of the lower M<sub>3</sub> is remarkable in the ATD6-96 mandible.

Lorenzo et al. (1999)'s conclusions about the study of the hand and foot remains suggest that the TD6 hominins exhibit a morphology more similar to modern humans than that of Neandertals and their predecessors from the European Middle Pleistocene. The long bones are fragmentary and their study (Carretero et al., 1999; Pablos et al., 2012) yielded some interesting indications about the phylogenetic position of the TD6 hominins (Tables 2 and 4). Thus, the clavicle ATD6-50 is described by Carretero et al. (1999) as "absolutely very long (maximum length), relatively slender (low robusticity index) and with pronounced shaft curvature and relatively small epiphyses", sharing its morphology with Neandertals. Similarly, the humeri ATD6-121 (subadult) and ATD6-148 (adult) exhibit a large olecranon fossa and very thin medial and lateral pillars, sharing these features with European Middle Pleistocene hominins, Neandertals and, interestingly, with the Bodo Middle Pleistocene humerus (Carretero et al., 2009; Bermúdez de Castro et al., 2012). Finally, the talus shows relatively narrower trochlea, a feature only shared with Neandertals (Pablos et al., 2012).

## 5. Discussion

Although the number of specimens of the TD6 hypodigm is still limited, there is enough information to offer proposals about the hypothetical phylogenetic position of *H. antecessor*. We expect that this information will be greatly increased in a near future, when we excavate the majority of the TD6-2 level (about 80 square meters).



The former hypothesis that *H. antecessor* could represent the last common ancestor of *H. neanderthalensis* and *H. sapiens* (Bermúdez de Castro et al., 1997) was formulated mainly due to the presence of a modern-like face in the TD6 hypodigm. However, the geographic position of the Iberian Peninsula in the westernmost extreme of the Eurasian continent, as well as the geological age of the TD6 level pose some difficulties to conciliate with the present paradigm about the origin of our species. In fact, genetic data point to a more recent divergence of modern humans and Neandertals (e.g. Noonan et al., 2006; Endicott et al., 2010; Krause et al., 2010). The molecular analyses made by Endicott et al. (2010) for the MCRA support the hypothesis of a widely-dispersed ancestral species during the middle part of the Middle Pleistocene, and a split that would have occurred in a time range between 0.34 and 0.54 Ma, with a mean age of 0.43 Ma. According to these authors, the split might have coincided with the severe climate of MIS 12 (ca. 0.48–0.42 Ma). Other results, however, suggest dates near to the MIS 21 (Ovchinnikov et al., 2002; Green et al., 2008; Langergraber et al., 2012). Concerning the genetic approach there is no consensus about the best method. Thus, recent analyses by Fu et al. (2013) suggest a nuclear substitution rate that is approximately half that of previous estimates based on fossil calibration. Therefore, and according to these authors, major events in human evolution occurred far earlier than previously thought. However, other specialists consider that the rate of mutation is slower than assumed so far and thus, it would affect the hypothetical split of hominin lineages (Hawks, 2012; Scally and Durbin, 2012). In consequence, it may be recommendable to wait for an agreement before using genetics arguments favouring or rejecting hypotheses on the split time of Neandertals and modern humans.

Concerning the modern-like face of *H. antecessor*, Freidline et al. (2013) proposed that evolution of modern-like facial morphology occurred independently in Africa, Asia and Europe and several times during the Early and the Middle Pleistocene. Freidline et al. (2013)'s evolutionary interpretation of ATD6-69 is clearly influenced by the most commonly accepted paradigm that the root of *H. sapiens* lies in the African Middle Pleistocene populations (e.g., Stringer and Andrews, 1988). However, their interpretation has been replied by Bermúdez de Castro and Martínón-Torres (2014). As we have previously explained (Bermúdez de Castro et al., 2003) and we also defend in this review, we agree that Gran Dolina-TD6 hominins may not represent the origin of modern human populations but a side branch restricted to Western Europe. However, from a cladistic point of view this lineage would stem out very close to the last common ancestor of *H. sapiens* and *H. neanderthalensis*.

On the other hand, we have showed that the hominins recovered from the Sima del Elefante cave site (TE9 level), dated to about 1.1–1.2 Ma (Carbonell et al., 2008) and only 500 m far from Gran Dolina, may represent a previous and different population dispersal than that represented in TD6. Since the TE hominin sample is very limited (Bermúdez de Castro et al., 2011; Martínón-Torres et al., 2011; Prado-Simón et al., 2011, 2012; Lorenzo et al., 2015) it is not possible to draw sound conclusions from the anatomical comparisons with the TD6 hominins. However, differences in the inferred behaviour and knapping strategies has led us to propose that the TE9 and TD6 hominins can belong to two different migrations into Western Europe (Bermúdez de Castro et al., 2013). Waiting for new evidence, the TE9 hominins have been assigned to *Homo* sp. (Bermúdez de Castro et al., 2011). In contrast to TE remains, the TD6 hominins exhibit enough information to posit phylogenetic hypotheses. They show a certain number of derived features, mainly shared with Eurasian hominins and, in particular, with the Middle Pleistocene and early Late Pleistocene populations. In this context, it is surprising the relatively high number of features exclusively

shared with Neandertals and with the Atapuerca-SH hominins (Table 4).

Gómez-Robles et al. (2013) have studied the dental morphology of a large sample of hominins by combining 2D geometric morphometrics method with the GLM method for estimating ancestral traits (e.g. Martins and Hansen, 1997; Polly, 2008). These authors concluded that no known fossil species is a suitable candidate for being the last common ancestor of Neandertal and modern humans. Thus, they exclude *H. antecessor*, but also other species like *H. heidelbergensis*. Since all the European hominins posterior to 1.0 Ma exhibit "Neandertal features" they consider the possibility that molecular estimates of the divergence between Neandertals and modern humans may be underestimated. We agree with this conclusion although, as we stated above, the time of divergence of different lineages using genetic estimations ought to be considered with caution. A second hypothesis suggested by Gómez-Robles et al. (2013) points to the possibility that the divergence in dental features between Neandertals and modern humans significantly predates the complete speciation. This decoupled phenotypic differentiation would have affected the dentition, but no other cranial and postcranial features. However, we have confirmed that *H. antecessor* shares some neurocranial, mandibular, and postcranial features with the Atapuerca-SH hominins and the Neandertals (Table 4). These features would be not Neandertal apomorphies, but traits appeared in an ancestral and polymorphic population during the Early Pleistocene (Bermúdez de Castro et al., 2012; Bermúdez de Castro and Martínón-Torres, 2013; Bermúdez de Castro et al., 2014).

The TD6 hominins exhibit a suite of features lost in their African ancestors and in the Dmanisi hominins (e.g. Martínón-Torres et al., 2008; Rightmire et al., 2008; Bermúdez de Castro et al., 2014). Moreover, the dental features are in line with the Eurasian pattern suggested by Martínón-Torres et al. (2007). Although the TD6 hominins show a significant number of derived features shared with Neandertals and modern humans, the hypothesis that *H. antecessor* represent the last common ancestor of both hominin lineages is not fully supported according to the dental morphology (Gómez-Robles et al., 2013), or the geographic location of the Sierra de Atapuerca. Nevertheless, all the evidences need to be reconciled in a credible scenario. Bermúdez de Castro and Martínón-Torres (2013) have presented this scenario considering geographic and climatic factors (see also Dennell et al., 2011; Martínón-Torres et al., 2011). Since it seems unlikely that Neandertal roots can stretch back as deep as 1.0 Ma, we favour the existence of a Eurasian clade. This clade would be the origin of some waves of populations into Europe during the late Early Pleistocene and the Middle Pleistocene. We also suggest that the settlement of Europe was complicated by climatic and geographic factors, favouring isolation and possible hybridation between paleodemes, including the first residents. This scenario would explain the considerable diversity observed in the European fossil record, evinced in the human samples recovered from Ceprano, Arago, Sima de los Huesos or Mala Balanica (e.g. Manzi, 2001; Roksandic et al., 2011).

Since the most accepted theory in the present paradigm is that modern humans originated in Africa and the lineage of Neandertals developed in Europe, the physical and genetic divergence of the two populations might have occurred either in Europe or in Africa. The latter has been the preferred option of many colleagues, perhaps because Africa has been traditionally considered as the source of different migrations towards the Eurasian continent (e.g. Stringer and Hublin, 1999; Hublin, 2009; Mounier et al., 2009; Abbate and Sagri, 2011). In parallel with the current paradigm concerning the origin of modern humans (Stringer and Andrews, 1988) it has also been suggested that the ancestors of

Neandertals come from a significant out of Africa dispersal during the Middle Pleistocene (Krause et al., 2010).

Nevertheless, and as we have stated in previous studies (Martinón-Torres, 2011; Bermúdez de Castro and Martinón-Torres, 2013), Southwest Asia represents a suitable region for the evolution of hominins during the entire Pleistocene (Hughes et al., 2007, 2008; Almogi-Labin, 2011). Furthermore, the Levantine Corridor is a geographical crossroad between continents, and has been identified as a true biodiversity hotspot (Carrión et al., 2011). This means that this region can be a source of phylogenetic diversity, inducing speciation and reduced extinction rates (Kingston, 2007; Spathelf and Waite, 2007; Ricklefs, 2010). Western Eurasia could be then the homeland of an early hominin population, origin of several migrations into Europe during the late Early and Middle Pleistocene. Rightmire (1998) suggested that a speciation event occurred in Africa during the very early Middle Pleistocene from *Homo erectus* s.l. This author identified the speciation event with the *H. heidelbergensis* species, and stated that it would be represented in both Africa (e.g., Bodo) and Europe (e.g., Petralona). During the late Middle Pleistocene, either in Africa or Western Eurasia, *H. heidelbergensis* species would have separated in would have splitted into two branches, leading to the modern humans and Neandertal lineages in Africa and Europe, respectively (Rightmire, 1998).

We agree with Rightmire (1998) in the general idea that there was an early speciation process during the Pleistocene. However, evidence from TD6 would push back in time this event. Also interesting in this topic, is the inclusion of Western Eurasia in the Rightmire's scenario as the possible region for the splitting of modern humans and Neandertals. In our view, the Western Eurasian–African region could have been connected at least until the so-called Middle Pleistocene Transition (MPT: 1.25–0.7 Ma) throughout the Levantine Corridor, yielding support to the physical and genetic continuity of this hypothetical African–Western Asian population. This is a prerequisite for the splitting sometime of the modern human and Neandertal lineages. According to new evidences (e.g. Arnold, 2014; Arsuaga et al., 2014) and putting aside the ongoing debates about the interpretation of the genetic data (see above), this splitting might have occurred earlier than assumed by Rightmire (1998). Furthermore, the Rightmire (1998)'s scenario might be more complex, with the possible formation of different Eurasian lineages during the Middle Pleistocene. Moreover and regarding these questions, future comparative studies with African late Early Pleistocene human fossils (Abbate et al., 1998; Manzi et al., 2003; Macchiarelli et al., 2004; Zanolli et al., 2014) would shed light to test this evolutionary scenario.

Concerning the geographic aspect of this scenario, it is very interesting the O'Regan et al. (2011)'s review on the Afro-Eurasian large-mammals dispersals during the Plio-Pleistocene. In their review, these authors conclude that the majority of the large-mammals migrations out of Africa occurred prior to 3.0 Ma or between 1.8 and 1.3 Ma. Later mammal movements out of Africa were possibly sporadic. The faunal record of Western Europe from 1.2 Ma onwards suggests transversal dispersals of large mammals originating in Asia (Crégut-Bonnoure, 1992 a,b; Kahlke, 1992; Kalkhe et al., 2011, 2011; Carrión et al., 2011; van der Made, 2011), obviously favoured by similar climatic conditions in Eurasia during the late Early and Middle Pleistocene. O'Regan et al. (2011) also conclude that a relatively small number of African Pleistocene taxa emigrate into Eurasia, and *viceversa*. The suggestion made by Clarke (2000) that the first Eurasian hominins could have moved back into Africa is a very interesting idea, also considered by Manzi (2004), Dennell and Roebroeks (2005), Rightmire et al., (2006), Martinón-Torres et al. (2007, 2008). These hypothetical population movements in both directions through the Levantine Corridor may have

diminished or ceased due to the worsening climate occurred during the MTP (see a detailed discussion in Bermúdez de Castro and Martinón-Torres, 2013 and references therein on geographical and climatic aspects of the region). The climatic changes associated to the MTP might be the main mechanism behind the physical separation of the African/Western Eurasian population, previously connected through the Levantine Corridor during the Early Pleistocene. This separation would have preceded the genetic divergence leading to modern humans and Neandertals.

## 6. Concluding remarks

*H. antecessor* exhibits a unique and very interesting mosaic of primitive and derived features. A significant number of derived features in this species points to a certain relationship with the modern human and Neandertal lineages. In order to reconcile these observations with the present fossil record, we suggest that *H. antecessor* could represent one of the successive waves of populations, which settled Europe during the Pleistocene and splitted away from an early population probably living in Western Eurasia or in Africa/Western Eurasia. This early population would be the result of a cladogenetic event occurred during the late Early Pleistocene. For this review, we prefer to avoid taxonomical questions about this hypothetical population, and we are aware that some colleagues may identify this cladogenetic event with *H. erectus* s.l.

Palaeogenetic studies ought to be refined in order to reduce the time range for the physical and genetic divergence of the modern humans and Neandertal lineages. However, we consider that this event occurred during the evolution of this hypothetical population. Independently from the name we could assign to the last common ancestor of Neandertals and modern humans, and according to the present evidence observed in the TD6 hominins, both lineages would belong to the same clade of *H. antecessor*. The recent genetic and morphological observations on the Atapuerca-Sima de los Huesos hominins (Meyer et al., 2014; Arsuaga et al., 2014) are very promising for understanding the evolutionary scenario in Europe.

As a corollary of this report, we consider that the variability observed in Asia (Anton, 2003; Vialet et al., 2010; Liu et al., 2013; Xing et al., 2014, 2015) ought to be reconsidered. Independently from taxonomical questions, the settlement of the Asian continent might have occurred during the Early and Middle Pleistocene from some successive migration population waves, some of them probably coming from Western Eurasia as well. Future comparative studies between *H. antecessor* and other Middle Pleistocene European hominins with the Chinese fossil record could shed light on these open questions.

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## BRIEF COMMUNICATION

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## Early Pleistocene hominin deciduous teeth from the *Homo antecessor* Gran Dolina-TD6 bearing level (Sierra de Atapuerca, Spain)

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### Abstract

**Objectives:** During the last 13 years, the late Early Pleistocene Gran Dolina-TD6-2 level (Sierra de Atapuerca, northern Spain) has yielded an additional sample of 26 dental specimens attributed to *Homo antecessor*. In this report, we present a descriptive and comparative study of the six deciduous teeth.

**Methods:** We provide external and internal morphological descriptions following classical terminology, as well as the mesiodistal and buccolingual measurements of the teeth. The internal morphology was described by means of micro-CT technique.

**Results:** The TD6 deciduous teeth preserve primitive features regarding the *Homo* clade, such as the presence of styles in lower and upper canines and developed anterior and posterior foveae in the dm<sub>2</sub>. However, other features related to the complexity of the crown morphology (e.g., cingulum) are not present in this sample. Furthermore, the great reduction of the talonid of the dm<sub>2</sub>s is also noteworthy. Despite the limited comparative evidence, the presence of a remarkably well-developed tuberculum molare in the dm<sup>1</sup> and dm<sub>2</sub>s from TD6 can be also considered a derived feature in the genus *Homo*. The TD6 hominins exhibit dental dimensions similar to those of other Pleistocene hominins. The dm<sub>2</sub>s are buccolingually elongated and the buccolingual diameter of ATD6-93 is the largest recorded so far in the *Homo* fossil record.

**Conclusions:** This study expands the list of plesiomorphic features of *H. antecessor*, and provides some information on the evolutionary status of this species. However, the identification of some advanced traits evinces a step towards the derived morphology of European Pleistocene teeth. The study of the deciduous dentition confirms the mosaic pattern of *H. antecessor* morphology revealed in previous studies of this hominin sample.

### KEYWORDS

deciduous teeth, *Homo antecessor*, Sierra de Atapuerca



## 1 | INTRODUCTION

The presence in the hominin fossil record of deciduous teeth is limited in comparison with the larger collections of permanent specimens recovered from many African and Eurasian sites. Therefore, any information concerning the morphology and dimensions of the hominin deciduous teeth is always welcomed by the scientific community (e.g., Benazzi et al., 2011; Crevecoeur et al., 2010; Howell & Coppens, 1973; Hublin, 2006; Keyser, Menter, Moggi-Cecchi, Pickering, & Berger, 2000; Mallegni & Ronchitelli, 1989; Peretto et al., 2015; Toussaint et al., 2010; Tillier, Hardy, David, Girard, & Dlatchenko, 2013; Zanolli, Bayle, & Machiarelli, 2010, 2012). Several studies suggest that deciduous nonmetric dental traits are useful tools in assessing the biological relationships of human populations (Tocheri, 2002, and references therein). Furthermore, it is generally accepted that the deciduous dentition is more evolutionarily conservative than the permanent dentition "and are thus relatively more useful for distinguishing specimens at various taxonomic levels" (Bailey, Benazzi, Buti, & Hublin, 2016 and references therein; Keyser et al., 2000, p. 194).

Here we describe unpublished deciduous teeth recovered from the Gran Dolina-TD6 site in Sierra de Atapuerca (Spain) during the last decade. Our aim is to present a descriptive and comparative study of these teeth which, apart from the specimen recovered from Barranco León [Orce, Spain (Toro-Moyano et al., 2013)], represent the only available information on the deciduous dentition in the European Early Pleistocene.

The TD6 level (Bermúdez de Castro, Rosas, & Nicolás, 1999a) has been divided in three sublevels: TD6-1, TD6-2, and TD6-3 (Bermúdez de Castro et al., 2012; Campaña et al., 2016). The human fossils, as well as more than 300 artefacts and several thousand micro- and macromammal fossil remains (Carbonell et al., 1999; Cuenca-Bescós, Laplana, & Canudo, 1999; García & Arsuaga, 1999; van der Made, 1999), come from the sublevel TD6-2. Parés and Pérez-González (1995, 1999) observed a polarity reversal between TD7 and TD8, interpreted as the Matuyama/Brunhes boundary, meaning that levels TD8 to TD11 were deposited during the Middle Pleistocene, whereas levels TD7 to TD1 were deposited during the Early Pleistocene. A combination of paleomagnetic data and ESR/U-series ages suggests an age range between 0.78 and 0.86 million years ago (Ma) for the TD6 level (Falgüeres et al., 1999). Thermoluminescence (TL) dates on samples taken at the TD7 level, one meter below the Brunhes/Matuyama boundary give a weighted mean age of  $0.96 \pm 0.12$  Ma for TD7 (Berger et al., 2008). The ESR dating applied to optically bleached quartz grains from TD6 gives dates between  $0.60 \pm 0.09$  Ma and  $0.95 \pm 0.09$  Ma (Moreno et al., 2015). These authors also obtained dates of  $0.73 \pm 0.13$  Ma and  $0.85 \pm 0.14$  Ma for the TD7 level from samples taken under the Matuyama/Brunhes boundary. Using thermally transferred OSL (TT-OSL) dating of individual quartz grains, Arnold et al. (2014) obtained a weighted mean age of  $0.84 \pm 0.06$  Ma for the TD6 level. Finally, Arnold and Demuro (2015) have undertaken a series of TT-OSL suitability assessments on known-age samples from TD6. Using this method, they obtained a weighted average age of

$0.85 \pm 0.04$  Ma for TD6-3. Summarizing, and taking into account the biostratigraphic information from TD6 (Cuenca-Bescós et al., 1999, 2015), we consider that the TD6 hominins could be assigned to the MIS 21.

## 2 | MATERIALS

The deciduous dental sample of the TD6 hominin assemblage includes eight *H. antecessor* specimens. In our first study of the TD6 teeth (Bermúdez de Castro et al., 1999a) we presented the description of the two deciduous teeth: the upper canine ( $dc^1$ ) and the first molar ( $dm^1$ ) preserved in situ in the maxilla ATD6-14. The other deciduous teeth are an upper lateral incisor ( $di^2$ ), an upper second molar ( $dm^2$ ), a lower canine ( $dc_1$ ), two lower first molars ( $dm_1$ ), and a lower second molar ( $dm_2$ ). One of the  $dm_1$ s and the  $dm_2$  belong to the immature mandible ATD6-112 (Bermúdez de Castro et al., 2010).

In previous papers (Bermúdez de Castro et al., 1999a), we suggested a minimum number of eleven individuals (MNI) for the current TD6 hominin assemblage. Due to the considerable fragmentation of the hominin remains (see Carbonell et al., 2010; Fernández-Jalvo, Díez, Cáceres, & Rosell, 1999; Saladié et al., 2012) we have serious difficulties to ascertaining this estimate. In Table 1 we present the specimens described in this study and a re-evaluation of the MNI.

The so-called Aurora Archaeostratigraphic Set (Bermúdez de Castro et al., 2008), which corresponds to the TD6-2 sublevel, includes at least two strata with human fossil remains. These and other strata are condensed near the wall of the cave, where a test pit was made during the 1990s. A new stratigraphic study confirms not only the complexity of the TD6 level, but also that the fossils and artefacts were accumulated in the cave by geological processes, derived from the adjacent slope above the cave or the cave entry (Campaña et al., 2016). Therefore, it is possible that the current *H. antecessor* hypodigm includes a combination of various human occupations of the Gran Dolina cave. Although the time elapsed among these hypothetically different occupations was relatively short, we must be aware that the identified individuals may not correspond to the same event and the MNI may be as high as fifteen. Awaiting clarification from future excavations at the TD6 level, this demographic assessment must be considered preliminary. However, it is interesting to note that between 70% (for the MNI) and 80% (if the maximum number of individuals is fifteen) of the individuals are immature.

It must be kept in mind that although the TD6 hominins exhibit a modern human pattern of dental development (Bermúdez de Castro et al., 1999b), the rates of dental growth in *H. antecessor* may be faster than those of *H. sapiens* and therefore the ages at death given in Table 1 may be overestimated.

## 3 | METHODS

The external morphology is described from direct observation following both classic and more recent studies (e.g., Grine, 1984; Johanson, White, & Coppens, 1982; Moggi-Cecchi, Grine, & Tobias, 2006; Tobias,

TABLE 1 Individuals represented in the TD6 hominin assemblage

Hominin	A/I	Specimens	Age at death <sup>a</sup>
H1	Immature	ATD6-1 (LC <sub>1</sub> ), ATD6-2 (LI <sub>2</sub> ), ATD6-3 (RP <sub>3</sub> ), ATD6-4 (RP <sub>4</sub> ), ATD6-5 (R mandible fragment (M <sub>1</sub> -M <sub>3</sub> ), ATD6-6 (fragment of RLC <sub>1</sub> ), ATD6-7 (RP <sub>7</sub> ), ATD6-8 (RP <sub>8</sub> ), ATD6-9 (LP <sub>9</sub> ), ATD6-10 (RM <sub>1</sub> ), ATD6-11 (LM <sub>1</sub> ), ATD6-12 (RM <sub>2</sub> ), ATD6-13 (Left maxillary fragment, C <sup>1</sup> -P <sup>3</sup> ), ATD6-5a,b,c (some small isolated fragments of the mandible ATD6-5).	13.5-14.5
H2	Immature	ATD6-14: left maxillary fragment with dc <sup>1</sup> -dm <sup>1</sup> , and some permanent germs I <sup>1</sup> , I <sup>2</sup> , C <sup>1</sup> , P <sup>3</sup> , and P <sup>4</sup> inside.	3.5-4.0
H3	Immature	ATD6-69: maxilla and left zygomatic bone with LP <sup>3</sup> , M <sup>1</sup> , and unerupted M <sup>2</sup> , M <sup>3</sup> , and R I <sup>2</sup> to M <sup>1</sup> .	10.0-11.0
H4	Adult	ATD6-48, LI <sub>2</sub> .	Young
H5	Immature	ATD6-94 (RM <sub>1</sub> ), ATD6-103 (RM <sub>1</sub> ).	5.0-6.0
H6	Adult	ATD6-96, left hemimandible with C <sub>1</sub> to M <sub>3</sub>	Young
H7	Adult	ATD6-113, left mandibular fragment with M <sub>2</sub> -M <sub>3</sub> .	Young
H8	Immature	ATD6-112, right mandibular fragment with dm <sub>1</sub> , dm <sub>2</sub> , and the germs of I <sub>2</sub> , C <sub>1</sub> , P <sub>3</sub> , P <sub>4</sub> , and M <sub>1</sub> .	3.5-3.9
H9	Immature	ATD6-102 (di <sup>2</sup> ).	2.5-3.0
H10	Immature	ATD6-125, right LP <sub>4</sub>	13.5-14.5

A/I: Adult/Immature.

<sup>a</sup>According to modern human standards.

1991; Zanolli, Grine, Kullmer, Schrenk, & Macchiarelli, 2015). When necessary, a binocular microscope was also used. Mesiodistal (MD) and buccolingual (BL) dimensions of the crowns were measured with a standard sliding caliper and recorded to the nearest 0.1 mm following the technique of Flechier, Lefèvre, and Verdène (Lefèvre, 1973). Morphological and metrical data were obtained from the literature, except in the case of the Arago sample and the dm<sub>1</sub> from Barranco León for which the originals were observed and measured by JMBC and MMT. A recent *H. sapiens* sample was also measured (CCG and JMBC). This sample is formed by naturally shed deciduous teeth of living Spanish children.

Concerning the internal morphology, we have made comparisons with two deciduous specimens of the Atapuerca-Sima de los Huesos (SH) dental collection, as well as with Neanderthal and *Homo sapiens* dental samples obtained from NESPOS, ESRF, and CENIEH databases. Additional information of the internal morphology (e.g., Barranco León, Qesem, and Sangiran) was obtained from the literature (Fornai et al., 2016; Toro-Moyano et al., 2013; Zanolli et al., 2012, 2015). It is a common practice that dental anthropologists use the expression of morphological features of both the permanent and deciduous teeth to study relationships between populations, assuming that this expression is genetically modulated. Usually, results based on permanent and deciduous morphology are very similar (see Edgar & Lease, 2007, for a review of the literature concerning this matter). Therefore, and as an orientation for the readers, in this report we have followed the Arizona State University Dental Anthropology System (ASUDAS; Turner, Nichol, & Scott, 1991) and Martínón-Torres, Bermúdez de Castro, Gómez-Robles, Prado-Simón, and Arsuaga, (2012) for the identification of morphological features. Additionally, for the trigonid crests we

employed Martínez de Pinillos et al. (2014) and for the assessment of the talonid crests and the entoconid mesial ridge we followed the standards by Martínón-Torres et al. (2014). Although these methods have been devised from permanent teeth we found they could be applied to the deciduous morphology as well.

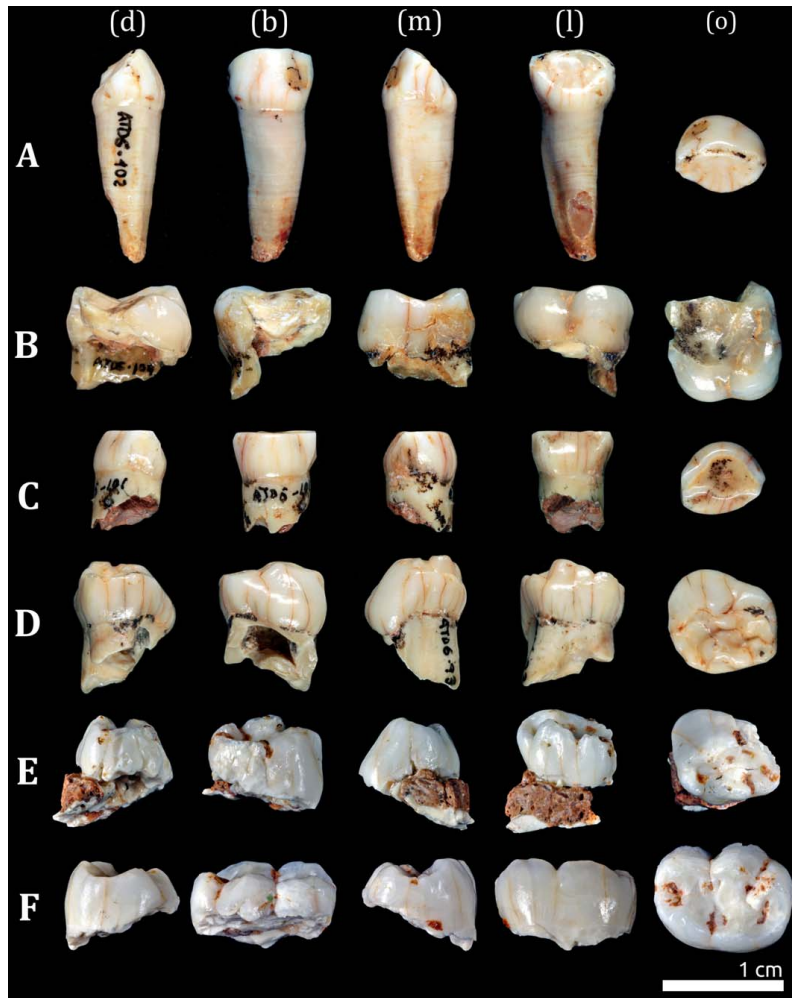
In order to study the dentine morphological characteristics of *H. antecessor*, the sample was scanned with a microtomographic Phoenix v/tome/xs of GE Measurement, housed at the CENIEH with the following parameters: 130 kV, 150 μA, and 0.2 Cu filter resulting in an isometric voxel size of 18 μm. Tomographic data were segmented and visualized with Amira 6.0.0.

## 4 | RESULTS

### 4.1 | External morphology

#### 4.1.1 | Deciduous left upper lateral incisor (ATD6-102)

The TD6 sample includes one specimen of this class (Figure 1A). ATD6-102 is remarkably well preserved. A thin flake, about 4 mm long, is missing from the lingual aspect of the root. Another thin enamel flake is missing from the mesiobuccal aspect of the crown. The latter probably occurred antemortem, since the edges of the damaged area are rounded and the surface shows fine striations, similar to those observed in the rest of the buccal surface. These striations are well visible under 5× magnification. ATD6-102 is slightly worn, showing a very narrow dentine strip on the incisal edge (degree 2 of Molnar's [1971] classification). In modern humans the di<sup>2</sup> finishes its formation (stage H2) at about 2.5 years of age (Liversidge & Molleson, 2004). Because this tooth exhibits minimal occlusal wear, the most probable age at



**FIGURE 1** Distal (d), buccal (b), mesial (m), lingual (l), and occlusal (o) aspects of (A) ATD6-102 (di2); (B) ATD6-104 (dm2); (C) ATD6-101 (dc); (D) ATD6-93 (dm1); (E) ATD6-112 (dm1), and (E) ATD6-112 (dm2)

death of this individual was between 2.5 and 3.0 years according to the standards of modern humans. A small mesial interproximal wear facet is present, but there is no a distal interproximal facet. In lateral view, the labial surface of this tooth is gently convex from the cervical line to the incisal rim. From the occlusal aspect, the labial convexity is gentle (corresponding to ASUDAS grade 3). The mesial and distal marginal ridges are weakly developed conforming a moderate shovel shape, and they merge with a moderate lingual basal eminence (grade 2, according to Martín-Torres et al., 2012). Two barely perceptible grooves run vertically from this eminence and disappear in the lingual surface, delimiting a smooth central ridge. The root is complete, slightly curved towards distal. It measures 13.0 mm at the buccal aspect from

the cementum–enamel junction (CEJ) to the apex. The cross-section of the root at the cervical level is ovoid in shape, with the longer axis oriented in a mesiobuccal to distolingual direction. A wide developmental groove runs along the lower half of mesial aspect of the root.

The comparative  $di^2$  hominin sample is small. From the morphological point of view there are no key features to distinguish between different taxa, except for the smaller size and simplified morphology of the *H. sapiens* specimens. The prominence of the mesial and distal marginal ridges and the cervical eminence is variable in all taxa and the shovel-shape is generally not well developed. The crown dimensions of ATD6-102 are somewhat smaller than in the Neandertal sample (Table 2).

**TABLE 2** Mesiodistal (MD) and buccolingual (BL) measurements of the deciduous upper lateral incisor, ATD6-102, the lower canine ATD6-93 and ATD6-112, and the lower second molar ATD6-112 compared with those of other deciduous teeth from different hominin specimens and samples

Species/specimen	N	di <sup>2</sup>				dc <sub>1</sub>				dm <sub>1</sub>				dm <sub>2</sub>						
		MD		BL		MD		BL		MD		BL		MD		BL				
		X	SD	X	SD	X	SD	X	SD	X	SD	X	SD	X	SD	X	SD			
Early Homo (SA) <sup>a</sup>	1	(4.6)	-	4.1	-	1	6.0	-	5.8	-	2	8.75	-	7.50	-	2	11.25	-	9.55	-
Early Homo (EA) <sup>b</sup>																				
Chinese <i>H. erectus</i> <sup>c</sup>					3	6.16	0.06	5.26	0.06	2	8.75	-	6.80	-	5	11.30	0.66	9.26	0.71	
PCG.2 Kabuh formation <sup>d</sup>																				
BL02-J54-100 <sup>e</sup>					1	10.05	-	8.48	-											
<i>H. antecessor</i> <sup>f</sup>	1	6.0	-	5.1	-	1	7.0	-	6.0	-	2	8.95	-	8.55	-	1	11.4	-	(9.2)	-
<i>H. heidelbergensis</i> <sup>g</sup>					3	6.56	0.87	6.13	0.72	3	9.43	0.66	8.03	0.40	3	10.36	0.30	9.56	0.50	
<i>H. neanderthalensis</i> <sup>h</sup>	9/11	6.43	0.61	5.52	0.43	13	6.77	0.61	6.06	0.54	24	8.83	0.44	7.56	0.47	32	10.55	0.52	9.40	0.48
Qesem QC2, QC3 <sup>i</sup>					1	9.10	-	7.10	-	1	11.1	-	9.7	-						
<i>H. sapiens</i> (pooled sex) <sup>j</sup>	32	5.17	0.29	4.75	0.27	21	5.82	0.45	5.40	0.33	18	7.91	0.36	6.90	0.39	18	10.03	0.40	8.67	0.41

<sup>a</sup>This sample (SA; South Africa) includes specimens from Sterkfontein and Drimolen (Keyser et al., 2000; Moggi-Cecchi et al., 2015, 1995).  
<sup>b</sup>This sample (EA; East Africa) includes specimens from Koobi Fora (Leakey & Wood, 1973, 1974; Wood, 1991).  
<sup>c</sup>This sample includes specimens from Zhoukoudian (Weidenreich, 1937).  
<sup>d</sup>From Zanolli et al. (2012).  
<sup>e</sup>From Toro-Moyano et al. (2013).  
<sup>f</sup>This study.  
<sup>g</sup>This sample includes the original specimens from the Arago site. Measurements taken by JMBC.  
<sup>h</sup>This sample includes specimens from the following sites: Amud, Archi, Arco-sur-Cure, La Chaise (Abri Suard), La Chaise (Bourgeois Delauney), Chateaufort, Combe-Grenal, Cova Negra, Ehringsdorf, Engis, Gibraltar 2, Kabara, Krapina, La Ferrassie, Roc de Marsal, Pech de l'Azé, Placard, Salaman, Shanidar, Spy, Staroselje, Subalyuk, Taubach, Teshik-Tash, Uluzzo, Zaskahaya. Data taken from: (Asuaga et al., 1989; Bailey and Hublin, 2006; Crevecoeur et al., 2010; Madre-Dupouy, 1985; Tillier, 1979; Wolpoff, 2012).  
<sup>i</sup>From Hershkovitz et al. (2016).  
<sup>j</sup>Recent human sample. Measurements taken by JMBC and CGC.

#### 4.1.2 | Deciduous left upper second molar (ATD6-104)

The only  $dm^2$  of the TD6 assemblage is poorly preserved (Figure 1B). A substantial part of the buccal cusps and the mesial crown of ATD6-104 are missing, and it is not possible to obtain the MD and BL measurements. Only a minimal part of the distal root is still preserved. The occlusal surface is worn, showing wide dentine patches (degree 4 of Molnar's [1971] classification). A wide and well-marked distal interproximal facet is present. According to modern human standards of dental development the owner of this tooth died between about 6.0 and 12.0 years (Al Qahtani, Hector, & Liversidge, 2010). In spite of the bad preservation, it is possible to see that the occlusal outline is a regular and symmetrical square, with a well-developed hypocone (grade 4 of ASUDAS). No metaconule is present. The lingual cusps of ATD6-104 are aligned transversely with the buccal cusps forming an approximately squared occlusal polygon and a regular contour. In contrast, the two preserved Arago  $dm^2$ s (Arago 12 and 27) show a relatively distal displacement of the lingual cusps forming a rhomboidal occlusal polygon. The same morphology is present in the rest of the Neandertals analysed (Chateauneuf 2, Roc de Marsal, and in all the Krapina  $dm^2$ s), as well as in the Pontnewydd PN4 specimen (Compton & Stringer, 2015). In ATD6-104 a crista obliqua connecting the protocone and metacone is present (grade 1 of Martínón-Torres et al., 2012). This tooth shows two small ridges and a small depression at the mesiolingual corner of the protocone (Carabellís complex grade 3 of ASUDAS), whereas a well-developed Carabellíscusp is observed in the Krapina  $dm^2$ s.

#### 4.1.3 | Deciduous left lower canine (ATD6-101)

The TD6 sample includes one deciduous left lower canine (Figure 1C). This tooth is severely worn (degree 5 of Molnar's [1971] classification) showing a broad dentine patch, as well as marked mesial and distal interproximal wear facets. At the buccal aspect, the preserved height of the crown measures about 3.5 mm. It is not possible to ascertain if the root resorption process began in this tooth. Without additional data we can only speculate that the age at death of the individual was between 6 and 10 years, following the modern human standard. Only about 4 mm of the root is preserved at the buccal aspect. The occlusal outline of the crown is ovoid in shape and asymmetrical. In spite of its advanced wear, the mesial and distal marginal ridges are still visible, suggesting a moderate shovel-shape. The lingual basal eminence is also moderate. A lingual central ridge is barely developed. In lateral view, the labial surface is gently convex from the cervical line to the incisal rim. From the occlusal aspect, the labial convexity is moderate. The expression of mesial and distal vertical grooves along the labial surface (ASUDAS grade 1) suggests the possible presence of mesial and distal cusplets or styles, as in the deciduous upper canine of ATD6-14 (Bermúdez de Castro et al., 1999a).

The morphology of ATD6-101 is not very different from that of Arago and Neandertal specimens. The lingual basal eminence and the mesial and distal marginal ridges in all these canines exhibit a moderate development, whereas the essential ridge can be present (Arago 50) or absent (Spy 645a). The main difference is the presence in ATD6-101 of

potential mesial and distal styles. At least a distal style seems to be present in the deciduous canines from Zhoukoudian (Weidenreich, 1937), as well as in some Neandertals such as Combe Grenal and Pech de LAzé (Madre-Dupouy, 1985). We have not noted the same features in our visual inspections of the Arago specimens. At the buccal face, the Zhoukoudian deciduous canines present a swollen rim at the basal aspect of the buccal face. It is well-differentiated from the rest of the buccal surface, and ascends to a higher level on both the mesial and distal borders forming an arch-like cingulum (Weidenreich, 1937, Plate XXI, Fig. 190). This primitive feature is not present in the deciduous canine of TD6. At the cervical level, the cross-section of the root of ATD6-101 is circular in shape.

Despite the marked interproximal wear facets, the MD dimension of ATD6-101 is larger than the mean values of the Arago, Neandertals, and Zhoukoudian samples (Table 2), whereas the BL dimension of ATD6-101 is similar to that of these samples.

#### 4.1.4 | Deciduous lower first molars (ATD6-93 and ATD6-112)

The TD6 sample includes two specimens of this class. ATD6-93 is an isolated right  $dm_1$  preserving the crown and a minimum part of the roots (Figure 1D). Nevertheless, we can observe that bifurcation of the mesial and distal roots occurs at about 2.0 mm under the cemento-enamel junction (CEJ). ATD6-112 lost a fragment of the distobuccal cusp (Figure 1E), as well as some of the enamel and dentine at the level of CEJ. For this reason, and although the two roots remain included in the mandible, it is not possible to fit the crown and roots. ATD6-93 exhibits small dentine patches in all cusps (degree 3 of Molnar's [1971] classification), whereas in ATD6-112 wear affects only the enamel, except that there is an almost negligible dentine patch at the protoconid (degree 2-3). A well-marked distal interproximal wear facet is present in ATD6-93, but the possible contact of this tooth with the deciduous canine is not apparent. In ATD6-112 there is no mesial interproximal facet and the distal part of the crown is broken. In modern humans the  $dm_1$  finishes its formation (stage H2) about 2.5 years (Liversidge & Molleson, 2004), whereas the  $dm_2$  finishes its formation about 2.9 years. Given the occlusal wear of ATD6-93, the owner of this tooth probably died between 4.0 and 6.0 years according to the standards of modern humans. ATD6-112 belongs to an immature individual (Bermúdez de Castro et al., 2010) who died at about 3.5-4.0 years according to the modern human standards. In both molars the occlusal outline is strongly asymmetrical, exhibiting a trapezoidal shape due to the marked buccal flaring of the tuberculum molare and the receding mesiolingual corner. The tuberculum molare is well-developed, being expanded both buccally and strongly cervically. Four cusps are present in ATD6-93 and ATD6-112. In these two specimens the protoconid is the largest and it is mesially displaced, followed by the metaconid, the hypoconid, and the entoconid, which is almost vestigial in ATD6-93. The mesial cusps are clearly higher than the distal ones and they occupy a greater portion of the crown. The essential crests of the mesial cusps are joined forming a mid-trigonid crest (MdTC) (type A, continuous MdTC with an absent or discontinuous distal trigonid crest [DTC], from Martínez de Pinillos et al., 2014). The

essential crest of the hypoconid is conspicuous and swollen. The mesial marginal ridge is well marked. An incipient mesioconulid (Grine, 1984: 46) is formed at the mesial aspect of the mesial marginal ridge. In ATD6-93 this ridge is separated by a buccolingually large anterior fovea from the mesial cusps (grade 1 according to Martín-Torres et al., 2012), whereas in ATD6-112 the anterior fovea is very deep, pit-like, and centrally placed (grade 2 according to Martín-Torres et al., 2012). In ATD6-93 the groove pattern is well defined. There is a clear contact between the metaconid and the hypoconid (Y-pattern). In this tooth a pit-like posterior fovea is placed between this ridge and the groove which separates the hypoconid from the entoconid. The mesio-buccal groove between the protoconid and the hypoconid ends in a short longitudinal groove, which ascends by the distal slope of the protoconid. A pit is also observed at the lingual slope of the metaconid. In ATD6-112, the groove pattern is less conspicuous due to the dental wear, but it is possible to observe a contact between the metaconid and the hypoconid. Although the posterior part of the crown is damaged, the morphology in this area seems to be similar to that of ATD6-93.

General features of the TD6 dm<sub>1</sub>s fit well the morphology of the genus *Homo* (see Hillson, 1996). The trigonid is clearly larger than the talonid, in contrast to the Early Pleistocene dm<sub>1</sub>s from Sangiran (FS 67) (Putjangan Formation), Barranco León (BLO2-J54-100), the African early *Homo* specimens, and the dm<sub>1</sub> from Qesem where both regions show a similar area (Grine, 1984; Hershkovitz et al., 2016; Leakey & Wood, 1973, 1974; Toro-Moyano et al., 2013). The tuberculum molare is particularly conspicuous in the TD6 dm<sub>1</sub>s. This feature is weak or absent in early *Homo* (Grine, 1984; Leakey & Wood, 1973, 1974; Toro-Moyano et al., 2013). In the Zhoukoudian specimens there is a swollen cervical rim that, according to Weidenreich (1937), would correspond to the tuberculum molare. He also describes the presence of a vestigial paraconid in the mesial marginal ridge of the Zhoukoudian dm<sub>1</sub>s. The same feature has been described in BLO2-J54-100 from Barranco León, which is separated from the metaconid by a deep V-shaped groove that opens towards the lingual face. This groove is also observed in the dm<sub>1</sub> from ATD6-112. The tuberculum molare is not especially marked in the Arago specimens (A11, 34, and 55), and exhibits a variable development in Neandertals (Bailey and Hublin, 2006; Madre-Dupouy, 1985; Mallegni and Ronchitelli, 1989; Tillier, 1979, 1980, 1982; Tillier and Genet-Varcin, 1980; Wolpoff, 1979), as well as in modern humans. The presence of a mesioconulid has been reported in FS 67 from Sangiran (Grine, 1984). A similar incipient swelling of the mesial marginal ridge at the protoconid level is observed in Arago 11 and 34. No other reference to this feature has been noted in the available literature. In TD6 dm<sub>1</sub>s molars, as in other *Homo* specimens, the protoconid is generally the largest cusp. In the TD6 dm<sub>1</sub>s the mid-trigonid crest is high and very conspicuous. The presence of this feature is variable in the *Homo* fossil record. It is present in BLO2-J54-100 from Barranco León (Toro-Moyano et al., 2013) and in the unworn Zhoukoudian 125 (Weidenreich, 1937), but absent in FS 67 from Sangiran (Grine, 1984). Similarly, the feature is present in Arago 11 and 34, and less conspicuous in Arago 55. The mid-trigonid crest is generally

well developed in Neandertals (Bailey and Hublin, 2006; Madre-Dupouy, 1985; Mallegni & Ronchitelli, 1989; Tillier, 1979; Tillier & Genet-Varcin, 1980), but absent in specimens from the Upper Paleolithic assigned to *H. sapiens* (Bailey & Hublin, 2006). In the dm<sub>1</sub> from Qesem the anterior fovea is connected to the central basin by a longitudinal fissure (Hershkovitz et al., 2016). Interestingly, in the recent *H. sapiens* studied here 17 out of 18 specimens (94.5%) exhibit a well-developed mid-trigonid crest.

Regarding the size of these deciduous molars (Table 2), ATD6-93 is comparatively broader (breadth: 8.8 mm) and in the range of the larger *Homo* specimens due to its strong tuberculum molare. The BL breadth of ATD6-112 (BL: 8.3 mm) is somewhat less, whereas the MD dimension of both TD6 specimens is similar (MD: 9.0 mm for ATD6-93, and 8.9 mm for ATD6-112). These measurements are in the range of variation of the genus *Homo*, in which the largest specimens are represented by the dm<sub>1</sub> from Barranco León (BLO2-J54-100) and Arago 66 (see Table 2). Surprisingly, the BL dimensions of the Zhoukoudian dm<sub>1</sub>s are low and similar to those obtained in the modern human sample. Although Weidenreich (1937, p. 5) clearly explains the method he used to obtain the dental measurements, there is no scale in the Plates to check his results.

#### 4.1.5 | Deciduous lower second molars (ATD6-112)

The TD6 assemblage includes one specimen belonging to the right hemimandible ATD6-112 (Figure 1F). The lower part of the crown at the mesial and buccal sides is missing, and it is not possible to fit the crown to the roots, which are included in the alveoli of the mandible. Wear has erased a part of the enamel in all cusps, but the dentine is only visible at the hypoconid (degree 2–3 of Molnar's [1971] classification). ATD6-112 shows the five principal cusps. They are well-developed and clearly separated. The buccal face is bilobed in occlusal view. The size of the protoconid, metaconid and hypoconid is similar, followed by a well-developed entoconid and a small hypoconulid (corresponding to ASUDAS grade 2). There is a deeply incised narrow mid-trigonid crest connecting the essential crest of protoconid and metaconid, crest type A from Martínez de Pinillos et al. (2014). An incised mid-trigonid crest, similar to that present in the dm<sub>2</sub> of ATD6-112 is observed in three specimens (16.6%) of the modern human sample, whereas one specimen exhibits a well-developed mid-trigonid crest. That is, the different expressions of mid-trigonid crest is present in 22.2% dm<sub>2</sub>s of the modern human sample used in this study. Metaconid and hypoconid of ATD6-112 show a minimum contact (Y-pattern). The mesial marginal ridge is well developed, and its central aspect forms a small cuspule or mesioconulid. The anterior fovea is particularly deep and broad due to the small development of the mid-trigonid crest. The essential crest of the hypoconulid joins with the essential crest of the entoconid. This crest and the broad distal marginal ridge delimit a deep, groove-like, and lingually placed posterior fovea. A pit-like posterior fovea is observed in 9 out of 18 modern human specimens (50%). The cusps tips of the dm<sub>2</sub> of ATD6-112 are not especially internally compressed, as reported in other fossil specimens (Bailey & Hublin, 2006; Toussaint et al., 2010; Weidenreich, 1937). There are no signs of buccal cingulum in the TD6 dm<sub>2</sub> sample.

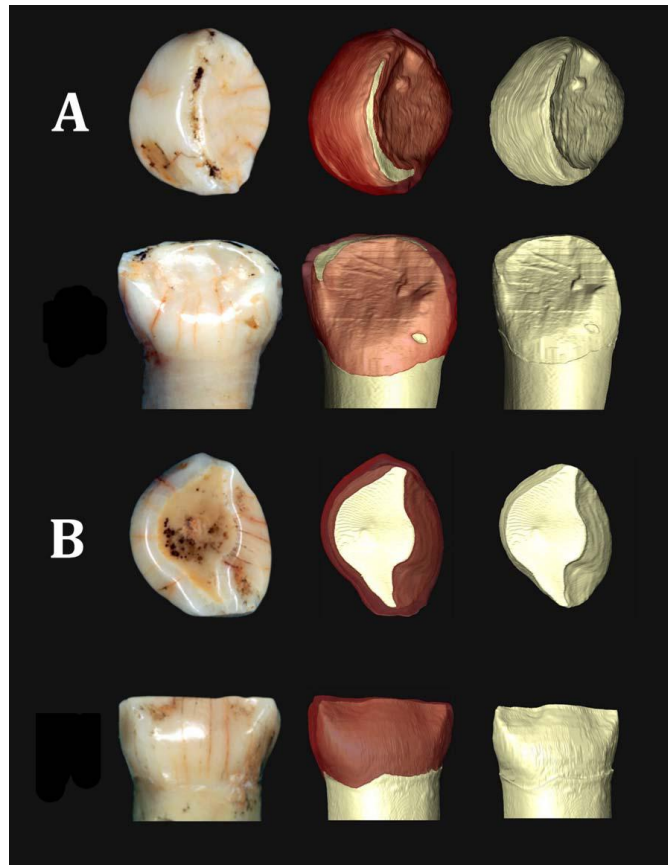


FIGURE 2 Inner morphology of A) ATD6-102 (di2); and B) ATD6-101 (dc)

The MD dimension (11.4) is large and similar to that of other Early Pleistocene *Homo* specimens (Table 2), and larger than the mean values of the Neandertal and Arago samples. The crown fracture of ATD6-112 prevents a precise measurement of its BL dimension.

## 4.2 | Internal morphology

### 4.2.1 | Deciduous left upper lateral incisor (ATD6-102)

The labial surface of ATD6-102 (Figure 2A) exhibits a pronounced convexity (grade 4 of ASUDAS) and the elevation of the marginal ridges is marked (grade 3 of ASUDAS). The mesial marginal ridge of the di<sup>2</sup> is more developed compared to the distal one. On the lingual surface of the EDJ we observed a small protuberance barely perceptible at the enamel to the naked eye.

### 4.2.2 | Deciduous left upper second molar (ATD6-104)

In the ATD6-104 EDJ (Figure 3A) the crista obliqua is present and continuous (grade 1 of ASUDAS). There are two small depressions delimit-

ing faint ridges at the mesiolingual corner of the protocone. They correspond to a Carabelli's complex grade 3 of ASUDAS that is less marked than at the enamel. There is a well-developed hypocone (grade 4 of ASUDAS) whereas the metaconule is absent.

### 4.2.3 | Deciduous left lower canine (ATD6-101)

In ATD6-101 (Figure 2B) the expression of features at the EDJ corresponds to that observed at the enamel. The occlusal outline of the crown is asymmetrical. The mesial and distal marginal ridges are still visible. The mesial ridge is larger than the disto-lingual (grade 1, according to Martín-Torres et al., 2012). On the contrary the distal accessory ridge is weakly developed (grade 1, according to Martín-Torres et al., 2012). The lingual basal eminence is moderate and the lingual surface also exhibits a mesial and a distal marked grooves. Finally, from the occlusal aspect, the labial and lingual surfaces exhibit moderate convexity.

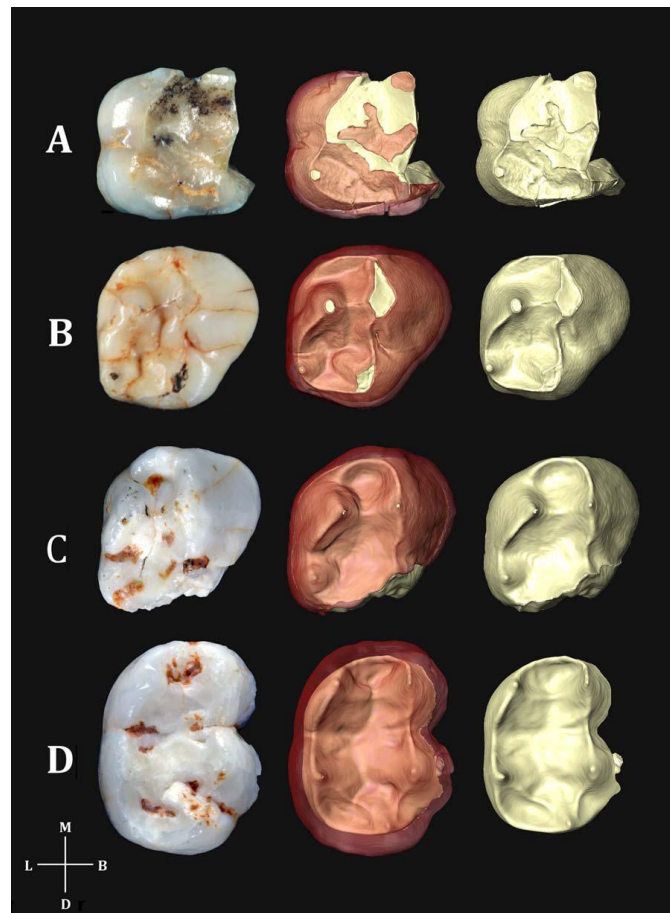


FIGURE 3 Inner morphology of (A) ATD6-104 (dm2); (B) ATD6-93 (dm1); (C) ATD6-112 (dm1); and (D) ATD6-112 (dm2)

#### 4.2.4 | Deciduous lower first molars (ATD6-93 and ATD6-112)

The right  $dm_1$  ATD6-93 (Figure 3B; Table 3) exhibits a well-developed tuberculum molare in the buccal part of the protoconid, giving a strongly asymmetrical shape to the occlusal outline of the molar. The tooth exhibits a marked mesial marginal ridge, with a small protuberance, which may correspond to a vestigial paraconid. The mesial marginal ridge is separated from the metaconid by a deep groove that extends lingually. This feature has also been identified in the Barranco León specimens (Toro-Moyano et al., 2013). The anterior fovea forms a slight linear depression (grade 1 according to Martín-Torres et al., 2012). Following Martínez de Pinillos et al. (2014) trigonid crest scoring system, we classified the crest exhibited by ATD6-93 as type 1, or continuous middle trigonid crest. There is no expression of talonid crest in the EDJ. Finally, on the disto-buccal surface of the protoconid there is

a ridge running distally. This trait could correspond to a moderate prostyloid at the EDJ (grade 4 of ASUDAS), or to a mesial protoconid ridge *sensu* Hlusko (2004), the latter being mostly identified so far in permanent molars of Asian *H. erectus* (Xing, Martín-Torres, Bermúdez de Castro, Xijjie, & Liu, 2015, 2016) and some isolated Sima de los Huesos (Martínez de Pinillos et al., 2014).

The fracture exhibited by the right  $dm_1$  of ATD6-112 (Figure 3C; Table 3) at its disto-buccal surface prevents the assessment of the hypoconid size, the presence of hypoconulid and the outline shape of the molar. The expression of the tuberculum molare is clear, but less developed than in ATD6-93. The anterior fovea is deep (grade 2 according to Martín-Torres et al., 2012) and the mesial marginal ridge, in contrast to that of ATD6-93, follows the occlusal outline and ends up in the metaconid. The expression of the trigonid crest corresponds to type 1 (Martínez de Pinillos et al., 2014) and we did not identify a talonid crest.



TABLE 3 Expression of some features of the EDJ in the dm<sub>1</sub>s and dm<sub>2</sub>s of *H. antecessor* and other hominin specimens

Site	Species	Specimen	Tooth	TgC	TM	C5	C6	C7	TIC	Protostylid	AF	Asy	EMR	
Sangiran	<i>H. erectus</i>	PCG.2	dm <sub>2</sub> L	1	-	x	x	-	-	x	x	NA	-	
Barranco León		BL02-J54-100	dm <sub>1</sub> L	1	-	x	-	-	-	-	-	x	-	
Gibraltar	<i>H. neanderthalensis</i>	HA-40.26	dm <sub>1</sub> R	1	-	x	-	-	-	-	x	-	-	
		HA-40.26	dm <sub>2</sub> R	1	-	x	x	-	-	-	x	-	x	
Abri Suard	<i>H. neanderthalensis</i>	S14 5	dm <sub>2</sub> R	1	-	x	x	-	-	-	x	-	x	
Krapina	<i>H. neanderthalensis</i>	d62	dm <sub>2</sub> L	1	-	x	-	-	-	-	x	-	x	
		d63	dm <sub>2</sub> L	1	-	x	-	-	-	-	x	-	x	
		d64	dm <sub>2</sub> L	1	-	x	-	-	-	-	x	-	x	
		d65	dm <sub>2</sub> L	1	-	x	-	-	-	6	-	x	-	x
		d66	dm <sub>2</sub> L	1	-	x	-	-	-	-	-	x	-	x
		d67	dm <sub>1</sub> L	1	-	x	-	-	-	-	-	x	x	x
		d68	dm <sub>2</sub> R	10	-	x	x	-	-	-	-	x	-	x
Atapuerca-Sima de los Huesos <sup>a</sup>		AT-2398	dm <sub>2</sub> L	1	-	x	-	-	-	-	x	-	x	
		AT-947 <sup>b</sup>	dm <sub>2</sub> R	1	NA	NA	NA	NA	NA	-	-	x	-	NA
Mirador	<i>H. sapiens</i>	MIR4_P22_294	dm <sub>1</sub> L	1	x	NA	-	-	-	-	NA	x	-	
		MIR4_P22_294	dm <sub>2</sub> L	NA	x	x	-	-	-	-	-	-	-	-
Qafezh	<i>H. sapiens</i>	15	dm <sub>1</sub> R	1	x	x	-	-	-	-	x	x	-	
		15	dm <sub>1</sub> L	1	x	x	-	-	-	-	x	x	x	
		15	dm <sub>2</sub> R	-	-	x	-	-	-	-	-	-	-	x
		15	dm <sub>2</sub> L	-	-	x	x	-	-	-	-	-	-	x
Lagar Velho	<i>H. sapiens</i>		dm <sub>2</sub> R	-	-	x	-	-	3	-	-	-	x	
La Madeleine	<i>H. sapiens</i>	4	dm <sub>1</sub> R	-	-	-	-	-	-	-	x	x	-	
		4	dm <sub>1</sub> L	1	x	x	x	x	x	x	x	x	x	
		4	dm <sub>2</sub> R	-	-	x	-	-	-	1	-	-	-	-
		4	dm <sub>2</sub> L	-	-	x	-	-	-	-	-	-	-	-
Qesem		QC2	dm <sub>2</sub> L	6	-	x	x	-	-	-	-	-	x	
Gran Dolina	<i>H. antecessor</i>	ATD6-93	dm <sub>1</sub> R	1	x	-	-	-	-	-	x	x	-	
		ATD6-112 <sup>c</sup>	dm <sub>1</sub> R	1	x	NA	NA	-	-	-	-	x	NA	-
		ATD6-112 <sup>d</sup>	dm <sub>2</sub> R	1	NA	x	-	-	-	-	-	x	NA	x

x: present; -: not present; NA: not assessed.

TgC: trigonid crest; TM: tuberculum molare; C5: cusp 5; C6: cusp 6; C7: cusp 7; TIC: talonid crest; AF: anterior fovea; Asy: asymmetry; EMR: entoconid mesial ridge.

<sup>a</sup>This hominin sample has been excluded from *H. heidelbergensis* (Arsuaga et al., 2014), but no other species has been proposed so far.

<sup>b</sup>AT-947: tooth heavily worn.

<sup>c</sup>ATD6-112: teeth fractured on the distal side.

<sup>d</sup>ATD6-112: teeth broken on buccal side.

4.2.5 | Deciduous lower second molars (ATD6-112)

The right dm<sub>2</sub> of ATD6-112 (Figure 3D; Table 3) presents a fracture that has damaged the buccal side of the crown. The five main cusps are expressed and the occlusal outline is symmetrical with a well-developed mesial marginal ridge. The EDJ presents a pronounced ante-

rior fovea (grade 2 according to Martín-Torres et al., 2012) and a mid-trigonid crest type 1 (Martínez de Pinillos et al., 2014), although it is lower than those of the dm<sub>1</sub>s. This type of crest is a common finding in the comparative sample, except for d68 (type 10) and QC2 (type 6) (see Table 3 and Fornai et al., 2016; Zanolli et al., 2012, 2015). The

distal fovea is well-developed, lingually displaced, and delimited by the distal marginal ridge and a continuous crest that joins the entoconid and the hypoconulid. We observed a mesial entoconid ridge that, according to Martínón-Torres et al. (2014), could be interpreted as a "trace" of Korenhof's talonid crest type 4.

The comparison of some morphological features of the EDJ in the deciduous first and second lower molars of *H. antecessor* and other available hominins is presented in Table 3. A continuous mid-trigonid crest like that of the *H. antecessor* deciduous molars is present in Barranco León and Qesem specimens, as well as in the totality of the Sangiran  $dm_2$  (Zanolli et al., 2012), *H. neanderthalensis* and Atapuerca-Sima de los Huesos samples, whereas only 4 out of 11 Pleistocene and Holocene *H. sapiens* specimens present a continuous mid-trigonid crest. The type 1 of this crest is also the most frequent in the comparative sample. The expression of tuberculum molare in the  $dm_1$ s and the concomitant asymmetry of the occlusal outline are shared with several fossil specimens, such as Qafzeh, La Madeleine and the modern *H. sapiens* specimen from El Mirador (Spain). The absence of a C6, C7, and protostylid is the common condition in our comparative sample, with the exception of the Sangiran specimens and the left  $dm_1$  from La Madeleine that express a protostylid. The expression of an entoconid mesial ridge in the  $dm_2$ s is common in all Neandertals, Atapuerca-Sima de los Huesos, and in *H. antecessor*, whereas this feature is absent in the two Sangiran specimens and in some Pleistocene and Holocene *H. sapiens* specimens.

## 5 | DISCUSSION AND CONCLUDING REMARKS

Some authors have emphasized the diagnostic value of the deciduous teeth (e.g., Bailey & Hublin, 2006; Benazzi et al., 2012; Keyser et al., 2000; Leakey, Feibel, McDougall, Ward, & Walker, 1998; White, Suwa, & Asfaw, 1994). Thus, it is advisable to further explore the utility of the features outlined in this study in larger hominin samples. Regarding the  $dm^2$  ATD6-104 the lingual cusps are aligned transversally with the buccal cusps forming an approximately squared occlusal polygon and a regular contour. According to Gómez-Robles et al. (2007), this is the plesiomorphic condition of the *Homo* clade for the  $M^1$ s, whereas a relatively distal displacement of the lingual cusps forming a rhomboidal occlusal polygon in which lingual cusps are distally displaced and the hypocone protrudes in the external outline is a derived condition in *H. antecessor*, *H. heidelbergensis*, and *H. neanderthalensis*. If we consider a theoretical genetic correlation between the morphology of the  $dm^2$ s and that of the  $M^1$ s (see Bailey, Benazzi, & Hublin, 2014 for a discussion on this matter; Edgar & Lease, 2007), it is interesting to observe that this derived condition is observed in the available Neandertal  $dm^2$  specimens, in Pontnewydd PN4, as well as in Arago 12 and Arago 27. Therefore, the possible correlation of this feature between the  $dm^2$ s and the  $M^1$ s of different hominin species/paleodemes should be explored in the future.

It has been stated that the size of the talonid and the trigonid is similar in the  $dm_1$ s of *Australopithecus* and early *Homo* (Hillson, 1996;

Leakey et al., 1998; White et al., 1994). However, this is not the case of later *Homo*, like TD6  $dm_1$ s, where the talonid is greatly reduced in comparison to the size of the trigonid (derived condition). It is interesting to note that the trigonid and the talonid of the 1.4 Ma old  $dm_1$  from Barranco León display a similar size. Thus, this specimen would be more primitive than TD6 in this regard (Toro-Moyano et al., 2013).

The tuberculum molare is extremely developed in the upper and lower  $dm_1$ s from TD6 (see Bermúdez de Castro et al., 1999a), whereas it is weak or absent in early *Homo* (Grüne, 1984; Leakey & Wood, 1973, 1974; Toro-Moyano et al., 2013). The absence or weak presence of this feature would be the primitive condition in hominins (see Keyser et al., 2000), whereas a well-developed tuberculum molare in the  $dm_1$ s could be a derived feature of later *Homo*. Regarding the mid-trigonid crest, Bailey and Hublin (2006) have emphasized the presence of this feature in the  $dm_1$ s of the Neandertals. According to these authors, this feature allows the distinction between these hominins and the Upper Paleolithic sample they observed. However, it is interesting to remark that the mid-trigonid crest in the  $dm_1$ s is an extremely variable feature in hominins, and its pattern of expression may be less clear-cut than previously thought. A mid-trigonid crest is present in Taung and Stw 296, but it is absent in Stw 104 (Moggi-Cecchi et al., 2006). Similarly and as we stated above, the presence of this feature is variable in Pleistocene *Homo* and extremely frequent in the modern sample studied here. Therefore, we must be very cautious regarding the taxonomic value of this trait.

The  $dm_2$  of ATD6-112 lacks any structure related to the buccal cingulum. Thus, ATD6-112 seems more derived than the Plio-Pleistocene specimens in this aspect, although more evidence would be necessary to evaluate the polarity of this feature in the genus *Homo*. The  $dm_2$  of ATD6-112 exhibits mid-trigonid crest and well-developed anterior and posterior foveae. Again, a mid-trigonid crest in the  $dm_2$  has been considered as a diagnostic feature of Neandertals in comparison to modern humans (Bailey & Hublin, 2006). This feature is only occasionally absent in Neandertals, like Chateaufort 2 and Combe-Grenal (Madre Dupouy, 1985). The mid-trigonid crest is also absent in the  $dm_2$ -QC2 from Qesem (Hershkovitz et al., 2011). A well-developed mid-trigonid crest has also been described in *A. afarensis* (e.g., A.L. 333 43b), and *A. africanus* (e.g., Stw 67, 97, 104, 315, and 428, as well as in Taung), (Johanson et al., 1982; Moggi-Cecchi et al., 2006) or in PCG.2 from Sangiran (Zanolli et al., 2012). In the absence of enough information about the  $dm_2$  variability in early *Homo* and modern humans, we suggest that the continuous mid-trigonid crest could be the primitive condition in the hominin clade. This feature could have been retained by Neandertals and probably lost in the  $dm_2$  of *H. sapiens* (Bailey & Hublin, 2006). In the  $dm_2$  sample studied here ( $n = 18$ ) we have found only one specimen with a continuous mid-trigonid crest (5.5%). It would be interesting the study of larger modern human samples to make an evaluation of this feature. We could ascertain if this feature is as diagnostic as in the permanent molars (Bailey, Skinner, & Hublin, 2011, and references therein). The presence of a pit-like posterior fovea in 50% of the recent  $dm_2$  also raises questions about the polarity of this trait.

The presence of mesial and distal styles in the deciduous upper and possibly in the lower canines (see Bermúdez de Castro et al., 1999a), as well as the large root of the  $d_1^2$  can be considered as primitive features of the TD6 deciduous teeth. Furthermore, and in agreement with the previous study of the permanent teeth (Bermúdez de Castro et al., 1999a), the size of the deciduous dentition remains within the range of variation of early *Homo*. The limited evidence points to a reduction of the deciduous molars, at least in the European Middle Pleistocene hominins and the Neandertals.

In general we can observe that there is a positive correspondence between the enamel (external) and the EDJ (internal) morphology. Specimen ATD6-102 presents similar morphology on both surfaces except for the small protuberance on the distal aspect of the lingual surface that is not reflected in the external enamel surface. The traits described for the external enamel surface on the mandibular molars (ATD6-93 and ATD6-112) are also found at the EDJ surfaces (e.g., a similar pattern of foveae, or number of cusps and crests). To fully understand the polarity of the traits expressed at the EDJ, however, it is desirable that more data on more hominin specimens is recovered in future studies.

The present study is a new contribution to our understanding of the TD6 hominins. Fieldwork in the coming years will allow to excavation of a surface of more than seventy square meters in each of the different sublevels of TD6. Until then, this study enlarges the list of primitive features of *H. antecessor* regarding the *Homo* clade, as well as the number of traits that this species shared with other *Homo* species including *H. sapiens* and *H. neanderthalensis*. Thus, the study of the deciduous dentition confirms the mosaic pattern of *H. antecessor* morphology revealed in previous studies of this hominin sample (e.g., Bermúdez de Castro et al., 2015).

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## 5.9. RESULTADOS INÉDITOS: ANÁLISIS ESTADÍSTICOS DE COMPARATIVA.

Para comprobar la variabilidad interpoblacional existente durante el Pleistoceno y evaluar el grado de neandertalización de la muestra de la Sima de los Huesos, vamos a comparar dicha población con otros grupos de homínidos del Pleistoceno Medio de Europa, África, Asia y Oriente Próximo, así como con *H. antecessor* y una amplia muestra de *H. neanderthalensis* y *H. sapiens* (ver Tabla 5.9.). Analizaremos la frecuencia de expresión de los primeros, segundos y terceros molares inferiores para el rasgo morfológico conocido como cresta del trigónido con fuertes implicaciones taxonómicas y filogenéticas (ver Tabla 5.10. y Gráfico 5.1. y 5.2.). Para ello vamos a utilizar el análisis estadístico de Escalado Multidimensional No Métrico (NMDS, de sus siglas en inglés) en el que aplicaremos el coeficiente de similitud de Gower (Hammer et al., 2001). Este método trata de reducir al máximo la dimensionalidad de los datos representando en un gráfico la distancia entre individuos, de tal forma que la proximidad entre los ellos indica su grado de afinidad fenética. Finalmente, los individuos pertenecientes a una misma población quedan agrupados mediante el polígono de menor tamaño posible (*convex hull*), permitiendo visualizar gráficamente la distribución resultante en base al rasgo morfológico estudiado.

Tabla 5.9. Muestra dental utilizada para el análisis de Escalado Multidimensional No Métrico (\* molares analizados gracias a las imágenes obtenidas de la bibliografía)

<i>H. antecessor</i>	Gran Dolina-TD6
Población de la Sima de los Huesos	Sima de los Huesos
Pleistoceno Inferior de África	Mulhuli-Amo
Pleistoceno Medio de Europa	Arago, Montmaurin, Mala Balanica*
Pleistoceno Medio de África	Tighenif
Pleistoceno Medio de Asia*	Hexian, Yiyuan, Sangiran, Zhoukoudian, Xujiayao
Pleistoceno Medio de Oriente Próximo*	Qesem Cave
<i>H. neanderthalensis</i>	Abri Suard, Abri Bourgeois-Delaunay, Regordou, Roc de Marsal, Engis, Ehringsdorf, Hunas, Krapina, Gibraltar Devil's Tower
<i>H. sapiens</i>	Qafzeh, Equus Cave, Lagar Velho, El Mirador, Muestras contemporáneas



### 5.9.1. Variabilidad inter poblacional de la Gran Dolina-TD6, Sima de los Huesos, *H. neanderthalensis* y *H. sapiens* mediante el análisis de las crestas de trigónido de los $M_1s$ . Comparativa con otras poblaciones del Pleistoceno.

Como podemos observar en la Figura 5.9.1.1., tras analizar el primer, segundo y tercer molar del grupo de *H. sapiens* vemos que, excepto un espécimen del yacimiento de El Mirador (MIR4-P22-205), todos los individuos, tanto arcaicos como modernos, caen dentro de la variabilidad de los humanos actuales. Por ello, de aquí en adelante, para los demás análisis de Escalado Multidimensional No Métrico (NMDS), agruparemos a Qafzeh, Equus Cave, Lagar Velho, La Madeleine, El Mirador y la Muestra Contemporánea en un único grupo sin diferenciar entre *H. sapiens* fósil y *H. sapiens* moderno.

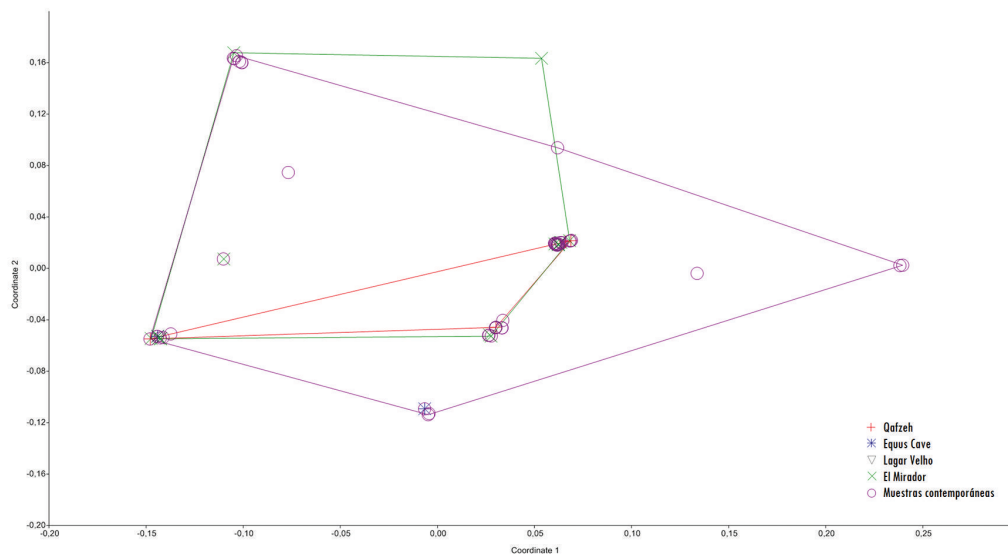


Figura 5.9.1.1. Escalado multidimensional no métrico (NMDS) y convex hulls para las crestas del trigónido en el esmalte y en la dentina de los  $M_1s$ ,  $M_2s$  y  $M_3s$  de los diferentes individuos de *H. sapiens* incluidos en la presente tesis doctoral.

La Figura 5.9.1.2. nos muestra el gráfico con los resultados del NMDS y los convex hulls para las crestas del trigónido en el esmalte y en la dentina de los  $M_1s$  de la Gran Dolina-TD6, la Sima de los Huesos (SH), *H. neanderthalensis* y *H. sapiens*. En él podemos observar que *H. sapiens* es el grupo con mayor variabilidad de todos, dentro del cual se encuentran los individuos del yacimiento de la Gran Dolina-TD6. Apenas existe solapamiento entre la población de la SH y los neandertales con el grupo de *H. sapiens* y los especímenes de *H. antecessor*. El 100% de la SH (n=14) cae en el mismo

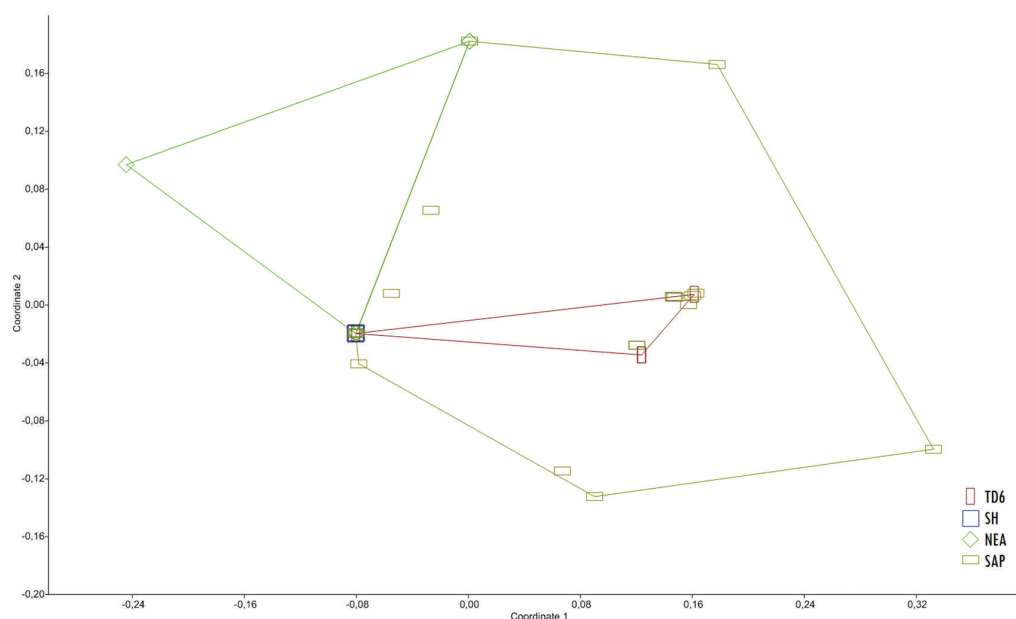


Figura 5.9.1.2. Escalado multidimensional no métrico (NMDS) y convex hulls para las crestas del trigónido en el esmalte y en la dentina de los  $M_3$  de Gran Dolina-TD6, Sima de los Huesos, *H. neanderthalensis* y *H. sapiens*.

punto, junto con el 75% de los *H. neanderthalensis* (12 de 16), un individuo de *H. antecessor* (ATD6-112) y cinco de los veintisiete especímenes de *H. sapiens* (Qafzeh-10, EQ-H8, MIR202-T34, IZ3 y AC82). Un individuo de *H. neanderthalensis* (Krapina\_D105) aparece separado del resto, al presentar ambas crestas del trigónido (media y distal) continuas, y otros tres (Krapina\_D79, Engis\_2 y HA-40.26) se alejan igualmente del conjunto compuesto por la SH y la mayoría de los neandertales, al mostrar crestas mesiales continuas.

En el gráfico de la Figura 5.9.1.3. el NMDS y los convex hulls nos muestran cómo dos de los tres individuos del Pleistoceno Medio europeo (Arago 40 y Montmaurin) caen dentro del grupo de la SH y de la mayoría de los neandertales. Sin embargo, Mala Balanica (BH-1), debido a su ausencia total de crestas, se encuentra dentro de la variabilidad de los *H. sapiens* agrupada con un individuo de *H. antecessor* (ATD6-96), Qafzeh-15, Lagar Velho y un individuo de la muestra contemporánea de comparativa. Por su parte, Tighenif\_2 aparece fuera pero próximo al conjunto de la SH y *H. neanderthalensis*, y asociado al grupo de *H. sapiens* junto con un individuo de la Edad del Bronce del yacimiento de El Mirador (MIR4-P22-294). Por otro lado, si consideramos al espécimen del yacimiento de Mulhuli-Amo (Buia, Eritrea) perteneciente al Pleistoceno Inferior, como un  $M_1$ , observamos que sus valores caen en el mismo lugar que todos los homínidos de la SH y la mayor parte de los neandertales,

estando por tanto alejado de los de sus coetáneos *H. antecessor*, excepto de ATD6-112 que presenta una cresta media del trigónido continua y una distal discontinua en el esmalte y en la dentina. Sin embargo, la interpretación de este espécimen debe ser tomada con cautela al tratarse de un individuo aislado. No obstante, es importante destacar el hecho de que, como ya se apunta en el trabajo realizado por Martínez de Pinillos y colaboradores (2017), el hasta entonces considerado rasgo autapomórfico de los neandertales, la cresta media del trigónido, aparece ya con una antigüedad cercana al millón de años, por lo que no puede considerarse un rasgo único y exclusivo del linaje neandertal.

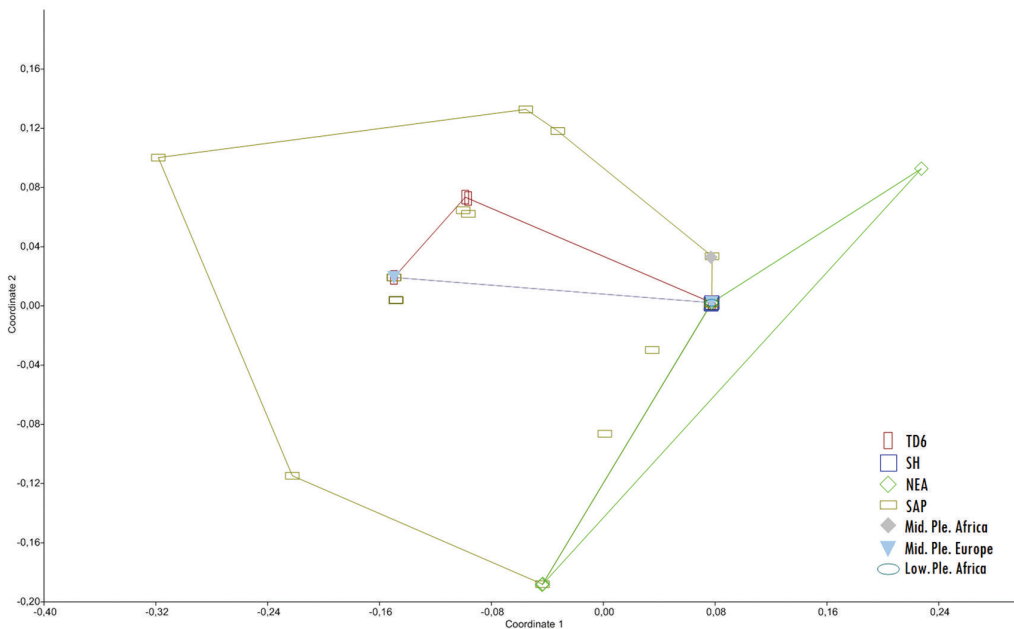


Figura 5.9.1.3. Escalado multidimensional no métrico (NMDS) y convex hulls para las crestas del trigónido en el esmalte y en la dentina de los  $M_3$  de Gran Dolina-TD6, Sima de los Huesos, *H. neanderthalensis*, *H. sapiens* y otros especímenes pleistocenos.

### 5.9.2. Variabilidad interpoblacional de la Gran Dolina-TD6, Sima de los Huesos, *H. neanderthalensis* y *H. sapiens* mediante el análisis de las crestas de trigónido de los $M_2$ s. Comparativa con otras poblaciones del Pleistoceno.

El NMDS y los convex hulls de la Figura 5.9.2.1. se basan en las frecuencias de expresión de las crestas del trigónido para el esmalte y la dentina de los  $M_2$ s de la Gran Dolina-TD6, la Sima de los Huesos (SH), *H. neanderthalensis* y *H. sapiens*. Al igual que ocurría con los  $M_1$ s, podemos ver de nuevo que el grupo de *H. sapiens* y *H. antecessor* aparecen separados de los neandertales y de la SH. En esta ocasión, la SH queda dividida en dos grupos diferentes: ocho de los once individuos se agrupan con cinco neandertales (Regourdou\_1, Krapina\_D3, Krapina\_D10, Krapina\_D86, Krapina\_D107) y tres *H. sapiens* (MIR4-P22-205, AC10, ISC2) al presentar una cresta media continua y una distal discontinua; mientras que los otros tres individuos de la SH aparecen asociados a dos neandertales (HA-40.26, Krapina\_D2) y dos humanos modernos por mostrar una cresta mesial continua y una distal discontinua. A su vez, dos especímenes de Krapina se encuentran separados del resto, uno por tener una cresta media discontinua y una distal continua (Krapina\_D6) y el otro por exhibir ambas crestas continuas (Krapina\_D104). Los cuatro  $M_2$ s de *H. antecessor* se sitúan dentro del grupo de *H. sapiens* y notablemente alejados de la SH y los neandertales.

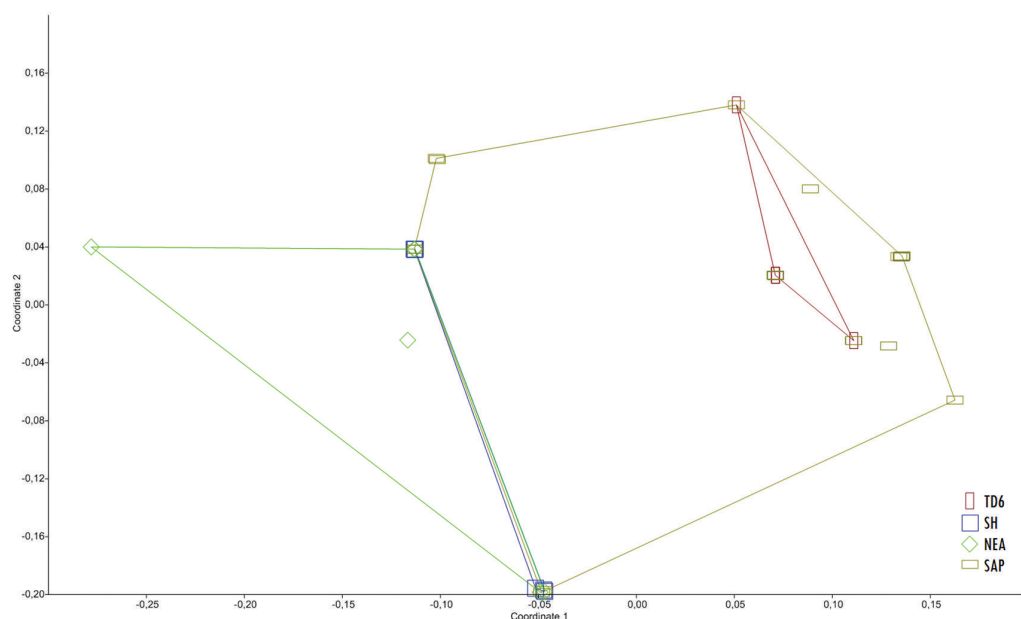


Figura 5.9.2.1. Escalado multidimensional no métrico (NMDS) y convex hulls para las crestas del trigónido en el esmalte y en la dentina de los  $M_2$ s de Gran Dolina-TD6, Sima de los Huesos, *H. neanderthalensis* y *H. sapiens*.

Así, ATD6-144 y TD6-96 se agrupan con 11 de los 32 (34%) *H. sapiens* al mostrar ambas crestas (medial y distal) discontinuas; ATD6-113 con 5 (16%) individuos que poseen una cresta distal discontinua y ATD6-5 aparece asociado a un único individuo de la Muestra Contemporánea que presenta una cresta media continua en la dentina pero no en el esmalte.

En el gráfico de la Figura 5.9.2.2. vemos que todos los especímenes del Pleistoceno Medio de Asia menos uno, que aparece fuera del resto de grupos (NG0802.3), están dentro de la variabilidad de *H. sapiens*. Los otros siete individuos quedan distribuidos de la siguiente manera: un espécimen de Sangiran Dome (NG92-D6-ZE-57s/d76), otro de Hexian (PA839), y uno de Yiyuan (Sh.y.072) se agrupan con un *H. antecessor* (ATD6-144) y once *H. sapiens* (Qafzeh-10, MIR201-7 y nueve humanos modernos) al mostrar ambas crestas del trigónido (media y distal) discontinuas. Otro espécimen de Sangiran Dome (NG92.3) que presenta tan solo una cresta distal discontinua, se sitúa junto con un *H. antecessor* (ATD6-113) y cinco *H. sapiens* (MIR4-P22-285 y cuatro humanos modernos). Otro individuo de Sangiran Dome (NG0802.2) queda agrupado con un *H. antecessor* (ATD6-96) y cinco *H. sapiens* (Qafzeh-15, MIR4-P22-230, MIR4-P22-108 y dos humanos modernos) al no presentar ningún tipo de cresta. El otro espécimen de Hexian (PA831) aparece junto a un humano moderno por presentar una cresta distal continua en la dentina pero no en el esmalte. Por otro lado, el espécimen de Zhoukoudian (PA70) que presenta una cresta mesial continua y una distal discontinua, se sitúa con tres individuos de la SH, dos *H. neanderthalensis* (Krapina\_D2 y HA-40.26) y dos humanos modernos. De nuevo, como ocurriera con los  $M_1$ s, Mala Balanica (BH-1) se encuentra dentro de la variabilidad de los *H. sapiens* junto con un humano moderno, mientras que el resto de los especímenes del Pleistoceno Medio Europeo (Arago y Montmaurin) se agrupan con el 73% (8 de 11) de los individuos de la SH, el 56% (5 de 9) de *H. neanderthalensis* y el 9% (3 de 32) de *H. sapiens*. Además, hay que destacar que junto a estos individuos también se encuentra el espécimen del Pleistoceno Medio de Oriente Próximo (QC12) y uno de los dos del Pleistoceno Medio africano (Tighenif\_1), mientras que el otro individuo (Tighenif\_2), como sucedía con los primeros molares, aparece asociado al grupo de *H. sapiens*. En esta ocasión, si consideramos al individuo del yacimiento de Mulhuli-Amo (Buia, Eritrea) como un  $M_2$ , de nuevo observamos que sus valores caen con la mayor parte de los *H. neanderthalensis* (5 de 9) y de los homínidos de la SH (8 de 11), junto con Arago, Montmaurin, Tighenif\_1 y QC12, pero esta vez alejado del 100% de sus coetáneos *H. antecessor*.

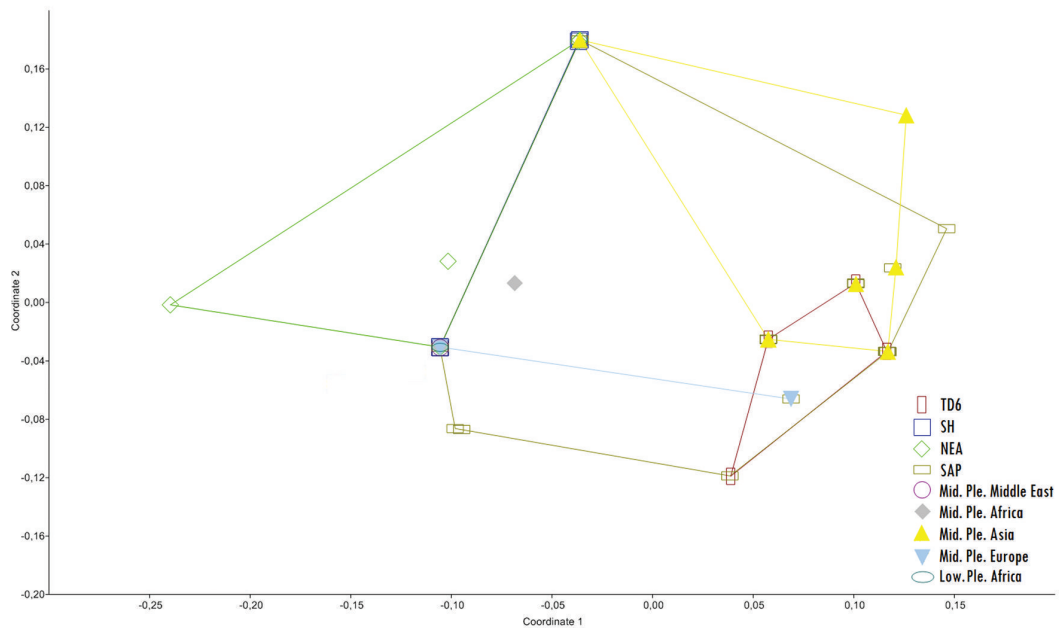


Figura 5.9.2.2. Escalado multidimensional no métrico (NMDS) y convex hulls para las crestas del trigónido en el esmalte y en la dentina de los  $M_3$  de Gran Dolina-TD6, Sima de los Huesos, *H. neanderthalensis*, *H. sapiens* y otros especímenes pleistocenos.

### 5.9.3. Variabilidad interpoblacional de la Gran Dolina-TD6, Sima de los Huesos, *H. neanderthalensis* y *H. sapiens* mediante el análisis de las crestas de trigónido de los $M_3$ s. Comparativa con otras poblaciones del Pleistoceno.

La Figura 5.9.3.1. ilustra el NMDS y los convex hulls de los  $M_3$ s de la Gran Dolina-TD6, la Sima de los Huesos (SH), *H. neanderthalensis* y *H. sapiens*, basándose en las frecuencias de expresión de las crestas del trigónido para el esmalte y la dentina. A diferencia de los anteriores gráficos, para esta clase dental hay un solapamiento general de los cuatro grupos con una mayor variabilidad en la expresión de crestas. Observamos que 6 de los 15 (40%) individuos de la SH y 5 de los 10 (50%) de *H. neanderthalensis* se encuentran dentro del grupo de los *H. sapiens*. En el caso de *H. antecessor*, los tres especímenes se integran dentro de la variabilidad de *H. sapiens* aunque uno de ellos (ATD6-113), al presentar una cresta media continua y una distal discontinua, se sitúa junto con el grupo formado por tres neandertales (Regourdou\_1, Abri Suard-S43 y Krapina\_D9) y un individuo de la SH. Mientras, los otros dos especímenes (ATD6-5 y ATD6-96) aparece junto a dos humanos modernos y al único *H. neanderthalensis* (Hunas\_I) que no exhibe ninguna cresta.

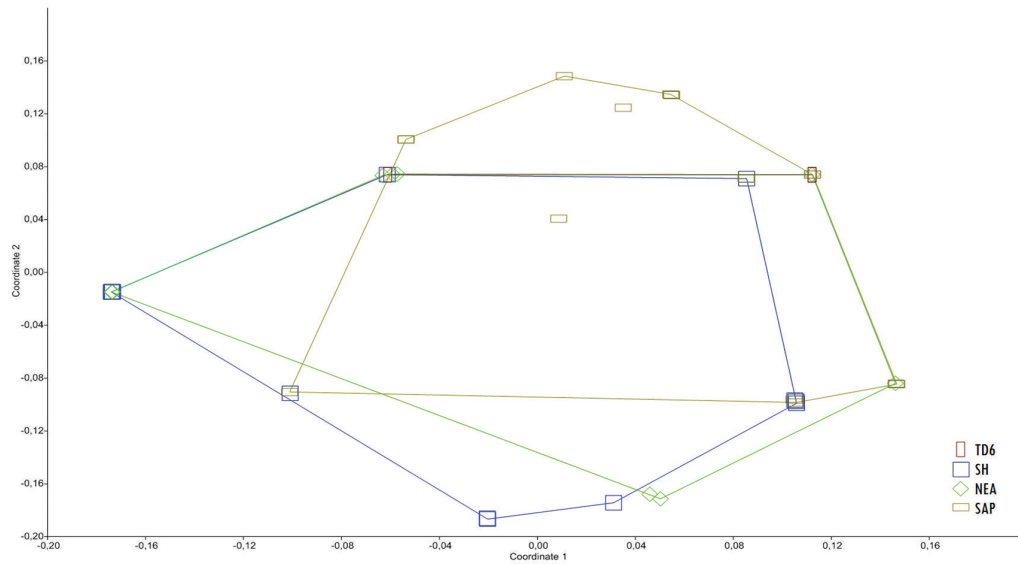


Figura 5.9.3.1. Escalado multidimensional no métrico (NMS) para las crestas del trigónido en el esmalte y en la dentina de los  $M_3$  de Gran Dolina-TD6, Sima de los Huesos, *H. neanderthalensis* y *H. sapiens*.

El NMS y los convex hulls de la Figura 5.9.3.2. muestran la amplia variabilidad existente en los  $M_3$ , donde la población de la SH cubre la práctica totalidad del resto de los homínidos analizados. Tan sólo el espécimen PA831 del Pleistoceno Medio de Asia se encuentra fuera de todos los grupos de variabilidad. En cuanto al resto de los individuos asiáticos, la única presencia de una cresta distal continua en el molar de Xujiayao (PA1500) lo sitúa junto a un homínido de la SH y a un humano moderno. Por otra parte, el individuo de Hexian (PA834-2) aparece asociado al espécimen de Arago (A-106) y a un humano moderno, mientras que el de Sangiran Dome (NG9107.2) se agrupa con un individuo de la SH, uno de la Edad del Cobre (MIR201-P37) y otro de la Muestra Contemporánea. Con respecto a los homínidos del Pleistoceno Medio africano, mientras que Tighenif\_2 aparece aislado, Tighenif\_1 se sitúa dentro de un amplio grupo compuesto por *H. antecessor* (ATD6-113), el espécimen de Montmaurin, un molar de la SH, tres *H. neanderthalensis* (Regourdou\_1, Abri Suard-S43 y Krapina\_D9), un individuo de la Edad del Bronce (MIR4-P22-230) y un humano moderno. Los otros dos individuos de *H. antecessor* (ATD6-5 y ATD6-96) se asocian con un neandertal (Hunas\_I) y dos molares de la Muestra Contemporánea de comparativa. Una vez más, Mala Balanica (BH-1) se sitúa dentro de la variabilidad de *H. sapiens* junto con un individuo de la Edad del Cobre (MIR201-7) y dos humanos modernos. Finalmente, el espécimen de Qesem Cave (QC13) aparece asociado a un individuo de la Muestra Contemporánea por presenta una cresta media del trigónido discontinua en el esmalte y continua en la dentina.

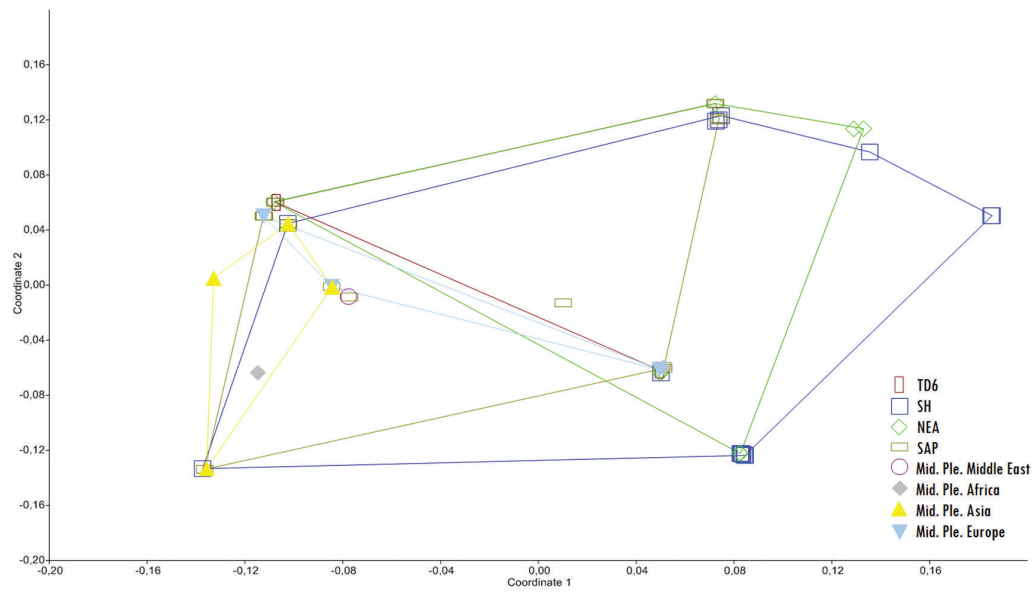


Figura 5.9.3.2. Escalado multidimensional no métrico (NMDS) y convex hulls para las crestas del trigónido en el esmalte y en la dentina de los  $M_3$  de Gran Dolina-TD6, Sima de los Huesos, *H. neanderthalensis*, *H. sapiens* y otros especímenes pleistocenos.



Tabla 5.10. Lista detallada de todos los molares utilizados en la presente tesis doctoral con su clasificación correspondiente para las crestas del trigónido y talónido.

ESPECIE / GRUPO	YACIMIENTO	ESPÉCIMEN	PIEZA DENTAL	OES	EDJ	TIC	EMR
-	Barranco León	BL02-J54-100	m <sub>1</sub> izq.	-	1	0	0
<i>H. antecessor</i>	Gran Dolina-TD6	ATD6-5	M <sub>1</sub> drch.	D	4	0	0
<i>H. antecessor</i>	Gran Dolina-TD6	ATD6-94	M <sub>1</sub> drch.	D	4	0	0
<i>H. antecessor</i>	Gran Dolina-TD6	ATD6-112	M <sub>1</sub> drch.	A	10	0	EMR
<i>H. antecessor</i>	Gran Dolina-TD6	ATD6-96	M <sub>1</sub> izq.	D	4	0	EMR
<i>H. antecessor</i>	Gran Dolina-TD6	ATD6-5	M <sub>2</sub> drch.	A	4	0	EMR
<i>H. antecessor</i>	Gran Dolina-TD6	ATD6-113	M <sub>2</sub> izq.	A	4	0	0
<i>H. antecessor</i>	Gran Dolina-TD6	ATD6-144	M <sub>2</sub> drch.	D	4	0	EMR
<i>H. antecessor</i>	Gran Dolina-TD6	ATD6-96	M <sub>2</sub> izq.	D	4	0	0
<i>H. antecessor</i>	Gran Dolina-TD6	ATD6-5	M <sub>3</sub> drch.	D	4	0	0
<i>H. antecessor</i>	Gran Dolina-TD6	ATD6-113	M <sub>3</sub> izq.	A	10	0	0
<i>H. antecessor</i>	Gran Dolina-TD6	ATD6-96	M <sub>3</sub> izq.	D	4	0	0
<i>H. antecessor</i>	Gran Dolina-TD6	ATD6-93	m <sub>1</sub> drch.	A	1	0	0
<i>H. antecessor</i>	Gran Dolina-TD6	ATD6-112	m <sub>1</sub> drch.	A	1	0	0
<i>H. antecessor</i>	Gran Dolina-TD6	ATD6-112	m <sub>2</sub> drch.	A	1	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-2	M <sub>1</sub> drch.	A	10	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-14	M <sub>1</sub> izq.	A	10	0	-
<i>SH hominins</i>	Sima de los Huesos	AT-21	M <sub>1</sub> izq.	A	7	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-22	M <sub>1</sub> izq.	A	1	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-101	M <sub>1</sub> drch.	A	10	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-141	M <sub>1</sub> drch.	A	7	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-272	M <sub>1</sub> drch.	A	12	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-286	M <sub>1</sub> izq.	A	12	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-556	M <sub>1</sub> izq.	A	10	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-561	M <sub>1</sub> drch.	A	8	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-576	M <sub>1</sub> izq.	A	8	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-829	M <sub>1</sub> izq.	A	8	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-943	M <sub>1</sub> drch.	D	4	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-1458	M <sub>1</sub> izq.	A	8	0	0
<i>SH hominins</i>	Sima de los Huesos	AT-1459	M <sub>1</sub> izq.	A	11	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-1759	M <sub>1</sub> izq.	A	10	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-2276	M <sub>1</sub> drch.	A	11	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-2438	M <sub>1</sub> drch.	A	8	0	0
<i>SH hominins</i>	Sima de los Huesos	AT-3175	M <sub>1</sub> drch.	A	11	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-3933	M <sub>1</sub> drch.	A	11	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-3934	M <sub>1</sub> izq.	A	10	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-4318	M <sub>1</sub> izq.	A	12	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-142	M <sub>2</sub> drch.	A	1	0	0
<i>SH hominins</i>	Sima de los Huesos	AT-169	M <sub>2</sub> izq.	A	1	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-271	M <sub>2</sub> drch.	A	13	0	0
<i>SH hominins</i>	Sima de los Huesos	AT-273	M <sub>2</sub> izq.	A	13	0	0
<i>SH hominins</i>	Sima de los Huesos	AT-284	M <sub>2</sub> drch.	A	11	0	0
<i>SH hominins</i>	Sima de los Huesos	AT-557	M <sub>2</sub> izq.	A	13	0	0
<i>SH hominins</i>	Sima de los Huesos	AT-941	M <sub>2</sub> izq.	A	12	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-946	M <sub>2</sub> izq.	A	11	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-1752	M <sub>2</sub> drch.	A	11	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-1756	M <sub>2</sub> drch.	A	12	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-1761	M <sub>2</sub> drch.	A	2	0	0
<i>SH hominins</i>	Sima de los Huesos	AT-2270	M <sub>2</sub> izq.	A	12	0	0

<i>SH hominins</i>	Sima de los Huesos	AT-2272	M <sub>2</sub> izq.	A	11	0	0
<i>SH hominins</i>	Sima de los Huesos	AT-2396	M <sub>2</sub> izq.	A	13	0	0
<i>SH hominins</i>	Sima de los Huesos	AT-3176	M <sub>2</sub> izq.	A	10	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-3179	M <sub>2</sub> izq.	A	13	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-3890	M <sub>2</sub> drch.	A	11	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-3889	M <sub>2</sub> drch.	A	11	0	0
<i>SH hominins</i>	Sima de los Huesos	AT-6579	M <sub>2</sub> izq.	A	12	0	EMR
<i>SH hominins*</i>	Sima de los Huesos	AT-11	M <sub>2</sub> izq.	-	-	0	-
<i>SH hominins</i>	Sima de los Huesos	AT-13	M <sub>3</sub> izq.	B	3	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-30	M <sub>3</sub> drch.	A	13	0	0
<i>SH hominins</i>	Sima de los Huesos	AT-100	M <sub>3</sub> izq.	C	3	0	0
<i>SH hominins</i>	Sima de los Huesos	AT-143	M <sub>3</sub> drch.	A	2	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-598	M <sub>3</sub> izq.	C	5	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-599	M <sub>3</sub> drch.	A	11	0	0
<i>SH hominins</i>	Sima de los Huesos	AT-811	M <sub>3</sub> drch.	C	14	0	0
<i>SH hominins</i>	Sima de los Huesos	AT-942	M <sub>3</sub> drch.	C	6	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-1468	M <sub>3</sub> drch.	A	10	0	0
<i>SH hominins</i>	Sima de los Huesos	AT-1473	M <sub>3</sub> izq.	D	4	0	0
<i>SH hominins</i>	Sima de los Huesos	AT-1945	M <sub>3</sub> izq.	B	3	0	0
<i>SH hominins</i>	Sima de los Huesos	AT-1959	M <sub>3</sub> drch.	C	5	2	0
<i>SH hominins</i>	Sima de los Huesos	AT-2271	M <sub>3</sub> izq.	C	5	1	0
<i>SH hominins</i>	Sima de los Huesos	AT-2273	M <sub>3</sub> izq.	C	9	2	0
<i>SH hominins</i>	Sima de los Huesos	AT-2277	M <sub>3</sub> drch.	C	6	2	0
<i>SH hominins</i>	Sima de los Huesos	AT-2385	M <sub>3</sub> izq.	B	3	0	0
<i>SH hominins</i>	Sima de los Huesos	AT-2438	M <sub>3</sub> drch.	C	9	0	0
<i>SH hominins</i>	Sima de los Huesos	AT-2760	M <sub>3</sub> izq.	C	6	0	0
<i>SH hominins</i>	Sima de los Huesos	AT-2777	M <sub>3</sub> drch.	A	13	0	0
<i>SH hominins</i>	Sima de los Huesos	AT-3182	M <sub>3</sub> drch.	A	8	0	0
<i>SH hominins</i>	Sima de los Huesos	AT-3943	M <sub>3</sub> drch.	A	11	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-6580	M <sub>3</sub> izq.	C	6	0	EMR
<i>SH hominins</i>	Sima de los Huesos	AT-947	m <sub>2</sub> izq.	A	1	0	0
<i>SH hominins</i>	Sima de los Huesos	AT-2398	m <sub>2</sub> drch.	A	1	0	EMR
<i>MP hominins Europe</i>	Arago	A-40	M <sub>1</sub> drch.	A	10	0	EMR
<i>MP hominins Europe</i>	Arago	A-68	M <sub>2</sub> drch.	A	12	0	EMR
<i>MP hominins Europe</i>	Arago	A-10	M <sub>2</sub> drch.	A	12	0	EMR
<i>MP hominins Europe</i>	Arago	A-32	M <sub>2</sub> izq.	A	12	0	EMR
<i>MP hominins Europe</i>	Arago	A-106	M <sub>3</sub> izq.	D	4	0	EMR
<i>MP hominins Europe*</i>	Arago	A-5	m <sub>2</sub> izq.	-	-	-	-
<i>MP hominins Europe</i>	Montmaurin	Montmaurin	M <sub>1</sub> drch.	A	1	0	EMR
<i>MP hominins Europe</i>	Montmaurin	Montmaurin	M <sub>1</sub> izq.	A	10	0	EMR
<i>MP hominins Europe</i>	Montmaurin	Montmaurin	M <sub>2</sub> drch.	A	7	0	EMR
<i>MP hominins Europe</i>	Montmaurin	Montmaurin	M <sub>2</sub> izq.	A	10	0	0
<i>MP hominins Europe</i>	Montmaurin	Montmaurin	M <sub>3</sub> drch.	A	10	0	EMR
<i>MP hominins Europe</i>	Montmaurin	Montmaurin	M <sub>3</sub> izq.	A	10	0	EMR
<i>MP hominins Africa</i>	Tighenif	Tighenif 1	M <sub>2</sub> drch.	A	7	0	0
<i>MP hominins Africa</i>	Tighenif	Tighenif 1	M <sub>2</sub> izq.	A	4	0	0
<i>MP hominins Africa</i>	Tighenif	Tighenif 1	M <sub>3</sub> drch.	D	4	0	0
<i>MP hominins Africa</i>	Tighenif	Tighenif 1	M <sub>3</sub> izq.	A	1	0	0
<i>MP hominins Africa</i>	Tighenif	Tighenif 2	M <sub>1</sub> izq.	A	1	0	EMR
<i>MP hominins Africa</i>	Tighenif	Tighenif 2	M <sub>2</sub> izq.	A	4	0	EMR
<i>MP hominins Africa</i>	Tighenif	Tighenif 2	M <sub>3</sub> izq.	B	4	0	EMR

<i>H. neanderthalensis</i>	Krapina	Krapina D77	M <sub>1</sub> drch.	A	10	0	EMR
<i>H. neanderthalensis</i>	Krapina	Krapina D79	M <sub>1</sub> drch.	A	13	0	EMR
<i>H. neanderthalensis</i>	Krapina	Krapina D80	M <sub>1</sub> drch.	A	8	0	EMR
<i>H. neanderthalensis</i>	Krapina	Krapina D84	M <sub>1</sub> drch.	A	10	0	EMR
<i>H. neanderthalensis</i>	Krapina	Krapina D105	M <sub>1</sub> drch.	C	6	4	0
<i>H. neanderthalensis</i>	Krapina	Krapina D81	M <sub>1</sub> izq.	A	12	6	EMR
<i>H. neanderthalensis</i>	Krapina	Krapina D82	M <sub>1</sub> izq.	A	10	0	-
<i>H. neanderthalensis*</i>	Krapina	Krapina D168	M <sub>1</sub> izq.	A	-	-	-
<i>H. neanderthalensis*</i>	Krapina	Krapina D1	M <sub>2</sub> drch.	D	-	-	-
<i>H. neanderthalensis</i>	Krapina	Krapina D3	M <sub>2</sub> izq.	A	10	0	-
<i>H. neanderthalensis</i>	Krapina	Krapina D86	M <sub>2</sub> izq.	A	12	0	EMR
<i>H. neanderthalensis</i>	Krapina	Krapina D107	M <sub>2</sub> izq.	A	10	0	EMR
<i>H. neanderthalensis</i>	Krapina	Krapina D2	M <sub>2</sub> drch.	A	14	0	-
<i>H. neanderthalensis</i>	Krapina	Krapina D6	M <sub>2</sub> izq.	B	3	0	EMR
<i>H. neanderthalensis</i>	Krapina	Krapina D10	M <sub>2</sub> drch.	A	12	0	EMR
<i>H. neanderthalensis</i>	Krapina	Krapina D104	M <sub>2</sub> drch.	C	6	0	0
<i>H. neanderthalensis</i>	Krapina	Krapina D4	M <sub>3</sub> izq.	C	2	0	0
<i>H. neanderthalensis</i>	Krapina	Krapina D5	M <sub>3</sub> izq.	C	5	1	0
<i>H. neanderthalensis</i>	Krapina	Krapina D9	M <sub>3</sub> izq.	A	8	0	EMR
<i>H. neanderthalensis</i>	Krapina	Krapina D85	M <sub>3</sub> izq.	C	6	0	0
<i>H. neanderthalensis</i>	Krapina	Krapina D106	M <sub>3</sub> izq.	C	2	5	0
<i>H. neanderthalensis</i>	Krapina	Krapina D7	M <sub>3</sub> drch.	C	6	4	0
<i>H. neanderthalensis*</i>	Krapina	Krapina D8	M <sub>3</sub> drch.	A	-	-	-
<i>H. neanderthalensis</i>	Krapina	Krapina D108	M <sub>3</sub> drch.	A	2	0	0
<i>H. neanderthalensis</i>	Krapina	Krapina D62	m <sub>2</sub> izq.	A	1	0	EMR
<i>H. neanderthalensis</i>	Krapina	Krapina D63	m <sub>2</sub> izq.	A	1	0	EMR
<i>H. neanderthalensis</i>	Krapina	Krapina D64	m <sub>2</sub> izq.	A	1	0	EMR
<i>H. neanderthalensis</i>	Krapina	Krapina D65	m <sub>2</sub> izq.	A	1	6	EMR
<i>H. neanderthalensis</i>	Krapina	Krapina D66	m <sub>2</sub> izq.	A	1	0	EMR
<i>H. neanderthalensis</i>	Krapina	Krapina D67	m <sub>1</sub> izq.	A	1	0	EMR
<i>H. neanderthalensis</i>	Krapina	Krapina D68	m <sub>2</sub> drch.	A	10	0	EMR
<i>H. neanderthalensis</i>	Engis	Engis 2	M <sub>1</sub> drch.	A	14	0	EMR
<i>H. neanderthalensis</i>	Devil's Tower	Gibraltar 2	M <sub>1</sub> drch.	A	7	0	EMR
<i>H. neanderthalensis</i>	Devil's Tower	Gibraltar 2	M <sub>1</sub> izq.	A	14	0	EMR
<i>H. neanderthalensis</i>	Devil's Tower	Gibraltar 2	M <sub>2</sub> izq.	A	14	0	EMR
<i>H. neanderthalensis</i>	Devil's Tower	Gibraltar 2	m <sub>1</sub> drch.	A	1	0	0
<i>H. neanderthalensis</i>	Devil's Tower	Gibraltar 2	m <sub>2</sub> drch.	A	1	0	EMR
<i>H. neanderthalensis</i>	Ehringsdorf	Ehringsdorf I 1048/69	M <sub>1</sub> izq.	A	10	0	EMR
<i>H. neanderthalensis*</i>	Ehringsdorf	Ehringsdorf G1 1010/69	M <sub>1</sub> izq.	A	-	-	-
<i>H. neanderthalensis*</i>	Ehringsdorf	Ehringsdorf G1 1010/69	M <sub>2</sub> izq.	A	-	-	-
<i>H. neanderthalensis</i>	Hunas	Hunas 1	M <sub>3</sub> drch.	D	4	0	0
<i>H. neanderthalensis</i>	Abri Suard	Abri Suard S5	M <sub>1</sub> izq.	A	12	0	EMR
<i>H. neanderthalensis</i>	Abri Suard	Abri Suard S14-7	M <sub>1</sub> drch.	A	11	0	EMR
<i>H. neanderthalensis</i>	Abri Suard	Abri Suard S49	M <sub>1</sub> drch.	A	7	0	EMR
<i>H. neanderthalensis</i>	Abri Suard	Abri Suard S43	M <sub>3</sub> drch.	A	11	0	0
<i>H. neanderthalensis</i>	Abri Suard	Abri Suard S15-5	m <sub>2</sub> drch.	A	1	0	EMR
<i>H. neanderthalensis</i>	Abri Bourgeois-Delaunay	Abri BDJ4C9	M <sub>1</sub> izq.	A	12	0	EMR

<i>H. neanderthalensis</i>	Regourdou	Regourdou 1	M <sub>1</sub> drch.	A	11	0	EMR
<i>H. neanderthalensis</i>	Regourdou	Regourdou 1	M <sub>1</sub> izq.	A	11	0	EMR
<i>H. neanderthalensis</i>	Regourdou	Regourdou 1	M <sub>2</sub> drch.	A	7	0	0
<i>H. neanderthalensis</i>	Regourdou	Regourdou 1	M <sub>2</sub> izq.	A	7	0	0
<i>H. neanderthalensis</i>	Regourdou	Regourdou 1	M <sub>3</sub> drch.	A	10	0	EMR
<i>H. neanderthalensis</i>	Regourdou	Regourdou 1	M <sub>3</sub> izq.	C	2	0	0
<i>H. neanderthalensis</i>	Roc de Marsal	Roc de Marsal	M <sub>1</sub> drch.	A	10	0	EMR
<i>H. neanderthalensis</i>	Roc de Marsal	Roc de Marsal	M <sub>1</sub> izq.	A	10	0	EMR
<i>H. sapiens</i>	Equus Cave	EQ-H5	M <sub>1</sub> drch.	D	11	0	EMR
<i>H. sapiens</i>	Equus Cave	EQ-H8	M <sub>1</sub> izq.	A	12	0	EMR
<i>H. sapiens</i> *	Equus Cave	EQ-H71/33	M <sub>3</sub> izq.	-	-	-	-
<i>H. sapiens</i>	Qafzeh	Qafzeh 10	M <sub>1</sub> drch.	A	7	0	0
<i>H. sapiens</i>	Qafzeh	Qafzeh 10	M <sub>1</sub> izq.	A	7	0	-
<i>H. sapiens</i>	Qafzeh	Qafzeh 15	M <sub>1</sub> drch.	D	4	0	0
<i>H. sapiens</i>	Qafzeh	Qafzeh 15	M <sub>1</sub> izq.	D	4	0	EMR
<i>H. sapiens</i>	Qafzeh	Qafzeh 10	M <sub>2</sub> drch.	D	4	0	0
<i>H. sapiens</i>	Qafzeh	Qafzeh 10	M <sub>2</sub> izq.	A	4	0	0
<i>H. sapiens</i>	Qafzeh	Qafzeh 15	M <sub>2</sub> drch.	D	4	0	0
<i>H. sapiens</i>	Qafzeh	Qafzeh 15	M <sub>2</sub> izq.	D	4	0	0
<i>H. sapiens</i>	Qafzeh	Qafzeh 15	m <sub>1</sub> drch.	A	1	0	0
<i>H. sapiens</i>	Qafzeh	Qafzeh 15	m <sub>1</sub> izq.	A	1	0	EMR
<i>H. sapiens</i>	Qafzeh	Qafzeh 15	m <sub>2</sub> drch.	D	4	0	EMR
<i>H. sapiens</i>	Qafzeh	Qafzeh 15	m <sub>2</sub> izq.	D	4	0	EMR
<i>H. sapiens</i>	Lagar Velho	Lagar Velho 1	M <sub>1</sub> drch.	D	4	0	EMR
<i>H. sapiens</i>	Lagar Velho	Lagar Velho 1	m <sub>2</sub> drch.	D	4	3	EMR
<i>H. sapiens</i>	La Madeleine	La Madeleine	m <sub>1</sub> drch.	D	4	0	0
<i>H. sapiens</i>	La Madeleine	La Madeleine	m <sub>1</sub> izq.	A	1	0	0
<i>H. sapiens</i>	La Madeleine	La Madeleine	m <sub>2</sub> drch.	D	4	1	0
<i>H. sapiens</i>	La Madeleine	La Madeleine	m <sub>2</sub> izq.	D	4	0	0
<i>H. sapiens</i>	El Mirador	MIR201-7	M <sub>1</sub> drch.	D	4	0	EMR
<i>H. sapiens</i>	El Mirador	MIR202-T34	M <sub>1</sub> drch.	A	1	0	0
<i>H. sapiens</i>	El Mirador	MIR202-T34	M <sub>1</sub> izq.	A	1	0	0
<i>H. sapiens</i>	El Mirador	MIR4 P22 294	M <sub>1</sub> izq.	A	1	0	0
<i>H. sapiens</i>	El Mirador	MIR4 P22 205	M <sub>1</sub> izq.	D	2	0	0
<i>H. sapiens</i>	El Mirador	MIR4 P22 108	M <sub>1</sub> izq.	D	4	0	0
<i>H. sapiens</i>	El Mirador	MIR4 P22 285	M <sub>1</sub> drch.	D	4	0	EMR
<i>H. sapiens</i>	El Mirador	MIR4 P22 190	M <sub>1</sub> izq.	D	4	0	EMR
<i>H. sapiens</i>	El Mirador	MIR201-7	M <sub>2</sub> drch.	D	4	0	EMR
<i>H. sapiens</i>	El Mirador	MIR202-T34	M <sub>2</sub> drch.	A	1	0	0
<i>H. sapiens</i>	El Mirador	MIR202-T34	M <sub>2</sub> izq.	D	4	0	0
<i>H. sapiens</i>	El Mirador	MIR4 P22 230	M <sub>2</sub> izq.	D	4	0	0
<i>H. sapiens</i>	El Mirador	MIR4 P22 205	M <sub>2</sub> izq.	A	10	0	0
<i>H. sapiens</i>	El Mirador	MIR4 P22 108	M <sub>2</sub> izq.	D	4	0	0
<i>H. sapiens</i>	El Mirador	MIR4 P22 285	M <sub>2</sub> drch.	D	4	0	EMR
<i>H. sapiens</i>	El Mirador	MIR201-7	M <sub>3</sub> drch.	D	4	0	EMR
<i>H. sapiens</i>	El Mirador	MIR201-P37	M <sub>3</sub> izq.	D	4	0	0

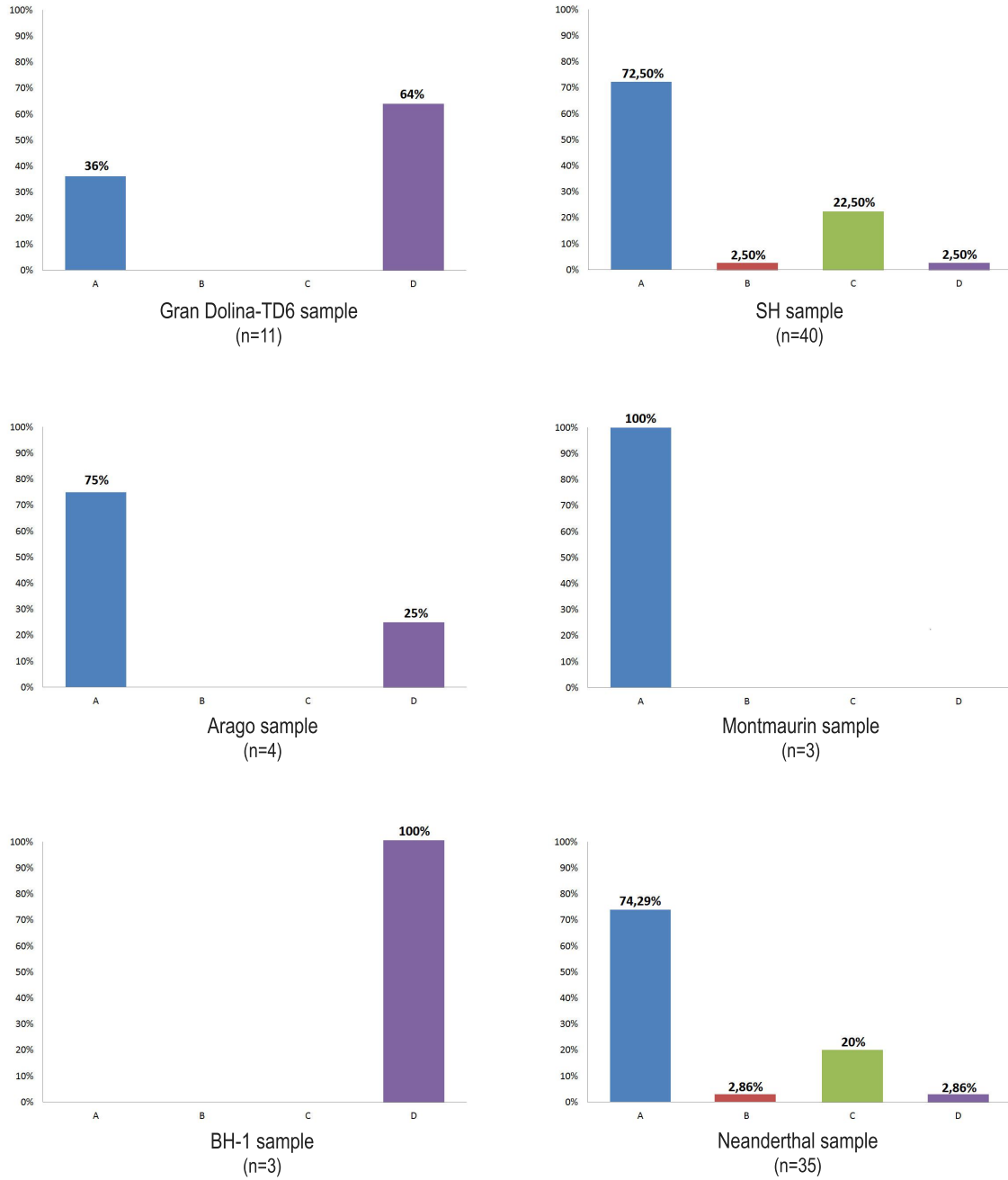
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<i>H. sapiens</i>	El Mirador	MIR4 P22 205	M <sub>3</sub> izq.	A	2	0	0
<i>H. sapiens</i>	El Mirador	MIR4 P22 294	m <sub>1</sub> izq.	A	1	0	0
<i>H. sapiens</i>	El Mirador	MIR4 P22 294	m <sub>2</sub> izq.	-	-	-	0
<i>H. sapiens</i>	Muestra contemporánea	IZ3	M <sub>1</sub> drch.	A	8	0	0
<i>H. sapiens</i>	Muestra contemporánea	HER8	M <sub>1</sub> izq.	D	4	0	EMR
<i>H. sapiens</i>	Muestra contemporánea	AC87	M <sub>1</sub> izq.	A	8	0	EMR
<i>H. sapiens</i>	Muestra contemporánea	BL4	M <sub>1</sub> izq.	D	4	0	EMR
<i>H. sapiens</i>	Muestra contemporánea	UCM16	M <sub>1</sub> izq.	D	4	0	EMR
<i>H. sapiens</i>	Muestra contemporánea	UCM38	M <sub>1</sub> izq.	D	4	0	EMR
<i>H. sapiens</i>	Muestra contemporánea	UCM48	M <sub>1</sub> izq.	A	2	0	0
<i>H. sapiens</i>	Muestra contemporánea	UCM10	M <sub>1</sub> izq.	B	3	0	EMR
<i>H. sapiens</i>	Muestra contemporánea	UCM28	M <sub>1</sub> izq.	D	4	0	EMR
<i>H. sapiens</i>	Muestra contemporánea	UCM38	M <sub>1</sub> drch.	D	4	0	EMR
<i>H. sapiens</i>	Muestra contemporánea	UCM51	M <sub>1</sub> drch.	D	4	0	EMR
<i>H. sapiens</i>	Muestra contemporánea	UCM53	M <sub>1</sub> drch.	A	4	0	EMR
<i>H. sapiens</i>	Muestra contemporánea	UCM67	M <sub>1</sub> drch.	D	4	0	EMR
<i>H. sapiens</i>	Muestra contemporánea	UCM26	M <sub>1</sub> drch.	D	4	0	EMR
<i>H. sapiens</i>	Muestra contemporánea	UCM44	M <sub>1</sub> drch.	D	4	0	-
<i>H. sapiens</i>	Muestra contemporánea	UCM65	M <sub>1</sub> drch.	D	4	0	EMR
<i>H. sapiens</i>	Muestra contemporánea	AC7	M <sub>2</sub> drch.	D	4	0	0
<i>H. sapiens</i>	Muestra contemporánea	AG1	M <sub>2</sub> drch.	D	4	0	EMR
<i>H. sapiens</i>	Muestra contemporánea	AC33	M <sub>2</sub> drch.	D	4	0	0
<i>H. sapiens</i>	Muestra contemporánea	AC12	M <sub>2</sub> izq.	D	4	0	0
<i>H. sapiens</i>	Muestra contemporánea	AC10	M <sub>2</sub> izq.	A	8	0	0
<i>H. sapiens</i>	Muestra contemporánea	ISC2	M <sub>2</sub> izq.	A	8	0	EMR
<i>H. sapiens</i>	Muestra contemporánea	BA12	M <sub>2</sub> izq.	D	4	0	0
<i>H. sapiens</i>	Muestra contemporánea	IZ14	M <sub>2</sub> izq.	D	4	0	0
<i>H. sapiens</i>	Muestra contemporánea	CR20080000017	M <sub>2</sub> izq.	D	4	0	0
<i>H. sapiens</i>	Muestra contemporánea	CR200800000113	M <sub>2</sub> izq.	D	3	0	0
<i>H. sapiens</i>	Muestra contemporánea	UCM3	M <sub>2</sub> izq.	D	4	0	EMR
<i>H. sapiens</i>	Muestra contemporánea	UCM3	M <sub>2</sub> drch.	D	4	0	0
<i>H. sapiens</i>	Muestra contemporánea	UCM58	M <sub>2</sub> izq.	D	4	0	0
<i>H. sapiens</i>	Muestra contemporánea	UCM58	M <sub>2</sub> drch.	D	4	0	EMR
<i>H. sapiens</i>	Muestra contemporánea	UCM22	M <sub>2</sub> drch.	D	1	0	0
<i>H. sapiens</i>	Muestra contemporánea	UCM67	M <sub>2</sub> drch.	A	2	0	0
<i>H. sapiens</i>	Muestra contemporánea	UCM59	M <sub>2</sub> izq.	D	4	0	0
<i>H. sapiens</i>	Muestra contemporánea	UCM65	M <sub>2</sub> izq.	D	4	0	EMR
<i>H. sapiens</i>	Muestra contemporánea	UCM9	M <sub>2</sub> izq.	D	4	0	EMR
<i>H. sapiens</i>	Muestra contemporánea	UCM10	M <sub>2</sub> izq.	A	2	0	0
<i>H. sapiens</i>	Muestra contemporánea	UCM69	M <sub>2</sub> izq.	D	4	0	EMR
<i>H. sapiens</i>	Muestra contemporánea	UCM24	M <sub>2</sub> izq.	A	1	0	0
<i>H. sapiens</i>	Muestra contemporánea	UCM28	M <sub>2</sub> izq.	D	4	0	0
<i>H. sapiens</i>	Muestra contemporánea	UCM38	M <sub>2</sub> izq.	D	4	0	0
<i>H. sapiens</i>	Muestra contemporánea	UCM44	M <sub>2</sub> izq.	D	4	0	0
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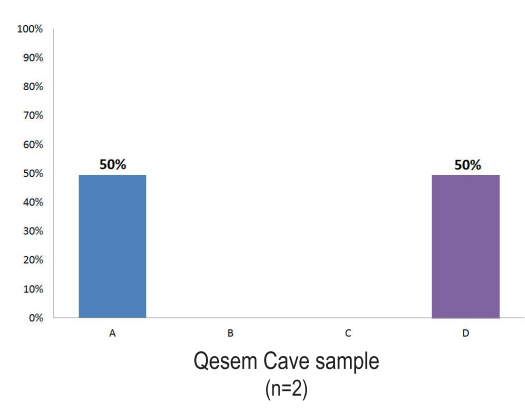
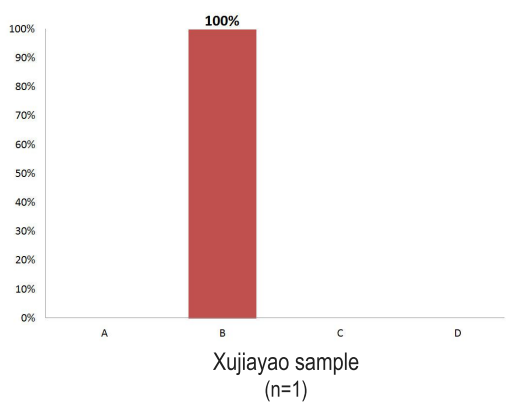
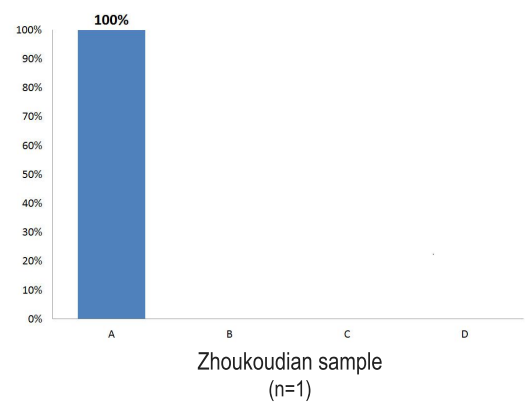
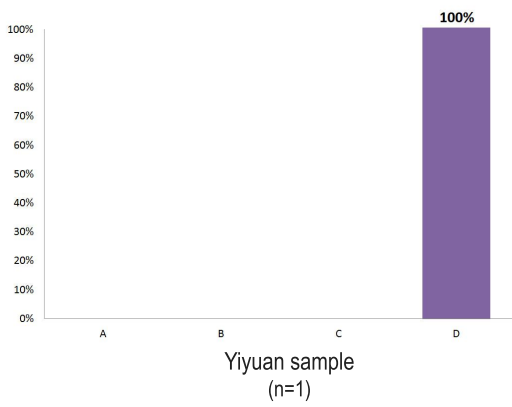
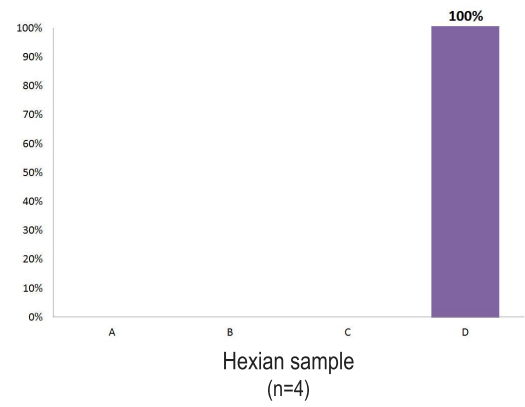
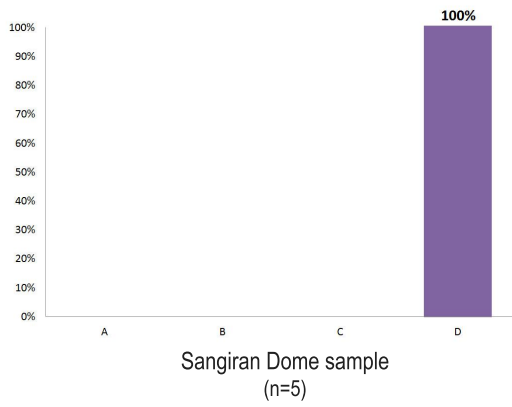
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<i>H. sapiens</i>	Muestra contemporánea	JB1	M <sub>3</sub> izq.	D	4	0	0
<i>H. sapiens</i>	Muestra contemporánea	CR20080000092	M <sub>3</sub> izq.	A	14	0	0
<i>H. sapiens</i>	Muestra contemporánea	CR20080000117	M <sub>3</sub> drch.	A	1	0	0
<i>H. sapiens</i>	Muestra contemporánea	CR20080000118	M <sub>3</sub> izq.	D	4	0	0
<i>H. sapiens</i>	Muestra contemporánea	CR20080000123	M <sub>3</sub> izq.	D	4	0	0
<i>H. sapiens</i>	Muestra contemporánea	UCM18	M <sub>3</sub> izq.	A	2	0	EMR
<i>H. sapiens</i>	Muestra contemporánea	UCM65	M <sub>3</sub> izq.	D	4	0	0
<i>H. sapiens</i>	Muestra contemporánea	UCM30	M <sub>3</sub> izq.	A	2	0	0
<i>H. sapiens</i>	Muestra contemporánea	UCM31	M <sub>3</sub> izq.	D	4	0	0
<i>H. sapiens</i>	Muestra contemporánea	UCM38	M <sub>3</sub> izq.	B	3	0	0
<i>H. sapiens</i>	Muestra contemporánea	UCM4	M <sub>3</sub> drch.	D	1	0	0
<i>H. sapiens</i>	Muestra contemporánea	UCM37	M <sub>3</sub> drch.	D	4	0	0
<i>H. ergaster</i>	Buia	MA 93	M <sub>1/2</sub> izq.	A	10	0	EMR
<i>H. erectus</i>	Sangiran Dome	NG0802.3	M <sub>2</sub> drch.	D	4	0	0
<i>H. erectus</i>	Sangiran Dome	NG92.3	M <sub>2/3</sub> izq.	D	4	0	EMR
<i>H. erectus</i>	Sangiran Dome	NG92 D6 ZE 57s/d 76	M <sub>2/3</sub> drch.	D	4	0	0
<i>H. erectus</i>	Sangiran Dome	NG0802.2	M <sub>2/3</sub> drch.	D	4	0	0
<i>H. erectus</i>	Sangiran Dome	NG9107.2	M <sub>3</sub> izq.	D	4	0	EMR
<i>H. erectus</i>	Sangiran Dome	PCG.2	m <sub>2</sub> drch.	A	1	0	0
<i>H. erectus</i>	Yiyuan	Sh.y.072	M <sub>2</sub> izq.	D	4	0	EMR
<i>H. erectus</i>	Hexian	PA838	M <sub>2</sub> izq.	D	-	0	-
<i>H. erectus</i>	Hexian	PA839	M <sub>2</sub> izq.	D	4	0	EMR
<i>H. erectus</i>	Hexian	PA834-2	M <sub>3</sub> izq.	D	4	0	-
<i>H. erectus</i>	Hexian	PA831	M <sub>2</sub> izq.	D	3	0	0
<i>H. erectus</i>	Hexian	PA831	M <sub>3</sub> izq.	D	3	0	0
<i>H. erectus</i>	Zhoukoudian	PA 70	M <sub>2</sub> izq.	A	2	0	EMR
-	Xujiayao	PA 1500	M <sub>3</sub> drch.	B	3	0	EMR
-	Qesem Cave	QC12	M <sub>2</sub> drch.	A	10	0	0
-	Qesem Cave	QC13	M <sub>3</sub> izq.	D	11	0	0
-	Qesem Cave	QC2	m <sub>2</sub> izq.	A	7	0	EMR
<i>H. heidelbergensis</i> s.l.	Mala Balanica	BH-1	M <sub>1</sub> izq.	D	4	0	0
<i>H. heidelbergensis</i> s.l.	Mala Balanica	BH-1	M <sub>2</sub> izq.	D	4	0	EMR
<i>H. heidelbergensis</i> s.l.	Mala Balanica	BH-1	M <sub>3</sub> izq.	D	4	0	EMR

\* molares cuyo estado de conservación o reconstrucción 3D no ha permitido una correcta visualización de los caracteres morfológicos  
 - sin asignación

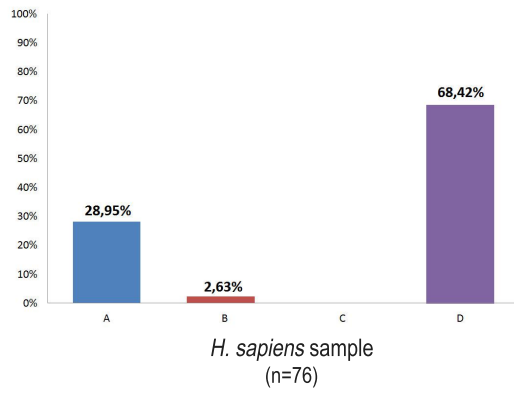
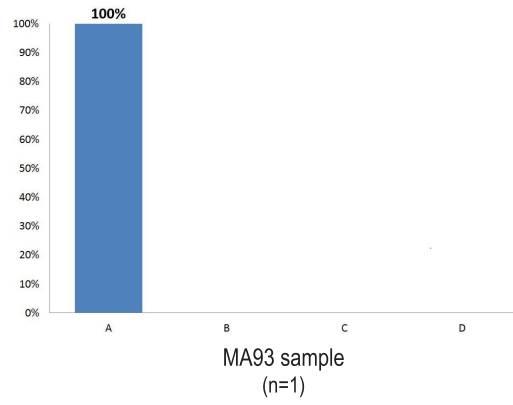
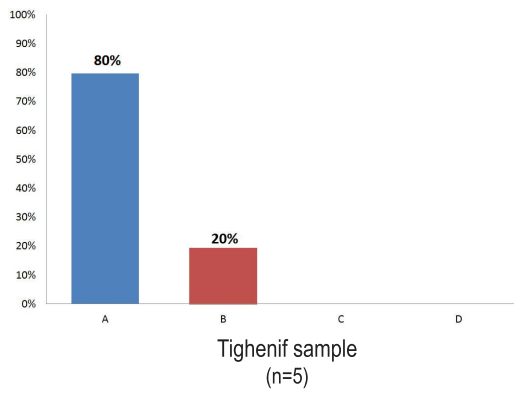
MP (Middle Pleistocene); OES (Occlusal Enamel Surface); EDJ (Enamel Dentine Junction); TIC (Talonid Crest); EMR (Entoconid Mesial Ridge)

Gráficos 5.1. Porcentajes de los diferentes tipos de crestas del trigónido en el esmalte de los molares permanentes para cada grupo de homínidos, siguiendo el método unilateral de Turner (1987).

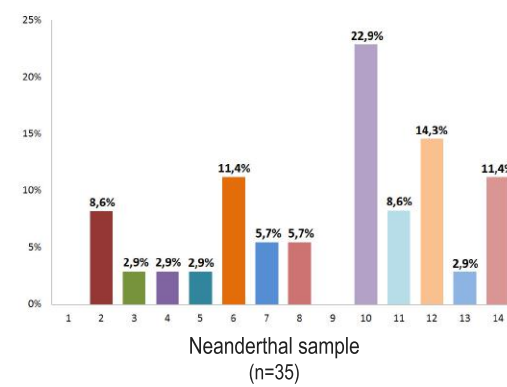
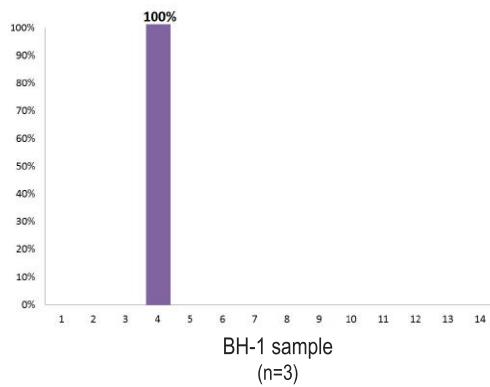
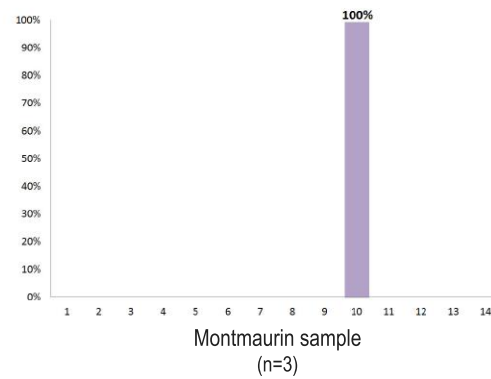
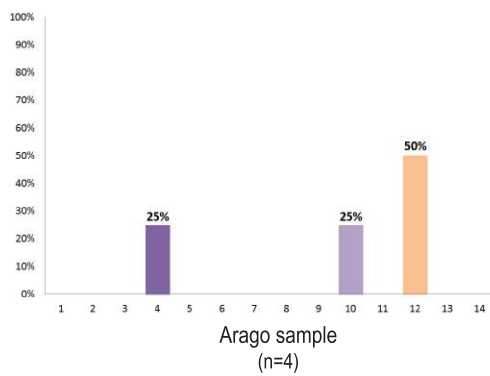
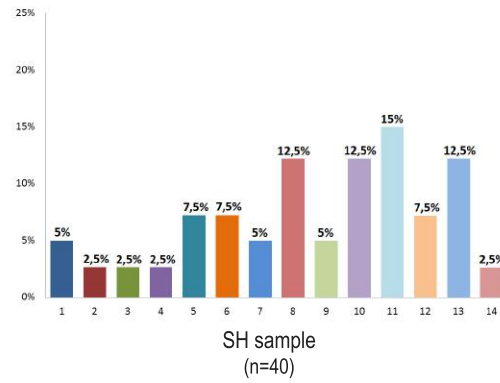
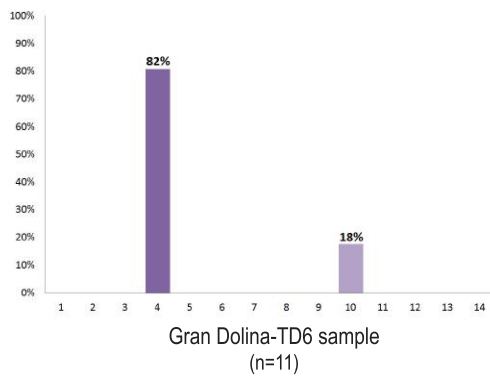


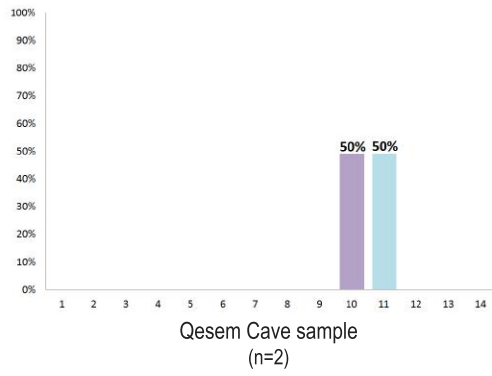
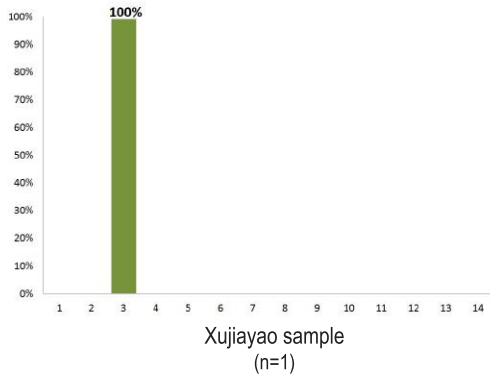
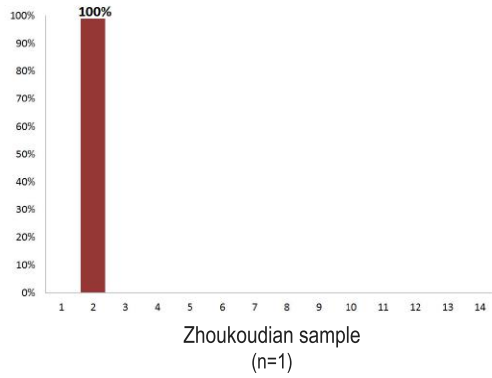
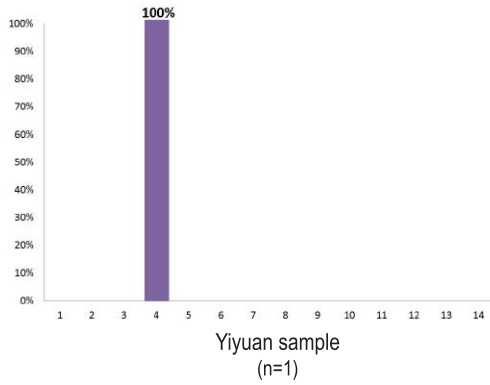
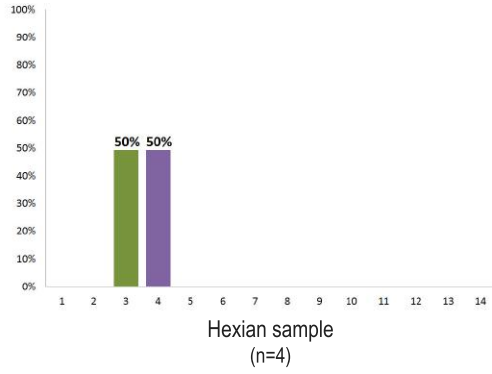
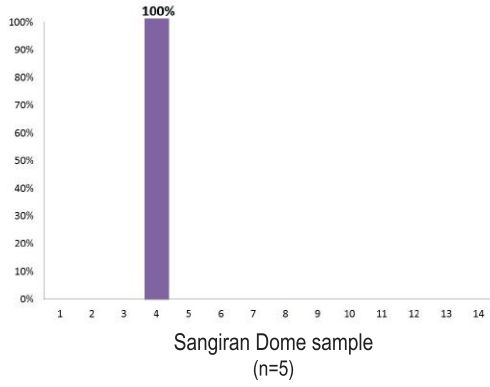


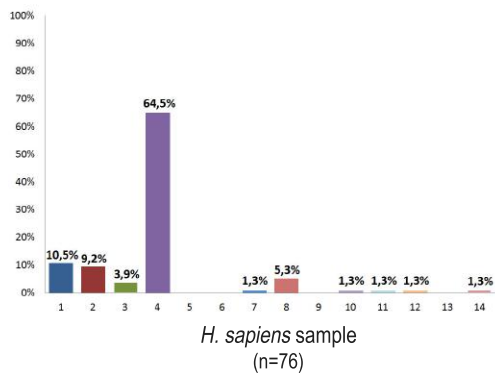
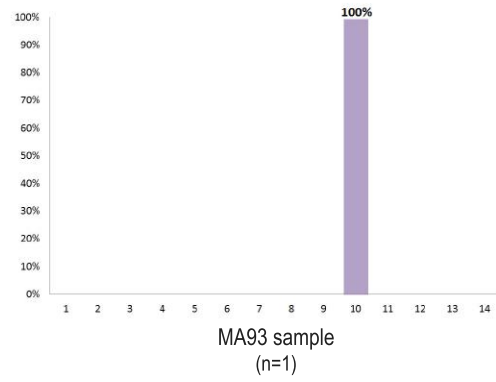
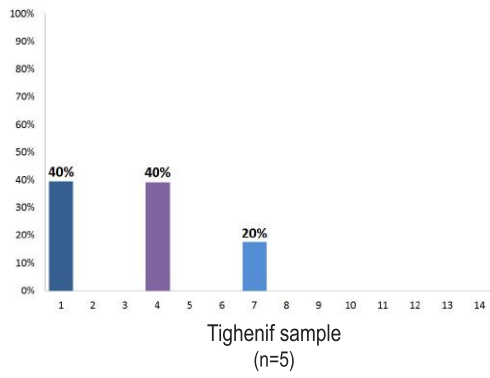




Gráficos 5.2. Porcentajes de los diferentes tipos de crestas del trigónido en la dentina de los molares permanentes para cada grupo de homínidos, siguiendo el método unilateral de Turner (1987). Los ejes de la "Y" para las muestras de la SH y los neandertales son diferentes con el fin de visualizar mejor los resultados.









06

DISCUSIÓN



## 6. DISCUSIÓN

La variación en la forma dental, así como las frecuencias y grados de expresión de muchos rasgos discretos se consideran altamente hereditarios (p. ej., Biggerstaff, 1973; Alvesalo et al., 1975; Blanco y Chakraborty, 1976), lo que hace que los dientes sean mucho más útiles que los restos esqueléticos para evaluar proximidades filogenéticas entre homínidos. Por ello, el estudio de los caracteres dentales se han convertido en una valiosa fuente de información a la hora de inferir relaciones evolutivas entre humanos modernos (p. ej., Scott y Turner II, 1997; Pilbrow, 2006), homínidos fósiles (p. ej., Bailey, 2002a; Bermúdez de Castro et al., 2003; Irish y Guatelli-Steinberg, 2003; Bailey, 2004; Guatelli-Steinberg y Irish, 2005; Kaifu et al., 2005; Martínón-Torres et al., 2006, 2012; Gómez-Robles et al., 2015; Skinner et al., 2016) y otros hominoideos (p. ej., Pilbrow, 2006; Skinner et al., 2008), así como para investigar el escenario en el que estas especies evolucionaron (p. ej., Martínón-Torres et al., 2007, 2011; Bermúdez de Castro y Martínón-Torres, 2013).

Aunque a día de hoy está ampliamente aceptado que la morfología de la dentina tiene una notable influencia en la morfología externa de un diente (Nager, 1960; Schwartz et al., 1998; Guy et al., 2003), la caracterización de los rasgos dentales se ha basado primordialmente en la superficie del esmalte. Sin embargo, desde 1960 algunos investigadores analizaron las estructuras internas en un intento de relacionar los caracteres morfológicos del esmalte con los de la dentina, pero para ello fue necesario, o bien aplicar técnicas destructivas, o bien estudiar los dientes incompletos o rotos (Nager, 1960; Korenhof, 1961, 1966; Sakai et al., 1967; Sakai y Hanamura, 1971, 1973; Korenhof, 1978, 1982; Corruccini, 1987a; b; Corruccini y Holt, 1989). Más recientemente y gracias a los avances en microtomografía axial computarizada (microCT), estos estudios se pueden llevar a cabo sin necesidad de dañar la muestra, lo que ha facilitado enormemente el estudio de ciertos rasgos con importante valor taxonómico y filogenético (Zubov, 1992a; Scott y Turner II, 1997; Irish, 1998; Martínón-Torres, 2006; Olejniczak et al., 2007; Le Cabec et al., 2013; Bailey et al., 2014; Xing et al., 2014; Bermúdez de Castro et al., 2016a; Skinner et al., 2016). Con esta tesis doctoral, pretendemos explorar la diversidad y las afinidades fenéticas existentes entre diferentes grupos de homínidos en cuanto a la expresión de los patrones de crestas expresados tanto en el esmalte como en la dentina.



## 6.1. LOS HOMININOS DE LA GRAN DOLINA-TD6: *HOMO ANTECESSOR*

### 6.1.1. Estatus taxonómico y filogenético de *Homo antecessor*. El estado de la cuestión.

Desde que en 1994 se hallaran en el nivel TD6 del yacimiento de la Gran Dolina restos fósiles humanos atribuidos a una especie nueva, *Homo antecessor* (Bermúdez de Castro et al., 1997a), el panorama de la evolución humana de nuestro continente ha cambiado considerablemente. Inicialmente, *H. antecessor* fue propuesto como el mejor candidato para representar al ancestro común de los neandertales y los humanos modernos por la presencia de diversas sinapomorfías compartidas entre ambos linajes (Bermúdez de Castro et al., 1997a; Martínez y Arsuaga, 1997). Años más tarde, diversos estudios comparativos entre la dentición de TD6 y los homínidos de la Sima de los Huesos (Bermúdez de Castro et al., 2003a; Martínón-Torres et al., 2012; Gómez-Robles et al., 2013; Bermúdez de Castro y Martínón-Torres, 2014; Martínez de Pinillos et al., 2017), planteaban la posibilidad de una discontinuidad poblacional entre *H. antecessor* y los homínidos del Pleistoceno Medio europeo. Estos análisis sugerían que las poblaciones del Pleistoceno Inferior de Europa habrían sido reemplazadas o genéticamente absorbidas por la llegada de nuevos grupos. Sin embargo, a su vez, también proponían algún tipo de relación filogenética entre *H. antecessor* y estos grupos del Pleistoceno Medio. La combinación única de caracteres primitivos y derivados que *H. antecessor* comparte con la Sima de los Huesos, con los neandertales y con *H. sapiens*, sugiere la posibilidad de que todos ellos hayan compartido un ancestro común el cual habría evolucionado en África o en el suroeste asiático (Bermúdez de Castro y Martínón-Torres, 2014; Bermúdez de Castro et al., 2017).

En la actualidad, el incremento del registro fósil de África y Eurasia está permitiendo, por un lado, obtener nuevas interpretaciones sobre la posición filogenética de los humanos de TD6 y, por otro, plantear hipótesis alternativas sobre el escenario evolutivo europeo (Martínón-Torres et al., 2007a; Carbonell et al., 2008b; Dennell et al., 2010; Bermúdez de Castro y Martínón-Torres, 2013). Uno de los debates más interesantes a día de hoy trata de aclarar la posible continuidad o discontinuidad existente en los grupos humanos de Europa durante el Pleistoceno (MacDonald et al., 2012; Bermúdez de Castro et al., 2013, 2016b; Rodríguez-Gómez et al., 2014).

Los datos climáticos y faunísticos demuestran que durante el Pleistoceno Inferior y en particular durante el Pleistoceno Medio, las migraciones entre África y Eurasia fueron escasas (van der Made, 2011). Del mismo modo, las evidencias craneales,

postcraneales y dentales sugieren que desde el Pleistoceno Inferior al Superior las poblaciones euroasiáticas y africanas pudieron seguir caminos relativamente independientes, favoreciendo un mayor impacto genético de Asia en la colonización de Europa que el proveniente de África (Martínez y Arsuaga, 1997; Arsuaga et al., 1999b; Carbonell et al., 2005; Martínón-Torres, 2006; Martínón-Torres et al., 2007a; Bermúdez de Castro et al., 2012). De esta manera, los homínidos europeos muestran mayores similitudes anatómicas con los grupos pleistocenos de Asia que con los de África, respaldando la hipótesis sobre el origen euroasiático y no africano de las poblaciones pleistocenas de Europa (Bermúdez de Castro y Martínón-Torres, 2013). Esta pérdida de caracteres africanos en los especímenes europeos anteriores al millón de años parece indicar que probablemente no fuesen descendientes directos de los homínidos que salieron del continente africano a finales del Pleistoceno Inferior, sino de una migración anterior (Bermúdez de Castro et al., 2011b). Bajo este contexto, el escenario más lógico y plausible es pensar que los homínidos de dicha migración anterior, representada a día de hoy por *Homo georgicus* (Gabunia et al., 2002), se hubiesen asentado en la zona del suroeste asiático desde donde, movidos principalmente por factores ecológicos y climáticos, se hubiesen expandido hacia otros territorios (Martínón-Torres et al., 2007a). Sin embargo, otros autores siguen defendiendo la hipótesis de un taxón Afro-Europeo (*H. heidelbergensis* s.l.) para el ancestro común de los humanos modernos y el linaje neandertal (Rightmire, 2008; Mounier et al., 2009; Stringer, 2012; Mounier y Mirazón Lahr, 2016).

En los últimos años, varios investigadores proponen un nuevo modelo de colonización de Europa en el que plantean que la historia evolutiva de las poblaciones africanas y euroasiáticas fue relativamente independiente durante el Pleistoceno Inferior, y casi totalmente independiente durante el Pleistoceno Medio (Dennell et al., 2010; Bermúdez de Castro y Martínón-Torres, 2013; Bermúdez de Castro et al., 2013, 2016b). Estos autores sugieren una colonización *no lineal* del continente, es decir, la existencia de pulsos migratorios de población desde un área de dispersión continuamente habitada (*CADE*, del inglés *central area of dispersals of Eurasia*), cuya localización más favorable se encontraría en Oriente Próximo por representar un verdadero cruce de caminos entre África, Europa y Asia. Este nuevo modelo implicaría la presencia en dicho área de dispersión de una “población madre”, que habría experimentado su propia evolución y cuyos cambios se verían reflejados en las diversas migraciones de paleo-demes que saldrían hacia otros territorios. Sin embargo, las complicadas barreras ecológicas, geográficas y climatológicas (Agustí et al., 2009;

Almogi-Labin, 2011; Cuenca-Bescós et al., 2011; Dennell et al., 2011; Finlayson et al., 2011; Leroy et al., 2011) que tuvieron que superar los distintos grupos humanos en su expansión hacia Europa -especialmente durante los periodos glaciales- pudieron favorecer procesos de deriva genética, con largos periodos de aislamiento, adaptaciones a las nuevas condiciones e incluso la posible hibridación entre paleo-demes (Dennell et al., 2010; Martín-Torres et al., 2011a; MacDonald et al., 2012; Bermúdez de Castro y Martín-Torres, 2013), lo que explicaría la notable diversidad existente en el registro fósil del Pleistoceno europeo (Manzi et al., 2001; Bermúdez de Castro et al., 2011b; Lorenzo et al., 2014; Bermúdez de Castro et al., 2015; de Lumley M.-A., 2015; Skinner et al., 2016).

### **6.1.2. Relación de *Homo antecessor* con los homínidos del Pleistoceno Medio y Superior de Europa y *Homo sapiens*.**

Tanto los restos fósiles como las evidencias arqueológicas y paleoambientales (Martín-Torres et al., 2007a; Bermúdez de Castro et al., 2011b; Dennell et al., 2011; Rodríguez et al., 2011; Moncel et al., 2013; Bermúdez de Castro et al., 2016b; Rocca, 2016) sugieren que durante el Pleistoceno Inferior, en la zona del suroeste asiático se produjeron uno o más eventos cladogenéticos que serían el origen de varias oleadas de población hacia Europa durante finales del Pleistoceno Inferior y Pleistoceno Medio. Una de esas oleadas se establecería en la zona más occidental de Eurasia dando lugar a la especie *H. antecessor* (Bermúdez de Castro et al., 1997a). Por otro lado, y a pesar de que los restos fósiles humanos de la Sima del Elefante-TE9 en la sierra de Atapuerca (Burgos, España) son escasos (Carbonell et al., 2008a; Bermúdez de Castro et al., 2011b; Martín-Torres et al., 2011b; Prado-Simón et al., 2012a; Lorenzo et al., 2014), todo apunta a que pudieran ser fruto de una dispersión anterior y diferente a la atribuida para *H. antecessor*, lo que permitiría hablar de, al menos, dos migraciones distintas hacia Europa occidental (MacDonald et al., 2012; Bermúdez de Castro et al., 2013). El estudio de la mandíbula (ATE9-1) recuperada en el año 2007 (Bermúdez de Castro et al., 2011b), permitió observar ciertas plesiomorfías dentro del género *Homo* (p. ej., un tubérculo marginal anterior situado entre el canino y el primer premolar, una marcada incisura submentalis, una clara asimetría de la superficie oclusal del segundo premolar con un gran talónido, etc.). Aunque, como es sabido, los caracteres primitivos no son útiles a la hora de establecer relaciones filogenéticas entre homínidos. Sin embargo, la mandíbula también presenta rasgos derivados con respecto al género *Homo* (p. ej., una

mínima inclinación del plano alveolar, la ausencia de un torus transversal superior, un menor grosor del cuerpo mandibular) sugiriendo que los homínidos de la Sima del Elefante debieron haberse separado de sus ancestros africanos, así como de *H. georgicus*, durante un periodo de tiempo prolongado (Bermúdez de Castro et al., 2011b; Martín-Torres et al., 2011a; b; Bermúdez de Castro et al., 2013; Bermúdez de Castro y Martín-Torres, 2013).

Volviendo a los restos de *H. antecessor*, el hecho de que estos homínidos presenten una combinación única de caracteres plesiomorfos dentro del género *Homo* (p. ej., premolares inferiores asimétricos con complejas raíces y cíngulo bucal, tamaño creciente de los molares, crenulaciones de esmalte en los molares, posición del foramen mentoniano) (Bermúdez de Castro et al., 1999c, 2016b, 2017; Martín-Torres, 2006; Gómez-Robles et al., 2008, 2015), junto con una serie de sinapomorfias compartidas por un lado con el linaje neandertal (p. ej., polígono oclusal reducido de los segundos premolares inferiores, forma romboidal del primer molar superior, tróclea del astrágalo relativamente estrecha, forma parabólica de la arcada alveolar de la mandíbula) (Martín-Torres et al., 2006, 2007a; Gómez-Robles et al., 2007; Bermúdez de Castro et al., 2012, 2016a; b, 2017; Pablos et al., 2012), por otro con *H. sapiens* (p. ej., patrón de remodelación ósea de la cara, escama temporal alta y convexa, canal incisivo vertical y en posición anterior) (Bermúdez de Castro et al., 1997b, 1999b, 2017; Arsuaga et al., 1999b; Lorenzo et al., 1999; Lacruz et al., 2013; Bermúdez de Castro y Martín-Torres, 2014) y por otro con algunos homínidos del Pleistoceno Medio de Asia (p. ej., marcada forma en pala de los segundos incisivos superiores, cíngulo bucal en los premolares superiores, mandíbulas gráciles, tubérculo cigomaxilar) (Arsuaga et al., 1999b; Carbonell et al., 2005; Martín-Torres et al., 2007a; Bermúdez de Castro et al., 2008; Vialet et al., 2010; Xing et al., 2014) ha llevado a plantear, desde hace años, la posibilidad de un origen euroasiático para la población de TD6 (Carbonell et al., 2005; Martín-Torres, 2006).

Así, *H. antecessor* podría ser una rama originada por un evento cladogenético acontecido en el suroeste asiático durante el Pleistoceno Inferior. Cada rama surgida de dicha cladogénesis evolucionaría de manera independiente adquiriendo una serie de rasgos únicos y exclusivos, combinados con otros heredados de dicha población ancestral (Martín-Torres et al., 2007a; Bermúdez de Castro y Martín-Torres, 2013, 2014; Bermúdez de Castro et al., 2013, 2015, 2017). Igualmente, esa hipotética “población madre” se caracterizaría por presentar también un mosaico de rasgos primitivos dentro del género *Homo*, junto con una serie de caracteres polimórficos

derivados que, en un primer momento, serían heredados por *H. antecessor* y más tarde por el linaje neandertal (Bermúdez de Castro et al., 2013).

El estudio de Bermúdez de Castro y colaboradores (2016b) refuerza la teoría sobre un escenario de continuidad en Europa durante el Pleistoceno Medio y Superior, apoyando la hipótesis de un linaje exclusivo y diferente al encontrado en los homínidos de África y el este de Asia. El análisis de las mandíbulas de diferentes homínidos pleistocenos reveló la presencia de un patrón derivado y exclusivo para los especímenes europeos del Pleistoceno Medio y Superior. El hecho de que *H. antecessor* carezca de ciertos rasgos morfológicos presentes en las poblaciones del Pleistoceno Medio de Europa, podría indicar una posible discontinuidad poblacional entre ambos grupos humanos. Sin embargo, la existencia de otros caracteres compartidos por ambas especies (p. ej., un tubérculo pterigoideo medio marcado, un índice bajo entre longitud/anchura de la arcada alveolar mandibular, una fosa oleocraneana grande) (Carretero et al., 1999; Bermúdez de Castro et al., 2012, 2015, 2016a), permite pensar en algún tipo de relación filogenética entre los homínidos de TD6 y los grupos europeos del Pleistoceno Medio.

Bajo este contexto tenemos que destacar que nuestro estudio confirma la presencia de crestas medias del trigónido continuas en *H. antecessor*, aunque con frecuencias de expresión menores y crestas menos elevadas que en las poblaciones del Pleistoceno Medio y Superior de Europa (Martínez de Pinillos et al., 2017). La manifestación de este patrón de crestas en los homínidos de TD6 ratifica, una vez más, los datos confirmados por otros investigadores sobre el mosaico de caracteres primitivos y derivados característico de *H. antecessor* (Arsuaga et al., 1999b; Carretero et al., 1999; Carbonell et al., 2005; Martín-Torres et al., 2007a; Bermúdez de Castro et al., 2012; Pablos et al., 2012; Lacruz et al., 2013; Gómez-Robles et al., 2015). La mayor parte de los rasgos plesiomórficos presentes en los homínidos de TD6 con respecto al género *Homo* se manifiestan en la dentición (p. ej., secuencia creciente de tamaño en premolares y molares, patrón *Dryopithecus*, molares de cinco cúspides, marcadas crenulaciones de esmalte en los molares) (Bermúdez de Castro et al., 1999c; Bermúdez de Castro y Martín-Torres, 2013). Sin embargo, también aparecen determinadas apomorfías compartidas con los neandertales y la Sima de los Huesos, tales como la forma romboidal del M<sup>1</sup>, el polígono oclusal reducido del P<sub>4</sub> y la forma en pala triangular incipiente de los incisivos superiores (Martín-Torres, 2006; Martín-Torres et al., 2006; Gómez-Robles et al., 2007).

Por tanto, en cuanto a la presencia de una cresta media continua del trigónido, rasgo considerado típico del linaje neandertal, *H. antecessor* se sitúa cerca de *H. sapiens* por presentar frecuencias más bajas y crestas menos elevadas que los neandertales y la Sima de los Huesos. Nuestros resultados, junto con otros estudios (p. ej., Arsuaga et al., 1999; Bermúdez de Castro et al., 1999a; Lacruz et al., 2013), hablan de una mayor afinidad fenética entre TD6 y *H. sapiens* y entre la población de la Sima de los Huesos y los neandertales (Martínez de Pinillos et al., 2017). Basándonos en los análisis estadísticos (ver Figuras 5.9.1.3., 5.9.2.2. y 5.9.2.3. del capítulo de Resultados), observamos que *H. antecessor* se encuentra dentro de la variabilidad de *H. sapiens*, y que tan sólo dos especímenes (un  $M_1$  y un  $M_3$ ) aparecen junto a homínidos del Pleistoceno Medio y Superior de Europa. Nuestro estudio afirma que la expresión de una cresta media del trigónido continua *per se*, tanto en el esmalte como en la dentina, no puede ser considerada una apomorfía neandertal propiamente dicha, puesto que aparece ya en especies anteriores como *H. erectus*, *H. georgicus* y *H. antecessor* (Martín-Torres et al., 2007a, 2008; Zanolli y Mazurier, 2013; Martínez de Pinillos et al., 2017). El patrón característico del linaje neandertal son en realidad las altas frecuencias de expresión y las crestas elevadas, lo que dificulta la valoración taxonómica de poblaciones de las que solo disponemos de dientes aislados (Bailey, 2000, 2002b; Martín-Torres, 2006; Bailey et al., 2011; Martín-Torres et al., 2012; Martínez de Pinillos et al., 2014).

En el año 2007, Martín-Torres y colaboradores definieron un patrón dental euroasiático que estaría ya presente en *H. antecessor*. Posteriores investigaciones (Dennell et al., 2011; Martín-Torres et al., 2011a; Bermúdez de Castro y Martín-Torres, 2013) planteaban la existencia de un clado en Eurasia desde donde diferentes grupos humanos se habrían dispersado hacia Europa durante finales del Pleistoceno Inferior y el Pleistoceno Medio. Dicho clado mostraría ya la presencia de una cresta media continua del trigónido en el esmalte y en la dentina, un rasgo que posteriormente se convertiría en característico del linaje neandertal. La presencia de este tipo de cresta continua en *H. antecessor* (Martínez de Pinillos et al., 2017), refuerza la teoría de que los homínidos de TD6 pudieran estar filogenéticamente situados muy cerca del último ancestro común de los neandertales y los humanos modernos.

Por otra parte, recientes estudios paleogenéticos basados en el análisis de ADN nuclear de los homínidos de la Sima de los Huesos, muestran una clara relación entre esta población y los neandertales (Meyer et al., 2016). Estos autores llegan a sugerir que los especímenes de la Sima de los Huesos podrían ser considerados neandertales tempranos. A la luz de estos nuevos datos, el origen del linaje neandertal habría que

llevarlo hasta mediados del Pleistoceno Medio o incluso antes. Los resultados de esta investigación apoyan, por tanto, la hipótesis ya planteada por Bermúdez de Castro y Martín Torres (2013) sobre la existencia de un evento cladogenético en el suroeste asiático, que hace aproximadamente 700 ka habría dado lugar al clado neandertal. Bajo este escenario, *H. antecessor* representaría una rama europea surgida de dicho evento cladogenético y situado muy cerca del nodo de divergencia que, hace entre 765-550 ka, daría lugar a *H. sapiens* y *H. neanderthalensis* (Bermúdez de Castro et al., 2016b). Los datos cronológicos y una combinación de caracteres modernos con otros típicos del linaje neandertal en los homínidos de TD6, respaldan esta teoría. Sin embargo, *H. antecessor* no necesariamente tuvo que extinguirse a finales del Pleistoceno Inferior, sino que la existencia en el sur de Europa de las denominadas *zonas refugio* durante épocas glaciales, pudo haber permitido su supervivencia durante un largo periodo de tiempo (Dennell et al., 2011), sin excluir la posible hibridación con los nuevos grupos humanos que llegaron al continente.

### 6.1.3. Relación de *Homo antecessor* con especímenes del Pleistoceno Inferior y Medio de África.

La presencia de una cresta media del trigónido continua como un rasgo existente ya en ciertas poblaciones del Pleistoceno Inferior (Martín-Torres et al., 2007a, 2008; Zanolli y Mazurier, 2013; Martínez de Pinillos et al., 2017) viene reforzada, una vez más, por el trabajo de Zanolli y colaboradores (2014). El estudio del espécimen del Pleistoceno Inferior del yacimiento africano de **Mulhuli-Amo** en Buia (Eritrea), muestra una cresta media continua del trigónido bien desarrollada hace 1 Ma. Los resultados obtenidos tras el análisis estadístico (ver Figuras 5.9.1.3. y 5.9.2.2. del capítulo de Resultados), indican que el molar de Buia se agrupa con la mayor parte de los neandertales y de las poblaciones del Pleistoceno Medio de Europa, por presentar una cresta media del trigónido continua. Ahora sabemos que muchos de los rasgos considerados típicos neandertales no son verdaderas apomorfías sino combinaciones exclusivas de rasgos aparecidos durante el Pleistoceno Inferior (p. ej., Franciscus y Trinkaus, 1995; Bailey, 2002a; Martín-Torres et al., 2006; Bermúdez de Castro et al., 2012).

Puesto que algunos investigadores plantearon que los fósiles de TD6 debían estar incluidos dentro de la especie *H. mauritanicus* (Hublin, 2001; Stringer, 2003),

consideramos importante hacer una comparativa con los homínidos del Pleistoceno Medio de **Tighenif** (Argelia) que dan nombre a dicha especie, clasificada originalmente como *Atlanthropus mauritanicus* (Arambourg, 1954). Estudios métricos y morfológicos llevados a cabo en los dientes y mandíbulas de ambas especies (Bermúdez de Castro et al., 2007, 2011a; Zanolli et al., 2010; Zanolli, 2011; Zanolli y Mazurier, 2013), revelan que los fósiles norteafricanos no muestran ninguno de los rasgos euroasiáticos identificados en los homínidos de TD6, pudiendo ser el resultado de una evolución aislada de *H. ergaster* en esta zona del continente (Martín-Torres, 2006). El análisis realizado por Bermúdez de Castro y colaboradores (2007) demostró que mientras los especímenes de *H. antecessor* poseen unas mandíbulas gráciles, similares a las de la mayoría de los homínidos del Pleistoceno Medio de China (Carbonell et al., 2005), las de Tighenif son extremadamente grandes y robustas, características presentes en la mayoría de las mandíbulas del Pleistoceno africano. Del mismo modo, la evidencia dental confirma que los grupos del Pleistoceno Medio del norte de África (Tighenif, Thomas Quarry y Oulad Hamida 1), muestran mayores similitudes con *H. ergaster* que con los homínidos de TD6, quienes poseen rasgos típicos de los grupos pleistocenos de Eurasia (Martín-Torres, 2006; Martín-Torres et al., 2007a; Bermúdez de Castro et al., 2017). Así, observamos que la morfología externa de los molares de Tighenif, a excepción del M<sub>3</sub> de Tighenif 2, es mucho más sencilla que la de exhibida por *H. antecessor* quien presenta marcadas crenulaciones, surcos y cúspides accesorias semejantes a las encontradas en algunos especímenes asiáticos analizados en esta tesis doctoral. Por tanto, aunque los fósiles de Tighenif y TD6 comparten algunos rasgos morfológicos, se trata en su mayoría de simplesiomorfias dentro del género *Homo* (p. ej., fosa pterigoidea poco profunda, posición lateral del cóndilo mandibular, cíngulo bucal en los caninos y premolares inferiores, asimetría del contorno oclusal en los P<sub>3</sub>s), las cuales carecen de utilidad a la hora de establecer relaciones filogenéticas.

Si consideramos las crestas del trigónido en la dentina de todos los molares de Tighenif 1 y 2, el porcentaje de crestas medias del trigónido continuas es menor (42.85%) que el de las discontinuas (57.14%). Sin embargo, si utilizamos el método unilateral (Turner, 1987), dicho porcentaje se invierte, mostrando un mayor número de crestas medias del trigónido continuas (60%) que de discontinuas (40%) (ver Gráfico 5.2.). Esto significa que algunos de los antímeros no presentan el mismo patrón de crestas, debiendo elegir aquel cuyo grado de expresión sea mayor. De esta manera, y de acuerdo con Zanolli y Mazurier (2013), el número de molares de Tighenif con una cresta media del trigónido continua en la dentina es mayor que aquellos que no la



presentan. No obstante, dicha cresta continua se corresponden con un grado 2 según Bailey y colaboradores (2011), cuya altura se reduce considerablemente en la zona del surco sagital. Por otro lado, nuestros resultados permiten observar que el porcentaje de crestas medias del trigónido continuas en la dentina de los molares de *H. antecessor* es mucho menor (18%) que el de las discontinuas (82%) (ver Gráfico 5.2.). Sin embargo y aunque dichas crestas continuas también se corresponden con un grado 2, hay que señalar que su elevación es algo mayor que la de los especímenes de Tighenif.

#### **6.1.4. Relación de *Homo antecessor* con homínidos del Pleistoceno Inferior y Medio de Asia.**

En cuanto a los homínidos del Pleistoceno Medio de **Qesem Cave**, recientes investigaciones llevadas a cabo sobre los dientes hallados en el yacimiento (4 deciduos y 9 permanentes), no han podido determinar el taxón al que perteneció esta población de Oriente Próximo (Fornai et al., 2016; Hershkovitz et al., 2016; Weber et al., 2016). Sin embargo, los autores de dichos estudios afirman que estos restos dentales presentan ciertos rasgos similares a algunos *H. sapiens* arcaicos como Skhul y Qafzeh (p. ej., tamaño relativamente pequeño, ausencia de tubérculo lingual y del hipoconúlido), pero a su vez muestran características más afines con los neandertales (p. ej., crestas medias del trigónido continuas, cúspides accesorias). Los resultados de nuestro estudio permiten observar que mientras el M<sub>2</sub> (QC12) muestra una buena correlación entre el tipo de cresta expresado en el esmalte (tipo A) con el de la dentina (tipo 10), el M<sub>3</sub> (QC13) carece de dicha correlación presentando una cresta media del trigónido discontinua en el esmalte (tipo D) y una continua en la dentina (tipo 11) (ver Gráfico 5.1 y 5.2.). Esta falta de correspondencia hace que en nuestros análisis estadísticos, mientras el segundo molar se sitúa junto a la mayoría de los especímenes del linaje neandertal, el tercero aparece asociado a un individuo de la Muestra Contemporánea (ver Figura 5.9.2.2. y 5.9.3.2. de Resultados). Sin duda, la existencia en ambos molares de crestas medias del trigónido continuas, reflejan una mayor afinidad con los neandertales que con *H. sapiens*. Sin embargo, hemos de ser conscientes de que este tipo de crestas aparecen ya, aunque en bajos porcentajes, en homínidos del Pleistoceno Inferior tales como *H. antecessor*, *H. georgicus* o el espécimen de Mulhuli-Amo en Buia, Eritrea (Martín-Torres, 2006; Zanolli et al., 2014; Martínez de Pinillos et al., 2017).

La ausencia de una cresta media continua del trigónido en los especímenes del yacimiento del **Sangiran Dome** en Java (Indonesia) de finales del Pleistoceno Inferior y comienzos del Pleistoceno Medio (Zanolli, 2015), así como en los del yacimiento del Pleistoceno Medio de **Yiyuan, Hexian y Zhoukoudian** (Xing, 2012; Xing et al., 2014, 2016), ratifica que la expresión de un patrón de crestas continuas del trigónido es más típico de los neandertales y de las poblaciones del Pleistoceno Medio de Europa que de las de Asia. Sin embargo, el M<sub>3</sub> de **Xujiayao** (PA1500), cuyas últimas dataciones lo sitúan en el Pleistoceno Medio tardío (Xing et al., 2015; Ao et al., 2017) y el M<sub>2</sub> y M<sub>3</sub> de Hexian (PA831) (Liu et al., 2017), a pesar de no presentar crestas medias continuas del trigónido, muestran una cresta distal continua. Este tipo de cresta (tipo 3), ausente en los homínidos de TD6, es poco común pero aparece ya en la Sima de los Huesos (22.5%), en *H. neanderthalensis* (17.2%) y en un porcentaje muy bajo de *H. sapiens* (3.9%) (ver Gráfico 5.2.).

Por otro lado, las múltiples crenulaciones de esmalte (“patrón dendrítico”) exhibidas por los especímenes de Yiyuan, Hexian, Zhoukoudian y Xujiayao, se asemejan a las existentes en los homínidos del Pleistoceno Inferior de la Gran Dolina-TD6, con la excepción de dos primeros molares (ATD6-5 y ATD6-96). Sin embargo, nuestros resultados también permiten observar que, en el caso de *H. antecessor*, dicha complejidad estructural tan sólo aparece en la superficie externa y no en la interna, mostrando una dentina mucho más simplificada sin un desarrollo extensivo de crenulaciones. A día de hoy no hay evidencia de *Australopithecus*, homínidos del Pleistoceno Medio norteafricano y del Pleistoceno Inferior y Medio de Europa, *H. erectus* de Sangiran, neandertales y *H. sapiens* que presenten este patrón dendrítico en la dentina (Skinner et al., 2008b, 2009, 2010; Bailey et al., 2011; Martínez de Pinillos et al., 2014; Martínón-Torres et al., 2014; Zanolli, 2015; Martínez de Pinillos et al., 2017). La persistencia de ciertos rasgos primitivos (p. ej., complejidad oclusal, raíces robustas, asimetría de la corona) en relación al género *Homo* expresados por los especímenes de Zhoukoudian, Hexian y Yiyuan, los distingue claramente de los humanos modernos, de los neandertales y de las poblaciones del Pleistoceno Medio europeo (Xing et al., 2014, 2016).

Sin duda, el hallazgo de nuevos fósiles humanos del Pleistoceno Inferior y Medio en África, Asia y Europa, ayudará a esclarecer las diferentes hipótesis propuestas a día de hoy sobre la evolución del género *Homo*.

## 6.2. LOS HOMININOS DE LA SIMA DE LOS HUESOS

### 6.2.1. Relación de la población de la Sima de los Huesos con *Homo neanderthalensis*.

Desde hace más de dos décadas, numerosos estudios se han centrado en caracterizar los rasgos dentales métricos y morfológicos de los neandertales (Patte, 1962; Zubov, 1992a; Bermúdez de Castro y Nicolás, 1995; Ramírez Rozzi, 1996; Tattersall y Schwartz, 1999; Bailey, 2002b; a; Kelley, 2004; Ramírez Rozzi y Bermúdez de Castro, 2004; Macchiarelli et al., 2006; Olejniczak et al., 2008; Smith et al., 2012). Muchos de estos rasgos han sido considerados como caracteres únicos y exclusivos de dicha especie (p. ej., forma en pala marcada en los incisivos superiores, menor grosor de esmalte, altas frecuencias de taurodontismo y crestas del trigónido). Sin embargo, el estudio de los fósiles de las poblaciones del Pleistoceno Medio europeo ha contribuido a aportar importantes datos al significado evolutivo de dichos caracteres. En este aspecto, la excepcional muestra del yacimiento de la Sima de los Huesos ha sido crucial a la hora de estudiar los posibles procesos evolutivos que condujeron a la aparición de los neandertales.

En el campo de la antropología dental, los homínidos de la Sima de los Huesos presentan la mayor parte de los caracteres morfológicos considerados típicos de *H. neanderthalensis* (Bermúdez de Castro, 1988, 1993; Martín-Torres, 2006; Martín-Torres et al., 2012), exhibiendo incluso rasgos aún más derivados que los propios neandertales (Bermúdez de Castro y Nicolás, 1995, 1996; Gómez-Robles et al., 2007, 2008, 2011a; b, 2012; Prado-Simón et al., 2012; Martín-Torres et al., 2013a; Martínez de Pinillos et al., 2014). Se han descrito numerosas similitudes tanto métricas como morfológicas en el aparato dental de la población de la Sima de los Huesos y los neandertales. Así, por ejemplo, el aumento del tamaño de la dentición anterior en relación a la posterior, la marcada forma en pala de los incisivos superiores, la presencia de un tubérculo lingual prominente y una fosa lingual profunda son características presentes tanto en *H. neanderthalensis* como en los homínidos de la Sima de los Huesos (Martín-Torres, 2006; Martín-Torres et al., 2012).

Con respecto a la dentición posterior, los primeros premolares superiores de los homínidos de la Sima de los Huesos y de *H. neanderthalensis* se caracterizan por presentar un contorno simétrico con una cara bucal abultada, cuya cúspide es claramente mayor que la lingual. Del mismo modo, los segundos premolares muestran una cara oclusal simétrica con una reducción, aunque no tan marcada como en los primeros, del talón y de la cúspide

lingual. En términos generales podemos decir que los premolares superiores tienden a la simetría y a la disminución de tamaño en la zona distal (Gómez-Robles et al., 2011b). Por su parte, los primeros premolares mandibulares muestran un contorno simétrico y redondeado con reducción e incluso ausencia del talónido (Gómez-Robles et al., 2008), mientras que los segundos premolares tienden a ser asimétricos, con un metacónido desplazado mesialmente, cúspides linguales accesorias y crestas transversas (Martinón-Torres et al., 2006).

El estudio de los primeros molares superiores de la Sima de los Huesos ha revelado la presencia de un mosaico de caracteres presentes tanto en *H. neanderthalensis* como en *H. sapiens* (Martinón-Torres et al., 2013b). Los homínidos de la Sima de los Huesos comparten con *H. neanderthalensis* un polígono oclusal pequeño en términos relativos, donde el desplazamiento distal de las cúspides linguales confiere al molar una forma romboidal característica. Además, poseen un hipocono abultado y prominente cuyo ángulo relativamente pequeño contrasta con el de mayor tamaño del metacono. Todas estas características están ya presentes en la población del Pleistoceno Inferior de la Gran Dolina-TD6 (Gómez-Robles et al., 2007, 2011a). Sin embargo, tanto el área total de la base de la corona como el tamaño en términos absolutos de las áreas de las cúspides (excepto el protocono, que está agrandado) son pequeños y caen dentro de la variabilidad de *H. sapiens* (Martinón-Torres et al., 2013b).

Los molares inferiores han sido ampliamente estudiados en el contexto de la evolución humana utilizando, entre otros, los análisis clásicos, la morfometría geométrica, los estudios radiculares y de la corona y la caracterización morfológica externa e interna. Así, diversos análisis morfométricos muestran que la Sima de los Huesos presenta una reducción de tamaño considerable (especialmente en los segundos y terceros molares) en comparación con los neandertales clásicos y otras poblaciones del Pleistoceno Medio europeo, que les sitúa dentro del rango de variación de los humanos modernos (Bermúdez de Castro y Nicolás, 1995; Martinón-Torres, 2006; Gómez-Robles et al., 2015; Martín-Albaladejo et al., 2017). En cuanto a la morfología externa de los molares inferiores, ya en 1992 A.A. Zubov y posteriormente S.E. Bailey (Bailey, 2000, 2002a; b), destacaron las altas frecuencias de expresión de las crestas medias del trigónido en *H. neanderthalensis*, siendo poco frecuentes en *H. sapiens*. Estos rasgos, característicos de las poblaciones del Pleistoceno Medio europeo y de los neandertales, venían acompañados de la aparición de una fosa anterior profunda y bien delimitada denominada *fóvea anterior*. Años después, un estudio detallado de las muestras dentales de los homínidos de la sierra de Atapuerca realizado por M. Martinón-Torres (Martinón-Torres, 2006), señalaba que la población de la Sima

de los Huesos también presentaba el desarrollo de dichos caracteres. Estos patrones de expresión coinciden con estudios anteriores sobre la morfología externa de los dientes de la Sima de los Huesos que demuestran que estos fósiles presentan una combinación de rasgos típicamente neandertales (p. ej., Bermúdez de Castro, 1986; Martín-Torres, 2006; Gómez-Robles et al., 2011b, 2012, 2015; Martín-Torres et al., 2012, 2013a).

A nivel de la dentina, nuestros resultados ratifican dichas semejanzas entre ambas poblaciones. Por un lado, observamos que la Sima de los Huesos presenta un mayor número de molares con crestas medias o mesiales del trigónido que sin ellas, siendo las primeras más frecuentes que las segundas. Y por otro, vemos que hay un claro predominio de molares con una cresta media o mesial alta y continua y una distal discontinua, el tipo de morfología más frecuente en *H. neanderthalensis* y mucho menos habitual en *H. sapiens*. Igualmente hay que destacar que la variabilidad y las frecuencias de expresión de los tipos de crestas del trigónido en la dentina son mucho mayores en la población de la Sima de los Huesos y los neandertales que en los humanos modernos. Dicha variabilidad es mayor en los terceros molares que en los primeros y segundos. Además, una alta frecuencia de las crestas distales del trigónido en los terceros molares de *H. neanderthalensis* ha sido definida como un carácter diagnóstico de esta especie con respecto a *H. sapiens* (Bailey, 2002a; b; Bailey et al., 2011). Este mismo patrón aparece en el esmalte y en la dentina de la Sima de los Huesos, lo que de nuevo nos lleva a ratificar la similitud entre ambas poblaciones (Martín-Torres et al., 2012; Martínez de Pinillos et al., 2014). En resumen, nuestro estudio sobre la morfología interna de los molares inferiores confirma que, al igual que ocurría en el esmalte, la dentina de los homínidos de la Sima de los Huesos presenta unas frecuencias de expresión de crestas similares a los existentes en la población neandertal y que difieren de los expresados en *H. sapiens*.

Con respecto a las crestas del talónido, a diferencia del estudio pionero realizado por C.A. Korenhof en los segundos molares deciduos de una población medieval de Sangiran (Korenhof, 1982), nuestros resultados muestran que este tipo de cresta no sólo aparece también en la población de la Sima de los Huesos y en *H. neanderthalensis*, sino que además está presente, y con frecuencias más altas, en la dentición permanente. Sin embargo, hemos de tener en cuenta que nuestros datos pueden verse condicionados por el menor número de piezas deciduas utilizado en nuestro análisis. Las altas frecuencias de crestas del talónido mostradas en el estudio de Korenhof (1982) en comparación con las nuestras, nos lleva a pensar que quizá la expresión de este tipo de cresta sea una particularidad de dicha población medieval de Sangiran que no puede ser extrapolada

a la especie *H. sapiens*. Además, es interesante destacar que en nuestro análisis hemos podido identificar la frecuente expresión de una protuberancia mesial del entocónido que, a pesar de no llegar a unirse al trigónido, podría ser interpretada como el vestigio de un tipo de cresta del talónido.

Muchos de los rasgos considerados “típicos neandertales” no son verdaderas apomorfias sino una combinación distintiva de caracteres primitivos que aparecen ya en especies anteriores pero en menor frecuencia (p. ej., Patte, 1962; Franciscus y Trinkaus, 1995; Bailey, 2002a; Martínón-Torres, 2006; Martínón-Torres et al., 2006; Bermúdez de Castro et al., 2012; Martínez de Pinillos et al., 2015). Por ello, en cuanto a la dentición, la similitud existente entre la Sima de los Huesos y los neandertales en sus altos grados de expresión y frecuencias de ciertos caracteres, apoyaría la hipótesis de que el linaje neandertal se originó al menos hace medio millón de años. Además, los últimos estudios realizados en paleogenética (Meyer et al., 2014, 2016), no sólo ratifican esta afirmación sino que aportan datos que apuntan incluso a un límite de hasta 700 ka para la separación de la genealogía de los neandertales y de los humanos modernos.

### 6.2.2. Relación de la población de la Sima de los Huesos con otros homínidos del Pleistoceno Medio de Europa.

Los fósiles humanos del Pleistoceno Medio se caracterizan por una gran variabilidad morfológica (Martínón-Torres et al., 2012; Zanolli y Mazurier, 2013; de Lumley M.-A., 2015; Hershkovitz et al., 2016; Rodríguez et al., 2016; Skinner et al., 2016; Daura et al., 2017; Liu et al., 2017) que ha dificultado su asignación taxonómica. Algunos de estos restos son considerados por ciertos investigadores como *H. heidelbergensis*, sin embargo a día de hoy aún es necesaria una definición clara y concisa de este taxón (p. ej., Stringer, 2012). Entre los diferentes grupos humanos que habitaron el continente europeo durante el Pleistoceno Medio, además de la extraordinaria colección del yacimiento de la Sima de los Huesos, hay que destacar los más de 140 fósiles humanos provenientes del yacimiento de la **Caune de l’Arago** en Tautavel (Francia). Estos restos humanos tienen una cronología similar a la de los fósiles de la Sima de los Huesos. Sin embargo, aunque presentan ciertas apomorfias que los relacionan con el linaje neandertal (Gómez-Robles et al., 2007, 2008, 2015; Bermúdez de Castro et al., 2011a, 2016b; Arsuaga et al., 2014) preservan también

algunos rasgos primitivos. Es interesante destacar que muchos investigadores están de acuerdo en afirmar que la muestra de Arago parece ser menos derivada que otras muestras contemporáneas como la de la Sima de los Huesos (p. ej., Bermúdez de Castro et al., 2003, 2011; Martín-Torres et al., 2012; Arsuaga et al., 2014; de Lumley M.-A., 2015). En particular, Bermúdez de Castro y colaboradores (2003) ya definieron los dientes de Arago como “intermedios” entre los de los homínidos del Pleistoceno Inferior de la Gran Dolina-TD6 y los de la población del Pleistoceno Medio de la Sima de los Huesos, sugiriendo un escenario evolutivo de discontinuidad entre los linajes humanos del Pleistoceno Inferior y Medio en Europa. Por su parte, debido a un cierto aspecto primitivo de los homínidos de Arago, la investigadora de Lumley M.-A. en un artículo publicado recientemente, los considera una subespecie de *H. erectus*, llegándolos a nombrar como *H. erectus tautavelensis* (de Lumley M.-A., 2015). Sin duda, tan sólo el hallazgo de nuevos restos fósiles permitirá entender la complejidad morfológica existente en las poblaciones europeas del Pleistoceno Medio.

La dentición de los homínidos de Arago es muy diversa, por lo que dependiendo de la clase dental presenta afinidades con diferentes grupos. La mayoría de los dientes permanentes de Arago son grandes, especialmente los de la mandíbula Arago 13 cuya dentición posterior es tan grande o más que la de *H. antecessor* (Bermúdez de Castro et al., 2004a). Es interesante destacar que el tamaño de algunos de los primeros premolares inferiores, como Arago 13, Arago 71 y Arago 75, están fuera del área de distribución de la Sima de los Huesos (Gómez-Robles et al., 2008). Así, la forma asimétrica y alargada del primer premolar de Arago 71 es similar al de *H. habilis* y ciertos australopitecinos; el tamaño medio del talónido y un polígono oclusal central sitúan a Arago 75 en una posición intermedia entre los humanos modernos y especies anteriores; y la simetría y ausencia de cíngulo y talónido de Arago 13 hacen que se parezca más a los de *H. neanderthalensis* y *H. sapiens* (Gómez-Robles et al., 2008). Sin embargo, en Arago 13 la zona apical de la raíz se divide en un componente mesiobucal y otro distolingual, cada uno con su propio conducto radicular, poniendo de manifiesto un patrón marcadamente primitivo para su cronología (Bermúdez de Castro et al., 2003a). Al igual que ocurre en el primer premolar de Arago 13, la raíz del segundo premolar también es doble, pero en este caso el componente mesiobucal presenta dos canales radiculares perfectamente delimitados, mostrando una morfología similar a la existente en el Homínido 1 de *H. antecessor*. Por otro lado, Arago 13 y Arago 21 muestran una secuencia creciente en los molares, y el segundo y tercer molar de Arago 13 son hipo y mesotauroodontos respectivamente (Bermúdez de Castro et al.,

2003a, 2011a). Además, la forma del primer molar superior en la mayoría de los especímenes de Arago es más primitiva que la exhibida por el resto de los homínidos del Pleistoceno Medio de Europa y *H. neanderthalensis*. Sin embargo, todas estas simpliomorfias se combinan con la existencia de otros caracteres derivados como la ausencia de la quinta cúspide en los segundos molares inferiores de Arago 5 y Arago 6 (Bermúdez de Castro et al., 2003a), o la presencia de elevadas frecuencias de crestas del trigónido como ocurre en los neandertales y en la población de la Sima de los Huesos (Martínón-Torres, 2006). Así, cuatro de los cinco molares de Arago estudiados en esta tesis doctoral presentan crestas medias del trigónido continuas, pero a diferencia de los neandertales y de los homínidos de la Sima de los Huesos, la variabilidad de expresión de los patrones de crestas en la dentina es menor. Sin embargo, hemos de ser prudentes ya que esto último puede ser debido al pequeño tamaño muestral y por tanto no representar la variabilidad real de la población original. Además, es curioso que el tercer molar analizado de Arago (A-106) no presente ninguna cresta del trigónido continua, ya que es esta clase dental la que exhibe los mayores porcentajes de crestas continuas mediales, y particularmente distales, en la población de la Sima de los Huesos y en *H. neanderthalensis* (Bailey et al., 2011; Martínez de Pinillos et al., 2014). Nuestros datos sobre los patrones de expresión de las crestas del trigónido de Arago apoyan estudios previos donde, por un lado, se observan afinidades con el linaje neandertal en cuanto a las frecuencias altas mientras que, por otro, la variabilidad en los tipos de crestas expresadas es menor, lo que les diferencia de la Sima de los Huesos y *H. neanderthalensis*; aunque, como ya hemos indicado, hemos de ser cautos puesto que puede ser consecuencia del tamaño muestral.

En cuanto a la mandíbula de **Montmaurin** (La Niche), a pesar de presentar unas características claramente primitivas (Billy y Vallois, 1977; Hublin, 1998), en lo referente a la dentición muestra notables afinidades con los especímenes del Pleistoceno Medio europeo y con *H. neanderthalensis*. En concreto, si comparamos los molares de Montmaurin con los de la población de la Sima de los Huesos, vemos que mesiodistalmente muestra también la serie decreciente en el primer y segundo molar, mientras que bucolingualmente el segundo molar es mayor que el primero (Bermúdez de Castro, 1986; Bermúdez de Castro et al., 2003a). Respecto al tercer molar, y a diferencia de lo que habitualmente sucede en los especímenes del Pleistoceno Medio, la mandíbula de Montmaurin presenta un tercer molar más grande que los otros dos (Bermúdez de Castro, 1986). Estos caracteres contrastan con los existentes en la mayoría de los fósiles del Pleistoceno Medio de África y Asia, que presentan una



dentición posterior de gran tamaño. En cuanto a las crestas del trigónido, podemos decir que los dientes de la mandíbula de Montmaurin muestran el patrón característico del linaje neandertal. Nuestro estudio revela que los seis molares exhiben una cresta media del trigónido continua y elevada tanto en el esmalte como en la dentina. Debido a los altos porcentajes de expresión de este tipo de cresta en la dentina, los molares de Montmaurin se asemejan a los de la Sima de los Huesos, los de La Caune de l'Arago y a los ejemplares de *H. neanderthalensis* analizados en la presente tesis doctoral (72%, 75% y 71% respectivamente) (ver Gráfico 5.2.). No obstante, aunque la cresta distal del trigónido continua ha sido descrita como un rasgo típico neandertal y está presente en la población de la Sima de los Huesos (22.5%) y en los *H. neanderthalensis* (17.2%), ni la mandíbula de Montmaurin ni los especímenes de Arago exhiben dicho patrón (ver Gráfico 5.2.), hecho que puede estar condicionado nuevamente al tamaño muestral. En conclusión, podemos decir que el espécimen de Montmaurin presenta un mosaico de caracteres, puesto que mientras que la morfología mandibular es claramente primitiva, sus molares muestran rasgos derivados más propios del linaje neandertal.

Respecto a la mandíbula del yacimiento de **Mala Balanica** (BH-1) en Serbia, hay que destacar que la morfología de los molares se encuentra fuera del rango de variación de la población de la Sima de los Huesos y de *H. neanderthalensis* por carecer de la tipología clásica neandertal de una cresta media del trigónido continua. Nuestros análisis estadísticos basados en las frecuencias de expresión de las crestas, sitúan a los molares de BH-1 dentro de la variabilidad de *H. sapiens* (ver Figura 5.9.1.3., 5.9.2.2. y 5.9.3.2 del capítulo de Resultados). Sin embargo, las semejanzas entre este espécimen y el holotipo de *H. heidelbergensis* en cuanto a la ausencia total de crestas es clara. Ambos individuos carecen de cualquier grado de afinidad neandertal como el expresado por la población de la Sima de los Huesos. El estudio llevado a cabo por Skinner y colaboradores (2016) sobre la dentición de BH-1, muestra una morfología primitiva y concluye que tanto los rasgos métricos como no métricos confirman una ausencia generalizada de caracteres derivados típicamente neandertales presentes en la población de la Sima de los Huesos. A pesar de este estatus plesiomórfico, según estos autores el espécimen BH-1 es más derivado en algunos aspectos que los homínidos de *H. antecessor*. Así, el P<sub>3</sub> de BH-1 presenta dos canales radiculares en lugar de tres, y el P<sub>4</sub> muestra una invaginación moderada de la raíz y no marcada como ocurre en *H. antecessor*. Sin embargo, también sostienen la existencia de ciertas similitudes con los especímenes del Pleistoceno Medio africano de Tighenif, como por ejemplo la invaginación de los premolares o la existencia de una sexta cúspide (entoconúlido) en

el  $M_2$  y  $M_3$  de Tighenif 2 (Skinner et al., 2016). Finalmente, estos autores concluyen que la mandíbula de Mala Balanica ha de ser clasificada como *H. heidelbergensis* s.l., lo cual se ve favorecido por su cronología, la situación geográfica y sus semejanzas con la mandíbula de Mauer.

En cuanto a la mandíbula de **Mauer**, a pesar de conocer únicamente la morfología interna del  $P_3$ ,  $P_4$  y  $M_2$  derecho (Weber et al., 2016), consideramos necesario e importante mencionar algunas de las características más relevantes del holotipo de la especie *H. heidelbergensis*. Este espécimen, el más antiguo de las poblaciones del Pleistoceno Medio europeo, presenta una mandíbula de aspecto primitivo cuya robustez se asemeja a las de Arago 2, Arago 13, Atapuerca 1-Sima de los Huesos y Montmaurin (Aguirre y de Lumley, 1977; Rosas, 1987). Sin embargo, también muestra algunas características claves para el posterior desarrollo de las apomorfias neandertales (Rosas y Bermúdez de Castro, 1998; Bermúdez de Castro et al., 2004). En cuanto a los primeros premolares, su contorno simétrico y la reducción de la cúspide lingual se asemeja a los de la Sima de los Huesos y *H. neanderthalensis*, mientras que el polígono oclusal amplio y más central es propio de *H. sapiens*. En los segundos premolares, la reducción del diámetro bucolingual entra dentro de la variabilidad de los neandertales y de las poblaciones del Pleistoceno Medio, pero la simetría de la corona es semejante al de los *H. sapiens* (Rosas y Bermúdez de Castro, 1998). Sin embargo, a pesar de que las proporciones entre la dentición anterior y posterior sitúan a la mandíbula de Mauer dentro del rango de la población de la Sima de los Huesos y *H. neanderthalensis*, la ausencia de ciertas apomorfias típicas del linaje neandertal (morfología de los segundos premolares, cresta media del trigónido, fóvea anterior) hace que sea el espécimen que menos se aproxime fenéticamente a los neandertales clásicos (Rosas y Bermúdez de Castro, 1998; Martín-Torres, 2006). La morfología externa de los molares inferiores permite observar con claridad un surco sagital ininterrumpido a lo largo de toda la cara oclusal del diente, que impide la presencia de una cresta continua de esmalte uniendo las cúspides mesiales. Sabiendo que existe una gran correspondencia entre los diferentes tipos de crestas del esmalte y la dentina, y a pesar de no haber podido analizar la morfología interna de los molares de Mauer, es razonable hipotetizar que la cresta media del trigónido también está ausente en la dentina. En definitiva, la mandíbula de Mauer, a pesar de ser el holotipo de la especie *H. heidelbergensis*, dista mucho de representar a la mayoría de las poblaciones del Pleistoceno Medio europeo (con la excepción del individuo de Mala Balanica) por carecer de las características morfológicas típicas presentes en estos grupos humanos.

### 6.2.3. Relación de la población de la Sima de los Huesos con especímenes del Pleistoceno Inferior y Medio de África.

El molar del yacimiento de **Mulhuli-Amo** en Buia (Eritrea) es el único espécimen del Pleistoceno Inferior de África analizado en la presente tesis doctoral. Este molar exhibe una mezcla de caracteres presentes en homínidos del Pleistoceno Inferior y Medio de Eurasia y África. Así, la secuencia del tamaño de sus cúspides con un protocónido mayor que el metacónido y una quinta cúspide (hipoconúlido) de gran tamaño coincidiría con el patrón más común en especímenes afro-europeos del Pleistoceno Inferior (Zanolli et al., 2014). Sin embargo, basándonos en los resultados obtenidos por Martín-Albaladejo y colaboradores (2017), esta secuencia es en realidad más típica de los especímenes euroasiáticos del Pleistoceno Inferior en vez de los africanos. Igualmente, la presencia de un pequeño metaconúlido o C7 en el espécimen de Buia (MA93) es compatible con las altas frecuencias de este rasgo observado en *H. ergaster* y *H. georgicus* (Martín-Torres et al., 2007a, 2008; Suwa et al., 2007). Por otro lado, mientras que la mayor parte de los especímenes del Pleistoceno Inferior africano muestran un patrón de surcos en “Y” (patrón *Dryopithecus*), el molar de MA93 presenta una configuración cruciforme (“+”), más típica de *H. erectus* de Java y de poblaciones euroasiáticas del Pleistoceno Medio y Superior (Martín-Torres et al., 2007a; Zanolli, 2013, 2015). Del mismo modo, el espécimen de Buia muestra el desarrollo de una cresta media del trigónido continua y elevada cuya expresión es poco frecuente en *H. ergaster*, donde generalmente está ausente o es discontinua (Martín-Torres et al., 2007a). Por tanto, hemos de tener en cuenta que, aunque la morfología de una cresta media continua junto con una distal discontinua es característica de *H. neanderthalensis* y de la mayor parte de los especímenes del Pleistoceno Medio Europeo (p. ej., Sima de los Huesos, Montmaurin, Aragón), aparece ya en poblaciones anteriores como *H. georgicus* y *H. antecessor*. Esto ratifica que no puede ser considerada una apomorfía neandertal propiamente dicha, sino un rasgo morfológico surgido durante el Pleistoceno Inferior pero convertido en típico del linaje neandertal por las altas frecuencias de expresión y la elevación de las crestas.

Los restos del Pleistoceno Medio africano de **Tighenif** (Argelia) fueron originalmente designados como *Atlanthropus mauritanicus* (Arambourg, 1954, 1955), posteriormente asociados a *H. erectus* (Le Gros Clark, 1964; Tillier, 1980; Rightmire, 1990) y finalmente atribuidos a *H. mauritanicus* (Hublin, 2001; Stringer, 2003) u *H. ergaster mauritanicus* (Martín-Torres, 2006; Bermúdez de Castro et al., 2007). Una

posterior revisión del hipodigma de *H. heidelbergensis* (Mounier et al., 2009), sugería que las semejanzas morfológicas entre los individuos de Tighenif con dicha especie posibilitaba su asignación a dicho taxón (Mounier et al., 2009; Stringer, 2012; Zanolli y Mazurier, 2013). Sin embargo, este mismo estudio destacaba también la existencia de algunos caracteres derivados como el desarrollo de una protuberancia a modo de mentón en Tighenif 2, que los situaba morfológicamente más cerca de *H. sapiens* que de los neandertales (Schwartz y Tattersall, 2000; Mounier et al., 2009; Schwartz y Tattersall, 2010), un hecho igualmente respaldado tras el análisis estructural de tres molares deciduos superiores (Zanolli et al., 2010). Las mandíbulas de Tighenif muestran, por tanto, un mosaico de caracteres primitivos y derivados con respecto al género *Homo*, junto con la presencia de rasgos únicos y exclusivos que caracterizan a esta población del norte de África. No obstante, las similitudes existentes entre los fósiles del Pleistoceno Medio de Europa y África responden a simplesiomorfias heredadas de un antepasado común cuyo representante más plausible a día de hoy es *H. antecessor* (Martín-Torres, 2006), aunque hemos de tener en cuenta que los caracteres primitivos no son de gran utilidad a la hora de realizar interpretaciones filogenéticas.

Según el estudio realizado por Zanolli y Mazurier (2013), las proporciones de los tejidos dentales del  $M_2$  y  $M_3$  de Tighenif 2 se aproximan a los valores expresados por los neandertales y sobre todo a los expresados por los miembros de *H. sapiens* del Pleistoceno Superior del norte de África. Sin embargo, mientras que sus análisis basados en la morfometría geométrica de la dentina indican que el  $M_2$  de Tighenif 2 se acerca al patrón neandertal, los resultados de nuestro estudio de las crestas del trigónido lo sitúan dentro del rango de variación de *H. sapiens* (ver Figura 5.9.2.2. del capítulo de Resultados). Del mismo modo, estos autores indican que los  $M_3$ s de Tighenif 1 y 2 aparecen fuera del rango de variabilidad de neandertales y humanos modernos, mientras que nuestros resultados los sitúan en el de los humanos modernos y la SH. Además, nuestros análisis sitúan también al  $M_3$  de Tighenif 1 dentro de la variabilidad de los neandertales y al de Tighenif 2 en la de los individuos del Pleistoceno Medio de Asia. Si utilizamos el método unilateral (Turner, 1987), el número de molares de Tighenif que exhiben una cresta media del trigónido continua en la dentina (60%) es mayor que aquellos que no la presentan (40%) (ver Gráfico 5.2.). Sin embargo, si tenemos en cuenta todos los molares, vemos que existen ciertas discrepancias entre la superficie externa e interna de algunos de ellos: dos  $M_2$ s con crestas medias continuas en el esmalte (tipo A), en la dentina se manifiestan como discontinuas (tipo 4) y

un  $M_3$  con cresta distal continua en el esmalte (tipo B) es discontinua en la dentina (tipo 4). Asimismo, es importante destacar que la cresta de los tres molares que la presentan continua es más baja (grado 2 según Bailey et al., 2011) que la mayoría de los neandertales y de los especímenes del Pleistoceno Medio europeo analizados en la presente tesis doctoral. Por tanto, algunos de los molares de Tighenif, a pesar de presentar crestas medias del trigónido continuas, su baja elevación no refleja el típico patrón característico del linaje neandertal, cuyas crestas suelen ser más pronunciadas.

#### **6.2.4. Relación de la población de la Sima de los Huesos con especímenes del Pleistoceno Inferior y Medio de Asia.**

En cuanto a los dientes hallados en el yacimiento del Pleistoceno Medio de **Qesem Cave** en Israel, diversos estudios (Fornai et al., 2016; Hershkovitz et al., 2016; Weber et al., 2016) nos han permitido valorar las diferencias y similitudes existentes entre éstos y los homínidos de la Sima de los Huesos. Con respecto a la dentición mandibular, los premolares muestran un tamaño que está dentro de la variabilidad de los humanos modernos pero con una morfología intermedia entre neandertales y *H. sapiens* (Weber et al., 2016). En contraste con los premolares, el segundo y tercer molar (QC12 y QC13 respectivamente) poseen características neandertales. Comenzando con la descripción morfológica del segundo molar (QC12), a pesar de carecer de la quinta cúspide, destaca por presentar una elongación mesiodistal que le confiere una forma rectangular típica de *H. neanderthalensis*. Sin embargo, la superficie oclusal relativamente simplificada (p. ej., ausencia de surcos, cúspides accesorias y crenulaciones) es más propia de *H. sapiens* que de los neandertales. No obstante, la presencia de una cresta media del trigónido continua y elevada tanto en el esmalte como en la dentina, sugiere una clara afinidad con el linaje neandertal (Hershkovitz et al., 2016; Weber et al., 2016). El estudio de la dentina muestra la existencia de una cresta distal discontinua que se corresponde con un tipo 10. Nuestros análisis estadísticos nos permiten observar que esta tipología (tipo 10) está presente en muy bajas frecuencias en *H. sapiens* (1,3%, un porcentaje que se corresponde con un único  $M_2$ ), mientras que es más habitual encontrarlo en *H. neanderthalensis* (22,9%, correspondiente a cinco  $M_1$ s, dos  $M_2$ s y un  $M_3$ ), en la Sima de los Huesos (12,5%, correspondiente a cuatro  $M_1$ s y un  $M_2$ ) y algunos individuos del Pleistoceno Medio europeo como la mandíbula de Montmaurin (100%, correspondiente a un  $M_1$ , un  $M_2$  y un  $M_3$ ) y Arago (25%, correspondiente a un  $M_1$ ). Sin embargo, hay que tener en cuenta que este tipo 10 aparece ya en un  $M_1$  y un  $M_3$

de *H. antecessor* (Martínez de Pinillos et al., 2017) y en el único molar hallado en el yacimiento de Buia, en Eritrea (Zanolli et al., 2014) (ver Gráfico 5.2.).

En cuanto a la caracterización morfológica del tercer molar (QC13), este posee un contorno oclusal cuadrado y una complejidad morfológica del tipo *mass-additive*, con crenulaciones, surcos y crestas, además de la presencia de la quinta (hipoconúlido) y séptima (metaconúlido) cúspide. Mientras que en la superficie externa la cresta media del trigónido parece estar ligeramente dividida por el surco central, la dentina nos muestra claramente la unión existente entre el protocónido y el metacónido, lo que junto con una cresta distal discontinua nos permite clasificar al tercer molar con el tipo 11. Al igual que sucedía con el segundo molar, el tipo 11 aparece en *H. sapiens* con la misma frecuencia (1,3%, correspondiente a un  $M_1$ ), y sigue siendo más característico de los neandertales (8,6%, correspondiente a dos  $M_2$ s y un  $M_3$ ) y de la Sima de los Huesos (15%, correspondiente a tres  $M_1$ s, tres  $M_2$  y un  $M_3$ ) (ver Gráfico 5.2.). Sin embargo, esta tipología está ausente en la mandíbula de Montmaurin, en Arago y en los especímenes de la Gran Dolina-TD6. En resumen, podemos decir que la combinación de una cresta media alta y continua y una distal discontinua sugiere afinidades entre Qesem y el linaje neandertal. No obstante, hemos de tener en cuenta una vez más que la presencia de una cresta media del trigónido continua, aunque en menor frecuencia y con grados de expresión menos elevados, aparece ya en poblaciones anteriores (p. ej., Gran Dolina, Dmanisi, Buia, Tighenif). Este hecho, unido a que el resto de las piezas dentales exhiben una mezcla de caracteres de *H. neanderthalensis* y humanos modernos, dificulta la asignación taxonómica de los individuos de Qesem Cave (Hershkovitz et al., 2016; Weber et al., 2016).

En cuanto a los homínidos del sur y este de Asia, vemos que los molares de **Zhoukoudian**, **Hexian** y **Yiyuan**, a diferencia de los de **Sangiran Dome**, se caracterizan por presentar una superficie oclusal compleja (p. ej., marcadas crenulaciones, rugosidades, cúspides accesorias, protoestílido, deflecting wrinkle). Estas crenulaciones o patrón dendrítico en la dentina parece ser distintivo de las poblaciones del Pleistoceno Medio de China, pudiendo ser considerado como una particularidad temporal y regional (Xing et al., 2014, 2016; Liu et al., 2017). Sin embargo, como ya indicamos anteriormente (apartado 6.1.4.), la mayoría de los molares de *H. antecessor* también exhiben este mismo patrón dendrítico de complejidad oclusal pero tan sólo en el esmalte, mostrando una dentina mucho más simple. Un conjunto de características primitivas con respecto al género *Homo* (p. ej., robustez radicular, complejidad oclusal, coronas asimétricas) hace que los homínidos de Zhoukoudian, Hexian y Yiyuan se

diferencien, en cierta medida, del linaje neandertal y de los humanos modernos (Xing et al., 2014, 2016).

Por otro lado, la ausencia de una cresta media del trigónido continua en los especímenes de Hexian, Yiyuan y Sangiran Dome (Xing et al., 2014, 2016; Zanolli, 2015), ratifica que la expresión del patrón de crestas continuas del trigónido es más característica de los neandertales y de las poblaciones del Pleistoceno Medio europeo que de especímenes asiáticos. Mientras, el segundo molar izquierdo de Zhoukoudian (PA70) (Xing, 2012) presenta una configuración de crestas del trigónido hasta ahora nunca observada. El desarrollo, tanto en el esmalte como en la dentina, de una doble cresta mesial continua mediante la unión de ambas cúspides mesiales al borde marginal mesial, representa una particularidad en el registro fósil. Asimismo, el segundo y tercer molar de la mandíbula de Hexian (PA831) exhiben una cresta distal continua tan sólo en la dentina (Liu et al., 2017). Igualmente, el tercer molar inferior derecho (PA 1500) del yacimiento del Pleistoceno Medio de **Xujiayao**, al norte de China (Xing et al., 2015; Ao et al., 2017), a pesar de no mostrar una cresta media del trigónido presenta una cresta distal continua (tipo 3). La existencia de una cresta distal continua, sola o combinada con una cresta mesial o media del trigónido, aparece ya en la población de la Sima de los Huesos (22.5%), en *H. neanderthalensis* (17.2%) y en algún humano moderno (3.9%) (ver Gráfico 5.2.). Además, los molares de Zhoukoudian, Hexian, Yiyuan, junto con algunos especímenes de la Sima de los Huesos, presentan una marcada cresta vertical en su cara bucal. Este rasgo morfológico podría ser una sinapomorfia existente en estas poblaciones euroasiáticas del Pleistoceno Medio (Xing et al., 2016). Todo parece indicar que las poblaciones del Pleistoceno Medio del este de Asia presentan una diversidad morfológica mucho mayor de lo que anteriormente se pensaba (Bailey y Liu, 2010; Xing, 2012; Liu et al., 2013) y que, por tanto, la asignación taxonómica de todos los especímenes asiáticos a *H. erectus* puede haber simplificado en exceso el escenario evolutivo de Asia (Xing et al., 2014, 2016).







07

CONCLUSIONES



## 7. CONCLUSIONES

Mediante la presente tesis doctoral hemos realizado una revisión exhaustiva de las crestas del trigónido y talónido para la mayoría de homínidos del Pleistoceno europeo. Los patrones de variación de las crestas del trigónido han demostrado ser taxonómica y filogenéticamente útiles, y su comparativa con otros grupos humanos nos ha ayudado a comprender la polaridad de dichos caracteres y a contextualizar la evolución de las poblaciones europeas. Por otra parte, las investigaciones realizadas sobre determinados caracteres morfológicos en *H. antecessor*, nos han permitido obtener datos importantes a la hora de plantear su posible posición filogenética, y a su vez proponer el escenario evolutivo más plausible para la colonización de Europa.

A continuación detallamos las conclusiones más relevantes obtenidas en la presente tesis doctoral:

1. Nuestros resultados demuestran que hay una **mayor variabilidad morfológica de la expresión de crestas del trigónido en la dentina que en el esmalte**. Sin embargo, y a pesar de dicha variabilidad, la correlación de los tipos de crestas entre ambas superficies es generalmente buena, de tal manera que la presencia de una cresta continua en el esmalte se corresponde con una cresta continua en la dentina.
2. La buena correlación existente entre la superficie del esmalte y la dentina es de gran utilidad ya que, en aquellos dientes en que el desgaste haya hecho desaparecer la morfología externa **se puede inferir, a partir de la dentina, el tipo de cresta que había en el esmalte**.
3. Con respecto al patrón de crestas del trigónido, nuestros resultados confirman que existe una **mayor afinidad fenética entre TD6 y *H. sapiens*** por una parte y entre la **Sima de los Huesos y los *H. neanderthalensis*** por otra.
4. Nuestros análisis demuestran que los **patrones de crestas del trigónido de los homínidos de la Sima de los Huesos coinciden con los exhibidos por *H. neanderthalensis*** en las altas frecuencias de expresión de una cresta media del trigónido continua, tanto en el esmalte como en la dentina. Además, nuestros resultados también revelan que la Sima de los Huesos presenta un

tipo de cresta del trigónido en la dentina (tipo 9) que, por el momento, parece ser exclusivo de esta población y podría evidenciar la existencia de patrones derivados propios de la Sima de los Huesos.

5. *H. antecessor* y *H. sapiens* se caracterizan por presentar altas frecuencias de crestas del trigónido discontinuas, difiriendo de la morfología típica manifestada por la población de la Sima de los Huesos y los neandertales.
6. A pesar de que *H. antecessor* muestra altos porcentajes de crestas del trigónido discontinuas, algunos especímenes exhiben crestas medias del trigónido continuas, lo que nos permite ratificar que este rasgo no es una apomorfia neandertal propiamente dicha. **Nuestros resultados revelan que lo que es típico del linaje neandertal no es la cresta media del trigónido continua *per se*, sino las elevadas frecuencias de expresión y una altura significativa de la cresta.**
7. Nuestros datos confirman que el patrón morfológico de una **cresta media del trigónido continua es característico de *H. neanderthalensis* y de las poblaciones del Pleistoceno Medio de Europa**, a pesar de estar ausente en Mauer y Mala Balanica (BH-1). Al igual que los molares de la Sima de los Huesos, los especímenes de Arago muestran altas frecuencias de crestas medias del trigónido continuas. Sin embargo, su variabilidad en los tipos de crestas es menor, aunque esto último puede ser debido al tamaño muestral. De entre todos los homínidos del Pleistoceno Medio de Asia analizados en la presente tesis doctoral, tan sólo los dos especímenes de Qesem Cave presentan una cresta media del trigónido continua. Esto nos lleva a afirmar que la expresión de una cresta media del trigónido continua es más propia de los neandertales y de las poblaciones del Pleistoceno Medio de Europa que de las de Asia. Además, con respecto a los especímenes del Pleistoceno Medio de Tighenif, aunque estos presentan un porcentaje mayor de crestas medias del trigónido continuas que de discontinuas, la cresta no es en ningún caso tan alta como la típica del linaje neandertal.
8. A excepción de los M<sub>1</sub>s de ATD6-5 y ATD6-96, los molares de *H. antecessor* se caracterizan por presentar una complejidad estructural en el esmalte semejante a la exhibida por los homínidos de Yiyuan, Hexian, Zhoukoudian y Xujiayao. Sin embargo, la dentina de *H. antecessor* no muestra las múltiples

crenulaciones y surcos que caracterizan a estos especímenes asiáticos, sugiriendo caminos evolutivos diferentes.

9. Los resultados de nuestras investigaciones reafirman la particularidad morfológica de *H. antecessor* **en cuanto a la existencia de un mosaico de caracteres primitivos y derivados** con respecto al género *Homo*. Las bajas frecuencias de crestas medias del trigónido continuas en *H. antecessor* sitúan a estos especímenes morfológicamente más próximos a *H. sapiens*. Aunque la mayor parte de los rasgos plesiomórficos aparecen en la dentición, *H. antecessor* también presenta algunas apomorfias craneales, postcraneales y dentales compartidas con el linaje neandertal y con los humanos modernos. Esta combinación apoyaría la idea de una posición filogenética de *H. antecessor* **próxima al nodo de divergencia de *H. sapiens* y *H. neanderthalensis***.
10. Nuestros datos refuerzan la teoría de que el **asentamiento de Europa pudo ser el resultado de varias oleadas migratorias**, en momentos diferentes, provenientes de una misma población madre localizada en el suroeste asiático. *H. antecessor* podría representar una dispersión de esta población madre que, durante el Pleistoceno Inferior, se establecería en la parte más occidental de Europa. Nuestros resultados permiten afirmar que existe un aumento en las frecuencias de expresión de las crestas medias del trigónido continuas para las poblaciones europeas del Pleistoceno Inferior al Medio. Sin embargo, la variabilidad existente entre los grupos del Pleistoceno Medio apunta a que el aumento no es totalmente progresivo, por lo que no encajaría con la “neandertalización” ordenada propuesta por la “hipótesis de la acreción”. Así, las poblaciones representadas por los especímenes de la Sima de los Huesos, Arago, Montmaurin o Mala Balanica, podrían evidenciar entradas en momentos diferentes y sin que podamos descartar hibridación entre los residentes y los nuevos emigrantes.



## 7. CONCLUSIONS

Through this PhD dissertation we have made a comprehensive review of the trigonid and talonid crests' expression for most European Pleistocene hominins. The variability in the trigonid crests patterns has proved to be taxonomically and phylogenetically useful. Their comparison with other hominins has helped us to understand the polarity of these features and to contextualize the evolution of the European populations in a wider frame. In addition, our study for some morphological traits in *H. antecessor* has allowed us to obtain important data to precise the phylogenetic position of this species and to assess the most plausible evolutionary scenario for the settlement of Europe.

Below, we detail the most relevant conclusions obtained in the present PhD dissertation:

1. Our results show that the **morphological variability of the trigonid crests expression at the dentine is higher than at the enamel**. Despite this variability, there is a general good correlation between both surfaces in such a way that continuous crests at the enamel correspond to a continuous crest at the dentine.
2. The good correlation between outer and inner surfaces of a tooth is very useful since from the dentine we can predict **the type of trigonid crest that there was at the enamel in excessively worn teeth**.
3. Regarding the trigonid crests patterns, our results confirm that there is a greater **phenetic affinity between TD6 and *H. sapiens***, and between **Sima de los Huesos and *H. neanderthalensis***.
4. Our data show that **Sima de los Huesos hominins matches *H. neanderthalensis*** in the high frequencies of continuous mid-trigonid crests expressed at both the enamel and the dentine surfaces. In addition, our study has identified a trigonid crest type at the dentine (type 9) that, to date, has been only identified in this population and could point to the presence of derived patterns specific to Sima de los Huesos.



5. *H. antecessor* and *H. sapiens* are characterized by the presence of high frequencies of discontinuous trigonid crests, differing from the typical morphology exhibited by Sima de los Huesos population and Neanderthals.
6. Although *H. antecessor* exhibits high percentages of discontinuous trigonid crests, some specimens display continuous mid-trigonid crests. This means that this feature cannot be considered a Neanderthal apomorphy. **Our results show that what is typical of the Neanderthal lineage is not the continuous mid-trigonid crests *per se*, but the high frequencies of expression and the pronounced height of the crest.**
7. Our data confirm that a **continuous mid-trigonid crest pattern is typical of *H. neanderthalensis* and of the European Middle Pleistocene populations**, despite being absent in Mauer and Mala Balanica (BH-1). Like Sima de los Huesos molars, the Arago specimens present high frequencies of continuous mid-trigonid crests. However, the variability at the dentine is lower, although the latter may be due to the small sample size. Among all of the Middle Pleistocene hominins from Asia analyzed in this PhD dissertation, only the two from Qesem Cave present a continuous mid-trigonid crest. This means that this feature is more common in Neanderthals and European Middle Pleistocene populations than in Asia. Concerning the Middle Pleistocene specimens of Tighenif, although they present higher percentages of continuous than discontinuous mid-trigonid crests, their heights are not as elevated as in the Neanderthal lineage.
8. With the exception of ATD6-5 and ATD6-96 M<sub>1</sub>s, ***H. antecessor* molars are characterized at the enamel by an occlusal complexity similar to that exhibited by the Yiyuan, Hexian, Zhoukoudian and Xujiayao hominins.** However, *H. antecessor* EDJ does not display the multiple crenulations and grooves that characterize these Asian specimens, suggesting different evolutionary paths.
9. Our results reinforce the idea of *H. antecessor* as a species that **displays a unique mosaic of primitive and derived features** regarding the *Homo* clade. The lower frequencies of continuous mid-trigonid crests in *H. antecessor* suggest that they are morphologically closer to *H. sapiens*. Although most of the dental features are plesiomorphic, *H. antecessor* also presents some

cranial, postcranial, and dental apomorphies shared with the Neanderthal lineage and modern humans. This combination would support a phylogenetic position of *H. antecessor* **close to the node of divergence of *H. sapiens* and *H. neanderthalensis*.**

10. Our data strengthen the hypothesis that **the settlement of Europe could be the result of several migrations**, at different times, coming from the same “mother population” located in Southwest Asia. *H. antecessor* could represent a dispersal from this mother population that settled in the westernmost part of Europe during the Early Pleistocene. We suggest that the frequency of continuous mid-trigonid crests increased in Europe from the Early to the Middle Pleistocene populations. However, the variability among the Middle Pleistocene hominins suggests that this increase is not lineal, so it would not fit with the “neanderthalization process” proposed by the “accretion hypothesis”. Thus, the populations represented by Sima de los Huesos, Arago, Montmaurin or Mala Balanica specimens could represent different migrations at different times and/or population fragmentation, and we cannot exclude the possible hybridization between residents and new settlers.



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BIBLIOGRAFÍA





## 8. BIBLIOGRAFÍA

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09

ANEXOS





## 9. ANEXOS

En este apartado hemos incluido otras publicaciones y trabajos presentados en Congresos Nacionales e Internacionales durante el periodo de realización de la tesis doctoral relacionados con la misma. A continuación hacemos un listado por orden cronológico.

**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., 2013. Los dientes al desnudo: patrones de crestas del trigónido en la unión esmalte-dentina de los molares de la Sima de los Huesos (Atapuerca). Oral Communication presented at the XVIII International Congress of the SEAF, Bilbao (Spain), June 19-21.

**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., 2013. Undressing teeth: trigonid crest patterns at the enamel dentine junction of the Sima de los Huesos lower molars. Poster presented at the 3rd Annual Meeting ESHE, Austria (Vienna), September 19-21.

Martín-Torres, M.; Bermúdez de Castro, J.M.; **Martínez de Pinillos, M.**; Martín-Francés, L.; Gracia-Téllez, A.; Martínez, I.; Arsuaga, J.L., 2013. Sima de los Huesos al dente: a “modern” Neanderthal? Oral Communication presented at the 3rd Annual Meeting ESHE, Austria (Vienna), September 19-21.

Rangel de Lázaro, G.; **Martínez de Pinillos, M.**; Modesto-Mata, M.; Martín-Francés, L.; de la Cuétara, J.M.; Martín-Torres, M.; Bruner, E., 2014. Computer tomography and microCT applications at CENIEH. Poster presented at the II International Conference on Research Infrastructures., Athens (Greece), April 2-4.

**Martínez de Pinillos, M.**; Martín-Torres, M.; Martín-Francés, L.; Bermúdez de Castro, J.M.; de Lumley, M.-A., 2014. On the dental variability of the early and middle Pleistocene populations of Atapuerca. Oral Communication presented at the Colloque International 50 anniversaire de la Caune de l’Arago à Tautavel 1964-2014, Tautavel (France), June 23-27.

Martín-Torres, M.; **Martínez de Pinillos, M.**; Martín-Francés, L.; Bermúdez de Castro, J.M.; Vialet, A.; de Lumley, M.-A., 2014. Microtomographic study of hominin lower molars. Gran Dolina, Arago and Sima de los Huesos comparison and evolutionary inferences. Oral Communication presented at the Colloque International 50 anniversaire de la Caune de l’Arago à Tautavel 1964-2014, Tautavel (France), June 23-27.

**Martínez de Pinillos, M.**; Martín-Torres, M.; Martín-Francés, L.; Bermúdez de Castro, J.M., 2014. Morphological comparison of the Pleistocene hominin lower molars from Atapuerca sites by means of microCT. Oral Communication presented at the XVII World Congress of the UISPP, Burgos (Spain), September 1-7.

Modesto-Mata, M.; Bermúdez de Castro, J.M.; Dean, C.; **Martínez de Pinillos, M.**; Martín-Torres, M., 2014. Crown formation times in Homo antecessor molars (Gran Dolina-TD6, Sierra de Atapuerca, Spain). Oral Communication presented at the XVII World Congress of the UISPP, Burgos (Spain), September 1-7.

**Martínez de Pinillos, M.**; Martín-Torres, M.; Martín-Francés, L.; Modesto-Mata, M.; García-Campos, C.; Bermúdez de Castro, J.M., 2015. Dental variability of the Pleistocene hominins from Sierra de Atapuerca. Expression of trigonid crest patterns in Homo antecessor and evolutionary inferences. Oral Communication presented at the 5th Annual Meeting ESHE, London (UK), September 10-12.

Bermúdez de Castro, J.M.; Martín-Francés, L.; Martín-Torres, M.; Modesto-Mata, M.; **Martínez de Pinillos, M.**; García-Campos, C., 2015. Virtual reconstruction of the mandible ATD6-96 (Gran Dolina-TD6, Sierra de Atapuerca, Spain) and the reassessment of the taxonomical signal of Homo antecessor mandibles. Oral Communication presented at the 5th Annual Meeting ESHE, London (UK), September 10-12.

Vialet, A.; **Martínez de Pinillos, M.**; Martín-Torres, M.; Bermúdez de Castro, J.M., 2016. The dentition from Montmaurin-La Niche cave (Haute-Garonne, France). New insights in the Homo heidelbergensis debate. Poster presented at the 6th Annual Meeting ESHE, Alcalá de Henares, Madrid (Spain), September 14-17.

Bermúdez de Castro, J.M.; Martín-Torres, M.; Martín-Francés, L.; **Martínez de Pinillos, M.**; Modesto-Mata, M.; García-Campos, C., 2016. Teeth: the “black box” Poster presented at the 6th Annual Meeting ESHE, Alcalá de Henares, Madrid (Spain), September 14-17.

García Campos, C.; Martín-Torres, M.; Martín-Francés, L.; **Martínez de Pinillos, M.**; Modesto Mata, M.; Bernardo, P.; Labajo, E.; Sánchez, J.A.; Ruíz, E.; Zanolli, C.; Bermúdez de Castro, J.M., 2016. Sexual dimorphism of the human permanent mandibular canine tissue proportions. Poster presented at the 6th Annual Meeting ESHE, Alcalá de Henares, Madrid (Spain), September 14-17.

Modesto-Mata, M.; García-Campos, C.; Martín-Francés, L.; **Martínez de Pinillos, M.**; García-González, R.; Quintino, Y.; Canals, A.; Lozano, M.; Dean, C.; Martín-Torres, M.; Bermúdez de Castro, J.M., 2016. New methodology to reconstruct in 2D the enamel of human lower molars and its application to Homo antecessor. Poster presented at the 6th Annual Meeting ESHE, Alcalá de Henares, Madrid (Spain), September 14-17.

Vialet, A.; **Martínez de Pinillos, M.**; Martín-Torres, M.; Bermúdez de Castro, J.M.; Bertrand, B.; Colard, T., 2017. Résultats préliminaires du récolement et de l'étude des fossiles humains des grottes de Montmaurin (Haute-Garonne, France). Poster presented at the Colloque annuel de la Société d'Anthropologie de Paris 1842e réunion scientifique, Paris (France), January 24-26.

Modesto-Mata, M.; García-Campos, C.; Martín-Francés, L.; **Martínez de Pinillos, M.**; García-González, R.; Quintino, Y.; Canals, A.; Lozano, M.; Dean, C.; Martín-Torres, M.; Bermúdez de Castro, J.M., 2017. New methodology to reconstruct in 2D the cuspal enamel of modern human lower molars. American Journal of Physical Anthropology 163:824-834.

García Campos, C.; Martín-Torres, M.; Martín-Francés, L.; **Martínez de Pinillos, M.**; Modesto Mata, M.; Bernardo, P.; Zanolli, C.; Bermúdez de Castro, J.M., 2017. Contribution of dental tissues to sex determination in modern human populations. Oral Communication presented at the XX Congress of the SEAF, Barcelona (Spain), July 12-14.

Modesto-Mata, M.; García-Campos, C.; **Martínez de Pinillos, M.**; Martín-Francés, L.; Romero, A.; Pérez-Pérez, A; Lozano, M.; Martín-Torres, M.; Dean, M.C.; Bermúdez de Castro, J.M., 2017. Perikymata counts and the enamel growth-pattern in a geographically diverse sample of modern Homo sapiens. Poster presented at the XX Congress of the SEAF, Barcelona (Spain), July 12-14.

**Martínez de Pinillos, M.**; Martín-Torres, M.; Martín-Francés, L.; García-Campos, C.; Modesto-Mata, M.; Bermúdez de Castro, J.M., 2017. Homo antecessor lower molars at a glance. Poster presented at the 7th Annual Meeting ESHE, Leiden, (Netherlands), September 21-23.

Martín-Torres, M.; **Martínez de Pinillos, M.**; Martín-Francés, L.; Modesto-Mata, M.; García-Campos, C.; Liu, W.; Xing, S.; Wu, X.; Bermúdez de Castro, J.M., 2017. New dental remains from Atapuerca-Gran Dolina TD6 level: Homo antecessor revisited. Poster presented at the 7th Annual Meeting ESHE, Leiden, (Netherlands), September 21-23.

Martín-Francés, L.; Martín-Torres, M.; **Martínez de Pinillos, M.**; García-Campos, C.; Modesto-Mata, M.; Bermúdez de Castro, J.M., 2017. 2D Enamel thickness in Early Pleistocene Homo antecessor (Atapuerca, Spain). Poster presented at the 7th Annual Meeting ESHE, Leiden, (Netherlands), September 21-23.

Vialet, A.; Bermúdez de Castro, J.M.; Modesto-Mata, M.; Martín-Torres, M.; **Martínez de Pinillos, M.**, 2017. A comparative study of the Late Middle European Pleistocene Montmaurin-La-Niche (MLN). Preliminary results. Poster presented at the 7th Annual Meeting ESHE, Leiden, (Netherlands), September 21-23.



## XVIII CONGRESO DE LA SEAF (Bilbao, 19-21 de Junio de 2013)

## COMUNICACIÓN ORAL

**Los dientes al desnudo: patrones de crestas del trigónido en la unión esmalte-dentina de los molares de la Sima de los Huesos (Atapuerca).**

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**Resumen**

Hasta el momento, el análisis de la superficie de la dentina en los molares inferiores dentro del género *Homo*, ha estado limitado a *Homo neanderthalensis* y *Homo sapiens*. En este estudio presentamos la tipología de crestas del trigónido que aparecen en los homínidos del Pleistoceno Medio de la Sima de los Huesos (SH), asignados a *Homo heidelbergensis*. La muestra ha sido escaneada con un microCT, así como digitalizada y analizada de manera tridimensional con el software Amira 5.3. Nuestro objetivo es caracterizar las expresiones de crestas del trigónido en el esmalte (OES) y en la dentina (EDJ) de los homínidos de la SH, para evaluar la relación existente de dicho patrón morfológico dental entre ambas superficies. Aunque nuestros resultados muestran una mayor variabilidad de los patrones de crestas del trigónido en la dentina (14 tipos) con respecto al esmalte (4 tipos) -así como en los M<sub>3s</sub> con respecto a los M<sub>1s</sub> y M<sub>2s</sub>- en casi todos los casos la existencia de una cresta continua en el esmalte se corresponde con una cresta continua en la dentina. Esta característica es ciertamente útil, ya que puede implicar la posibilidad de inferir el tipo de cresta del trigónido que existía en el esmalte de dientes desgastados. Nuestro análisis ratifica las similitudes encontradas en los patrones de crestas del trigónido entre la SH (*H. heidelbergensis*) y los Neanderthales, así como las diferencias con *H. sapiens*. Esta investigación permitirá conocer mejor la variabilidad intra-poblacional de la SH, así como explorar los orígenes del linaje Neanderthal.

**Palabras clave:** molares inferiores permanentes; Sima de los Huesos; *Homo heidelbergensis*; microtomografía; patrones de crestas del trigónido.

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# Undressing teeth: Trigonid Crest patterns at the EDJ of the Sima de los Huesos molars.

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## INTRODUCTION

Trigonid crest (TC) refers to the expression of a crest that connects lower molar mesial cusps, and it can start from any lobe segment or from the marginal ridge and occupy mesial or distal positions. TC patterning is taxonomically informative and can be distinctive among Late Pleistocene hominins. In this study, we present an examination of TC patterning in the Middle Pleistocene permanent lower molar sample from Atapuerca-Sima de los Huesos (SH). Crest expression was assessed from 3D models of the enamel and the dentine surfaces (OES and EDJ) that were produced using microtomography. We aim to 1) characterize the pattern of TC expression at the OES and the EDJ surfaces, 2) evaluate the concordance of expression between both surfaces and, 3) place TC variation in SH into a phylogenetic context.

## MATERIAL AND METHODS

The total sample comprised 131 lower permanent molars from three different groups: Sima de los Huesos (n=62), *H. neanderthalensis* (n=37) and *H. sapiens* (n=32) (Table 1). Each molar of SH, the contemporary *H. sapiens* and El Mirador samples was scanned with a Scaano Medical AG Micro-Computed Tomography 80 (parameters: peak energy of 70 kV, intensity of scanning of 114µA, and 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.

Regarding the terminological considerations and scoring procedures, we consider a **cusp** the occlusal projection of the crown (White and Folkens, 2005), that is always made up of three different segments: mesial, middle or essential, and distal. The middle segment is the lobe bearing the cusp (Carlson, 1987; Scott and Turner II, 1997), and the free apex on top of the essential segment will be called **cusp tip**. The linear rounded edge of enamel that forms the mesial border of occlusal surface is called the **mesial marginal ridge** (Fig. 1).

## RESULTS AND DISCUSSION

### Trigonid crest types at the OES and EDJ of the SH sample

Figure 2 displays the types of trigonid crests found at the OES (following the scheme of Korenhoj, 1982) and the EDJ of the SH sample. Our study reveals that majority of SH molars (93%) express a MeTC or a MdTC; that the MdTC (72%) is more frequent than the MeTC (21%); and that there is a high proportion of lower molars with a continuous MeTC or MdTC and a discontinuous DTC (74%).

### Variability of the TC types at the OES and EDJ

The four basic types of TC at the OES contrast with a wider spectrum of crests combinations (14 types) at the EDJ (Table 2). However, in almost all cases there is a concordance between the presence of a continuous MeTC and/or DTC at the OES and the presence of a continuous MeTC or MdTC and/or DTC, respectively, at the EDJ. We can also observe that, in both enamel and dentine, there is a higher variability in M<sub>2</sub>s compared to M<sub>1</sub>s and M<sub>3</sub>s.

### Taxonomical implications

The expression at the OES of a continuous MdTC has been classically considered as typical of Neanderthals (Bailey, 2002; Martínón-Torres et al., 2012). This feature is present in the 93% of the SH sample and a 97% of *H. neanderthalensis* versus a 39% in *H. sapiens*. At the EDJ there is almost a constant expression of a continuous MdTC with a discontinuous DTC in the SH sample (74%). This pattern is present in a 81% of *H. neanderthalensis* and only in a 46% of our *H. sapiens* sample, and it is in concordance with the results obtained by Bailey et al. (2011) (Fig. 3). The differences are significant between SH and *H. sapiens* and Neanderthals and *H. sapiens* (p<0.05). Concerning to the TC types at the EDJ, the most representative for the SH sample is type 11 (16%); for the Neanderthals is type 10 (21%) and for the *H. sapiens* sample is type 4 (53%). Additionally, there are three 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. In addition, there are six TC types (types 3, 5, 6, 9, 13 and 14) that are expressed in the SH and *H. neanderthalensis* that are absent in the *H. sapiens* group.

## CONCLUSIONS

Our study reveals 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 a continuous middle or distal TC at the OES corresponds with a continuous mesial/middle or distal TC at the EDJ. This aspect is useful in dental studies as it may imply the possibility of predicting the TC type that would be at the OES in the case of worn teeth. Moreover, our analysis reveals that at the EDJ the SH sample matches broadly the TC patterns displayed by *H. neanderthalensis* and differs significantly from those exhibited by *H. sapiens*, particularly in the almost constant expression of a continuous middle TC. However, SH also displays some patterns that have not been found so far in our *H. neanderthalensis* and *H. sapiens* samples.

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Table 1: Study sample of lower molars.

Species	Origin	N total	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>
<i>H. heidelbergensis</i>	Sima de los Huesos <sup>1</sup>	62	22	18	22
<i>H. neanderthalensis</i>	Engis <sup>2</sup>	1	1	-	-
	Gibraltar <sup>3</sup>	3	2	1	-
	Ebrindorff <sup>4</sup>	1	1	-	-
	Abri Bourgeois-Delaunay <sup>4</sup>	1	1	-	-
	Regourdou <sup>1</sup>	6	2	2	2
	Abri Suard <sup>5</sup>	4	3	-	1
	Krapina <sup>6</sup>	20	7	6	7
	Hunas <sup>7</sup>	1	-	-	1
<i>H. sapiens</i>	Equus Cave <sup>8</sup>	2	2	-	-
	Qafzeh <sup>9</sup>	8	4	4	-
	Lagar Velho <sup>9</sup>	1	1	-	-
	El Mirador <sup>1</sup>	9	3	3	3
	CENIEH <sup>1</sup>	12	4	7	1

<sup>1</sup>CENIEH microCT data base <sup>2</sup>ESM<sup>2</sup> data base <sup>3</sup>NESPOS data base

Table 2: Variability of the TC at the OES and EDJ

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

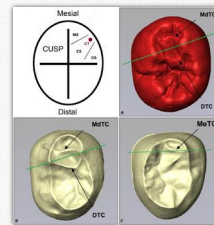


Fig. 1: To score the trigonid crests we draw a straight line from the protoconid to the metaconid tip (green line). Any TC lying distal to this line is classified as a distal trigonid crest (DTC) (Fig. 1A and 1B), and over to this line as a middle (MeTC) (Fig. 1A and 1B) or mesial trigonid crest (MeTC) (Fig. 1C). If one of the ends of the crest goes to the mesial marginal ridge, we classify it as MeTC instead of MdTC.

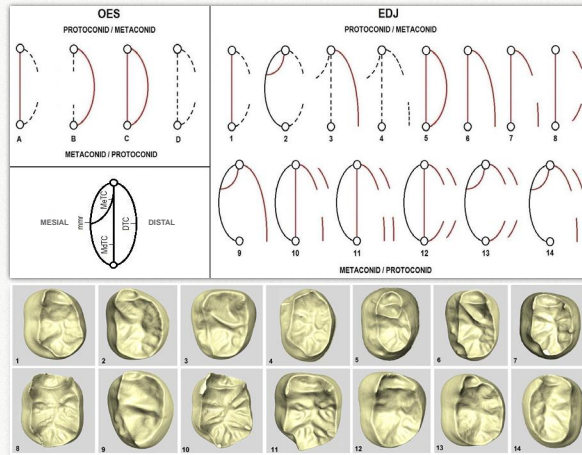


Fig. 2: Top: occlusal surface schemes of the OES (upper left) and EDJ (upper right) including the tips of the dentine horn (represented by circles) of the protoconid and metaconid and the mesial marginal ridge (represented by the continuous black line). Dashed lines mean that the crest is absent or discontinuous. Red lines mean that the crest/ridges are present in the form they are depicted. Bottom: examples of different types of TC on dentine with the mesial part at the top and the distal part at the bottom (virtual reconstruction computer models based on microCT).

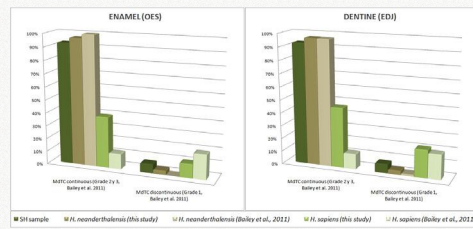


Fig. 3: Comparison between the data of our samples and those from Bailey et al. (2011) regarding continuous or discontinuous MeTC at the OES and EDJ.

Podium Presentation: Session 11, Sa (15:00)

### Sima de los Huesos *al dente* : a “modern” Neanderthal?

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Previous dental analyses have already pointed out the highly derived state of the Sima de los Huesos (SH) hominins compared to other Middle Pleistocene populations. SH dentitions present all the morphological features that either in their degree of expression, frequency or particular combination have been classically considered typical of *Homo neanderthalensis*. These studies have also revealed that SH dentitions are morphologically “more Neanderthal” than other penecontemporaneous Middle Pleistocene samples such as Mauer or Arago and even more derived in some traits than some Upper Pleistocene Neanderthals (Gómez-Robles et al., 2007; Martínón-Torres et al., 2012; Prado-Simón et al., 2012). However, these dental derived traits are combined with other dental and skeletal characters that do not display such derived states such as cranial, facial and postcranial features, which show intermediate or primitive conditions with respect to classic Neanderthals (Arsuaga et al., 1997). In our opinion, the evolution of the dentition would be in favor of a less gradual and anagenetic process for the evolution of the European Middle Pleistocene populations towards Neanderthals, than suggested in the *accretion model* (Hublin, 1998). Alternatively, we proposed that the morphological variability of the European Middle Pleistocene hominins and their apparent non-linear evolution to *Homo neanderthalensis* would fit better a “sink and source” model (Dennell et al., 2011) with repeated dispersals, fragmentations, regional extinctions and recombinations driven by the climatic conditions. However, a recent analysis on the cusp proportions of SH upper first molars (M1s) adds complexity to this scenario. Surprisingly, our study reveals that SH M1s present a mosaic of *Homo neanderthalensis* and *Homo sapiens* features. Regarding cusp angles and the relative occlusal polygon area, SH matches *H. neanderthalensis* pattern (Gómez-Robles et al., 2007). However, the total crown base area and the pattern of cusp proportions of SH M1s coincides with that of *H. sapiens*, presenting a small crown area, and a relative protocone enlargement and hypocone reduction. This “modern” pattern would match the *signal* of other dental features such as the small size of the postcanine dentition and the qualitative traits derived from this metric reduction (e.g., significant reduction or even absence of the hypoconulid/hypocone) that have been classically considered typical and even exclusive to *H. sapiens* (Bermúdez de Castro and Nicolás, 1995, Martínón-Torres et al., 2012). To the light of this evidence, we re-evaluate the state of art of the taxonomic and phylogenetic position of the SH population with regard to *H. heidelbergensis*, *H. neanderthalensis* and *H. sapiens*. Our dental analyses oblige to reconsider the “uniqueness” not only of the Neanderthal features, but also of the so-called modern traits.

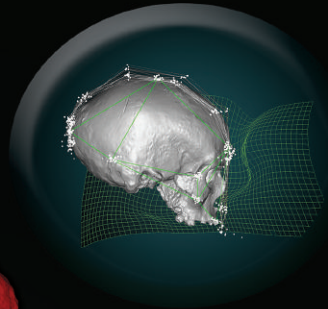
**References:** Arsuaga, J.L., Carretero, J.M. et al. (1991). Cranial remains and long bones from Atapuerca/Ibeas (Spain). *J Hum Evol* 20, 191-230. Bermúdez de Castro JM, Nicolás ME (1995) Posterior Dental Size Reduction in Hominids: The Atapuerca Evidence. *American Journal of Physical Anthropology*, 96, 335-356. Dennell, R., Martínón-Torres, M., Bermúdez de Castro, J.M. (2011). Hominin variability, climatic instability and population demography. *Quat Sci Rev* 30, 1511-1524. Martínón-Torres, M., Bermúdez de Castro, J.M. et al. (2012). Morphological description and comparison of the dental remains from Atapuerca-Sima de los Huesos site (Spain). *J Hum Evol* 62, 7-58. Gómez-Robles, A., Martínón-Torres, M., Bermúdez de Castro, J.M. et al. (2007). A geometric morphometric analysis of hominin upper first molar shape. *J Hum Evol* 53, 272-85. Hublin, J.J. 1998. Climate change, paleogeography and the evolution of the Neandertals. In *Neandertals and Modern Humans in Western Asia* (eds Akazawa T, Aoki K, Bar-Yosef O), pp. 295-310. New York: Plenum Publishing. Prado-Simón, L., Martínón-Torres, M., Baca, P. et al. (2012). Three-dimensional evaluation of root canal morphology in lower second premolars of early and middle pleistocene human populations from Atapuerca (Burgos, Spain). *American Journal of Physical Anthropology*, 147, 452-461.



## Computed Tomography and MicroCT applications at CENIEH

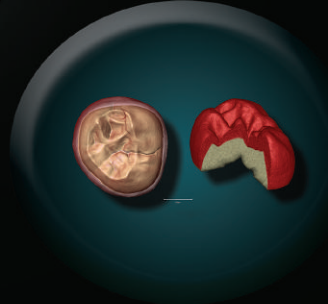
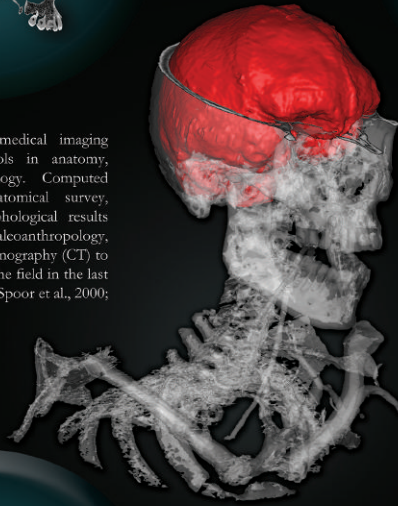
Gizéh Rangel de Lázaro,<sup>1</sup> Marina Martínez de Pinillos González,<sup>2</sup> Mario Modesto Mata,<sup>2,3</sup> Laura Martín-Francés,<sup>2</sup> José Manuel de la Cuétara,<sup>4</sup> María Martín-Torres,<sup>2</sup> Emiliano Bruner.<sup>2</sup>

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Computed statistics and biomedical imaging currently represent basic tools in anatomy, anthropology, and paleontology. Computed models allow complete anatomical survey, supporting reproducible morphological results and quantitative modeling. In paleoanthropology, the application of computed tomography (CT) to fossils was a major advance in the field in the last decades (Zollikofer et al., 1998; Spoor et al., 2000; Gunz et al., 2009).

Fossil remains can be CT scanned, cleaned and reconstructed using the tools of biomedical imaging (Zollikofer and Ponce de León, 2005). At the same time, computed statistics supply powerful tools to analyze anatomy and morphology taking into consideration multiple factors and the integration among different elements. Digital anatomy is employed in dental anthropology, craniology and paleoneurology, linking anthropological and biomedical fields.



New generation of non-invasive imaging tools has helped to address the conflicting requirements of safeguard versus exploitation of the fossil record and allows a virtual sharing and handling of fossils, ensuring its integrity

Virtual reconstruction of enamel (red) and dentine (beige) surface of *Homo heidelbergensis* molar from Atapuerca-Sima de los Huesos site. Digital models were made using a Scanco Medical AG Micro-Computed Tomography 80, housed at the CENIEH, and Amira 5.3.3 software



Gunz, P., Mitteroecker, P., Neubauer, S., Weber, G., & Bookstein, F. (2009). Principles for the virtual reconstruction of hominin crania. *Journal of Human Evolution*, 57, 48-62. Spoor, F., Jeffery, N., & Zonneveld, F. (2000). Using diagnostic radiology in human evolutionary studies. *J. Anat.*, 197, 61-76. Zollikofer, C., Ponce de León, M., & Martin, R. (1998). Computer-Assisted Paleoanthropology. *Evolutionary Anthropology*, 641-54. Zollikofer, C., Ponce de León. (2005). *Virtual Reconstruction: A Primer in Computer-Assisted Paleontology and Biomedicine*. Wiley.

*Colloque international 50 anniversaire de la Caune de l'Arago (1964-2014)*

Podium Presentation: Session 5, 16:50

**On the dental variability of the early and middle Pleistocene populations of Atapuerca.**

Marina **Martínez de Pinillos**<sup>1</sup>, María **Martinón-Torres**<sup>1</sup>, Laura **Martín-Francés**<sup>1</sup>, José María **Bermúdez de Castro**<sup>1</sup>, Marie-Antoinette **de Lumley**<sup>2</sup>.

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As the variation in dental form is highly heritable, teeth are more useful than other skeletal remains to assess resemblances between extant and extinct human populations, and to investigate phylogenetic relationships and the scenario in which these species evolved. The extraordinary human fossils found in different archaeological sites of Sierra de Atapuerca (Burgos, Spain), such as Gran Dolina-TD6 and Sima de los Huesos, give us the opportunity to explore the inter and intra-population variability of the Early and Middle Pleistocene dental collections from Atapuerca<sup>1</sup>. Up to date, the Gran Dolina-TD6 site has yielded a minimum number of individuals (MNI) of 11 whereas Sima de los Huesos (SH) has provided the largest hominin collection worldwide coming from one site with a MNI of 28. Due to this exceptional dental sample of SH, we have the possibility of not only performing comparisons between groups, but also assess the variability within one population<sup>2</sup>. By studying the Atapuerca samples as well as other comparative groups such as *Homo neanderthalensis* and *Homo sapiens*, we aim to investigate the Trigonid Crest pattern in these populations in order to make some possible evolutionary inferences<sup>3</sup>. This morphological feature has been classically studied at the enamel, but now we are able to reconstruct tridimensionally the inner surfaces by means of non-destructive techniques such as the microtomography (mCT)<sup>4</sup>. Our results reveal a higher variability in the expression of trigonid crests at the dentine compared to the enamel but, despite this variability, in almost all cases there is large general correlation between the expressions of crests at both surfaces. Besides, the analysis reveals that the SH sample matches broadly the trigonid crest patterns displayed by *Homo neanderthalensis* and differs from those exhibited by *Homo antecessor* and *Homo sapiens*. Other aspects of the variability of the trigonid crest expression at the dentine are presented and discussed.

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2. Martinón-Torres, M. *et al.* Morphological description and comparison of the dental remains from Atapuerca-Sima de los Huesos site (Spain). *Journal of Human Evolution*. 62, 7–58 (2012).
3. Martínez de Pinillos, M. *et al.* Trigonid crests expression in Atapuerca-Sima de los Huesos lower molars: Internal and external morphological expression and evolutionary inferences. *Comptes Rendus Palevol* 13, 205–221 (2014).
4. Bailey, S. E. *et al.* What lies beneath? An evaluation of lower molar trigonid crest patterns based on both dentine and enamel expression. *American Journal of Physical Anthropology* 145, 505–518 (2011).

*Colloque international 50 anniversaire de la Caune de l'Arago (1964-2014)*

Podium Presentation: Session 5, 17:10

**Microtomographic study of hominin lower molars. Gran Dolina, Arago and Sima de los Huesos comparison and evolutionary inferences.**

María **Martinón-Torres**<sup>1</sup>, Marina **Martínez de Pinillos**<sup>1</sup>, Laura **Martín-Francés**<sup>1</sup>, José María **Bermúdez de Castro**<sup>1</sup>, Amélie **Vialet**<sup>2</sup>, Marie-Antoinette **de Lumley**<sup>3</sup>.

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Due to new discoveries and interpretations, the evolution of the genus *Homo* during the Early and the Middle Pleistocene in Europe has become a topic of great interest. The archaeological, paleontological and molecular evidences<sup>1,2</sup> suggest that the settlement of the European continent depended upon the non-linear recruitment of populations and complex interactions among them, including the possibility of interbreeding. The aim of this study is to contribute to the analysis of the affinities between the Early and the Middle Pleistocene populations in Europe by analyzing the external and internal morphology of the lower molars by means of microtomography (mCT). In particular, we will focus in the pattern of trigonid and talonid crests expression, since these features are known to provide significant taxonomic and phylogenetic information<sup>3-5</sup>. We will present a comparative study of the outer enamel surface (OES) and enamel dentine junction (EDJ) surfaces of *H. antecessor*, *H. heidelbergensis* (Arago and Sima de los Huesos samples), *H. neanderthalensis* and *H. sapiens*. Previous studies revealed that Sima de los Huesos (SH) and the Arago specimens show clear dental Neanderthal affinities<sup>6</sup>. However, Arago teeth have been also described as more primitive than SH and somehow intermediate between SH and the Gran Dolina-TD6 fossils<sup>7</sup>. Morphological comparisons at the dentine level among the only human remains known from the Early Pleistocene of Europe (*H. antecessor*) and the largest and more representative samples for the Middle Pleistocene of Europe (Arago and Sima de los Huesos) together with *H. sapiens* and *H. neanderthalensis* will provide new and valuable information to explore the evolutionary scenario of the European settlement. Our study reveals that Arago lower molars share some EDJ features with SH (and thus, are close to the Neanderthal lineage) but in other traits its pattern of expression is closer to that of the Early Pleistocene fossils from Gran Dolina-TD6. The polarity (primitive-derived gradient) of the features is discussed with regard to *H. sapiens* and *H. neanderthalensis* trigonid and talonid crest expression. To the light of our mCT study, we present some evolutionary interpretations of the relationship between the Arago hominins and the Early and Middle Pleistocene hominins of Europe.

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## ORAL

**9. MORPHOLOGICAL COMPARISON OF THE PLEISTOCENE HOMININ LOWER MOLARS FROM ATAPUERCA SITES BY MEANS OF MICROCT.**

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Since the Atapuerca fossils are the most representative remains to understand the evolution of the genus *Homo* in Europe during the Early and Middle Pleistocene, the study of their dentition is becoming increasingly important. Several discoveries (Bermúdez de Castro and Martínón-Torres, 2013; Martínón-Torres et al., 2007a; Meyer et al., 2014) propose that the human occupation of Europe during the Pleistocene depended upon the non-linear recruitment of populations from the central area of dispersals of Eurasia. Morphological comparisons between those populations will provide new and valuable information to investigate the evolutionary scenario of the first European settlement.

The aim of this study is to explore the affinities between extant and extinct human population in Europe. For this purpose, and knowing that the expression of trigonid and talonid crest pattern seems to be of significant taxonomic and phylogenetic value (Bailey, 2002; Martínez de Pinillos et al., 2014; Martínón-Torres et al., 2014), we present a comparative study of these traits at the outer enamel surface (OES) and enamel dentine junction (EDJ) for *H. antecessor*, *H. heidelbergensis* (Sima de los Huesos samples), *H. neanderthalensis* and *H. sapiens* by means of microtomography (microCT).

Our results reveals that despite of the wider variability of trigonid crests types at the EDJ compared to the OES, the correlation in the morphology of the inner and the outer surface of the lower molars is high. Furthermore and in accordance with previous works (e.g. Bermúdez de Castro et al., 2003; Martínón-Torres et al., 2013), we highlight a more primitive dental conformation in Gran Dolina TD6 hominins in comparison with more derive features in the European Middle Pleistocene hominins from Sima de los Huesos.

To the light of our microCT study, we present some evolutionary interpretations of the relationship among the Early and Middle Pleistocene hominins of Europe, where the divergence of the features -primitive or derived- is considered regarding to H. sapiens and H. neanderthalensis trigonid and talonid crest expression.

signed to three individuals: two lower molars (one M1 and one M3) and five upper molars (three M1, one M2 and one M3). Environmental scanning electron microscope (ESEM) was used to estimate the imbricational enamel formation time and microtomography (microCT) was used to estimate the appositional enamel formation time.

Crown formation times of Homo antecessor molars fit within the variability of other hominin species.

Molar crown formation times are relatively stable throughout hominid evolution at least from the last common ancestor with chimpanzees, regardless dental morphological differences. Thus, differences in the eruption times might be mostly based on differences in the root extension rates.

ORAL

**10. CROWN FORMATION TIMES IN HOMO ANTECESSOR MOLARS (GRAN DOLINA-TD6, SIERRA DE ATAPUERCA, SPAIN)**

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Human remains from Atapuerca-Gran Dolina TD6 level represent at least 11 individuals that are dated to approximately 0.9 million years. These fossils were recovered in different seasons since 1994 and were the base to name a new human species, Homo antecessor. There are several publications regarding the morphological features of this hominin, including teeth. However, information available about Homo antecessor dental development is scarce, and those studies did not employed histological variables. Here, we studied the crown formation times of Homo antecessor lower molars. Our results are compared with molar crown formation times in other hominin species and great apes obtained from the literature. We studied seven Homo antecessor molars that are as-



Podium Presentation: Session 6A, Fr (14:40)

**Dental variability of the Pleistocene hominins from Sierra de Atapuerca. Expression of trigonid crest patterns in *Homo antecessor* and evolutionary inferences**

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1 - CENIEH

Teeth are considered a valuable source of morphological characters with taxonomic and phylogenetic utility. Here we will focus on the dentition of the human fossils recovered from the Gran Dolina-TD6 site, assigned to *Homo antecessor* species and dated to MIS 21 or MIS 25. To date, Gran Dolina-TD6 stratum has provided more than 150 human remains characterized by a unique combination of plesiomorphic and apomorphic traits. This unique combination, as well as new hominin fossil findings in Africa and Eurasia, has helped us to refine the phylogenetic position of *H. antecessor* regarding the Early and Middle Pleistocene hominins from those continents. The main purpose of our study is to contribute to a better understanding of the human evolution in Europe during the Early and Middle Pleistocene transition with the help of the valuable Atapuerca fossil samples. Thus, using micro-computed tomography (microCT) and knowing that the trigonid crest pattern expression bears a significant taxonomic and phylogenetic value, we have analysed the enamel and dentine surfaces of different hominins. Our sample includes *H. antecessor*, Sima de los Huesos (SH), *H. neanderthalensis* and *H. sapiens* specimens. Regarding the trigonid crest pattern, our results confirm that SH and Neanderthal samples share the highest frequencies of the typical continuous middle trigonid crest (MdTC) at both the enamel and the enamel-dentine junction, a feature that has been considered as a "Neanderthal feature". The identification of this feature in the *H. antecessor* dental samples means that a continuous MdTC cannot be considered as a Neanderthal apomorphy. However, the lower frequencies of expression suggest that *H. antecessor* is phenetically closer to *H. sapiens* who would have preserved a primitive pattern. Recent studies suggest that *H. antecessor* is at (or close to) the node of divergence of *H. sapiens* and *H. neanderthalensis*, and this would explain that TD6 hominins share features with both the modern humans and the Neanderthal lineages.

Acknowledgements: This research was supported with funding from the Dirección General de Investigación 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. M.M-P. has the benefit of a predoctoral contract of the Junta de Castilla y León under the Regional Strategy for Scientific Research, Technological Development and Innovation 2007-2013 co-financed by the European Social Fund (BOCYL-D-20122012-38).

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Podium Presentation: Session 2, Th (13:40)

### Virtual reconstruction of the mandible ATD6-96 (Gran Dolina-TD6, Sierra de Atapuerca, Spain) and the reassessment of the taxonomical signal of *Homo antecessor* mandibles

José María Bermúdez de Castro<sup>1</sup>, Laura Martín-Francés<sup>1</sup>, María Martínón-Torres<sup>1</sup>, Mario Modesto<sup>1</sup>, Marina Martínez de Pinillos<sup>1</sup>, Cecilia García<sup>1</sup>

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ATD6-96 is the left half of a gracile mandible of an adult individual with premolars and molars in place. It was found in 2003 in the TD6 level (OIS 21, 0.85 Ka) of the Gran Dolina cave site of the Sierra de Atapuerca, northern Spain. The specimen is broken at the level of the lateral incisor-canine septum. A first study of this specimen was published two years later. In order to obtain additional information, we have made a virtual reconstruction of the mandible. The specimen ATD6-96 was scanned with a Tomographic system (Tomograph YXILON Compact Yxlon International, X-Ray GmbH) housed at the University of Burgos, using the following settings: voltage 130 kV, amperage 4 mA and resultant voxel size of 0.109mm x 0.109mm x 0.20mm. The resulting images were imported into Amira (Visage Imaging) software to obtain the 3D volume of the mandibular left side. Following, a second reconstruction was made by mirror-imagining the original stack of images (left hemimandible) to obtain the right hemi-mandible and create the 3D volume. As the canine alveolus is not complete (due to a post-depositional breakage) it was necessary to mirror the remaining half. The reconstructed 3D volume was then aligned and placed resulting in an entire alveolar rim; this was also performed on the right side. Despite the 3D reconstruction of the mandibular fragments, the symphyseal region is still missing. To reconstruct the symphysis, we defined two landmarks placed at the interdental septum, between the canine and the lateral incisor. In order to complete our reconstruction, we have obtained information taking as a reference: 1) a modern human sample, 2) a fossil hominin sample, and 3) the size of the root of the TD6 permanent lower incisors. We rotated the created volumes (right and left hemi-mandibles) on the "x, y and z" planes until the anatomical position was obtained, trying that the wear plane of all teeth is positioned approximately in the same plane, perpendicular to a vertical line. Finally, all the measurements were taken on the 3D volume models for comparative purposes. In our first study, it was concluded that ATD6-96 shows a primitive structural pattern shared with all African and Asian specimens. Furthermore, ATD6-96 is very small and exhibits a remarkably gracility, like the other TD6 mandibles. In this aspect, *H. antecessor* has clearly diverged from the African hominins, and ATD6-96 shares his/her gracility particularly with the Early and Middle Pleistocene Chinese specimens. Moreover, ATD6-96 shows a remarkable medial pterygoid tubercle, which is very frequent in Neandertals and in the Middle Pleistocene Sima de los Huesos hominins. Concerning the digital reconstruction, the main finding is that ATD6-96 had a derived parabolic dental arcade, measured by the index of the alveolar arcade. Interestingly, the value obtained for this index in ATD6-96 is similar to the mean values of Neandertals and the Sima de los Huesos hominins, and higher than that obtained in other Middle Pleistocene African, Asian and European specimens. Thus, the value of the alveolar arcade index adds to the list of the "Neandertal" features observed in the ATD6 hypodigm so far. As we have concluded in previous studies, all these features cannot not be considered as Neandertal autapomorphies, but traits which may have appeared much earlier than we had previously considered, in an Early Pleistocene hominin population. Summarizing and in general terms, the TD6 mandibles clearly diverged from the Pleistocene African pattern and show more affinities with the Eurasian specimens.

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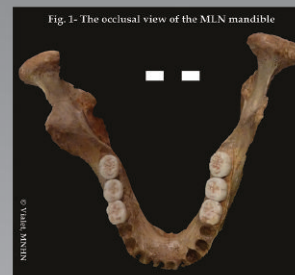


## The dentition from Montmaurin-La Niche cave, Haute-Garonne, France. New insights in the *Homo heidelbergensis* debate.

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### Context

The Montmaurin karstic system (South-West of Toulouse) is composed by 8 caves. Among them, the Montmaurin-La Niche (MLN) has yielded one mandible (Fig.1), a tibia and a cervical vertebra in 1949 during the R. Cammas' excavation [1]. A recent work on the geomorphological context and the fauna [2] attributed the layer bearing human fossils (C3) to the MIS 7, around 200 ka. In continuity with the study done in 1977 [3], the MLN mandible, considered as more archaic than Neandertal, is now assigned to *Homo heidelbergensis* [4] while this species is hotly debated.



### Material and methods

We carried out a deeper study comparing the MLN mandible with Middle Pleistocene fossils such as the Arago and Sima de los Huesos (SH) specimens which are the closest, geographically and chronologically speaking. We focused on dental morphological features which are known to have a high genetic component of expression and, among them, trigonid crest patterns which bear a significant taxonomic signal, particularly for the identification of the Neanderthal lineage [5, 6, 7]. We analyzed the morphology of the outer enamel surface (OES) of the six molars of the MLN mandible using the Korenhof's scoring system [8] and the trigonid crests expression at the enamel dentine junction (EDJ) using micro-CT data following the scoring system described in Martínez de Pinillos et al. [9]. The MLN mandible was scanned with a RTP Tomo3D-Tomographie RX in the AMIS-Faculty of Medicine in Toulouse and the segmentation was done with Amira 6.0 (Vivage Imaging, Inc.).

### Results



		MLN	Arago	SH	HN	HS
		n=6	n=5	n=63	n=40	n=37
OES	type A	100	75	72	77	33
EDJ	type 1	17	0	7	3	6
	type 7	17	0	5	9	3
	type 10	67	25	12	23	6

Fig. 2- Left: occlusal enamel surface (upper) and enamel dentine junction (lower) of AT2271 from SH illustrating the middle (MTC) and distal (DTC) trigonid crests. Right: virtual reconstruction of the enamel (upper) and dentine surfaces (lower) of the MLN molars.

Table 1- Percentages of the trigonid crest patterns at the OES (type A) and at the EDJ (types 1, 7, 10) of the MLN molars and other fossils (Arago, SH-Sima de los Huesos, HN-Neandertalis and HS-*Homo sapiens*).

Our study (Fig. 2) reveals that all the MLN teeth display a continuous MdTC at the OES (type A) that is also high and continuous at the EDJ (types 1, 7, 10). In this feature, MLN would be similar to Arago, SH and the Neanderthal samples lineage in presenting high prevalence of continuous MdTC (Table 1). However, in both MLN and Arago, a continuous DTC is absent whereas this feature has been described as typical of the Neanderthal lineage and is present in a 23.2% and 14.7% of our SH and Neanderthal samples, respectively. The absence of continuous DTC could be interpreted as a more primitive condition. Such results on dental features fit well with other mandibular traits which make the MLN mandible closer to the Arago ones than the more derived SH mandibles.

### References

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## Teeth: the "black box"

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### INTRODUCTION

Teeth represent the best source of information to address different questions regarding growth, development and hominins' lifestyle, including cultural and behavioural aspects. Moreover, teeth are very useful tools in paleodemographic, paleopathological, and paleoenvironmental studies. They are safe DNA containers and exhibit a suite of key features that can be used to characterize paleodememes. In summary, we can consider that teeth are a true "black box" to ascertain and document the events that happened during our ancestors' and our own life, as well as to establish reliable relationships between past and present populations.

The recent recovering of nuclear DNA sequences from two specimens from the Atapuerca-Sima de los Huesos (SH) Middle Pleistocene site has confirmed the close relationship between these hominins and the Neanderthals [1]. All previous morphological studies of the about 6,500 human remains recovered so far in SH reached a similar conclusion. In particular, pioneering morphological and metrical studies of the teeth [2, 3, 4] showed a close phylogenetic relationship between the SH hominins and the Neanderthals. Additional studies using larger samples and different methodological approaches confirmed previous results [e.g., 5].

Although we are aware that a substantial part of the dental morphology and dimensions are conditioned by environmental factors, it is also true that teeth are the skeletal part carrying the strongest taxonomical signal. Some of the dental derived features we identify in the fossils are highly reliable to characterize paleodememes.

### OBJECTIVE

The aim of this study is to test the accuracy of the dental external morphology for relating species.

### METHODOLOGY

To do so we want to challenge dental and non-dental specialists to participate in a quiz.

We have selected several mandibular first premolars ( $P_3$ ) and described the typical Neanderthal characteristics that are shared by some of these specimens. Moreover, other specimens not presenting the same features have also being included for differentiation.

Please, read carefully the typical Neanderthal external morphology. Following, identify which of the specimens present Neanderthal-like features and which do not.

### TYPICAL NEANDERTHAL-LIKE EXTERNAL MORPHOLOGY

The Neanderthal-like features identified in mandibular first premolars ( $P_3$ ) are the following:

1. Large and tall buccal cusp, particularly at its buccal surface. This cusp is strongly projected onto the occlusal plane, so that its tip is centered and close to the tip of the lingual cusp. Thus, the occlusal polygon is small and occupies a lingual position within the tooth contour.
2. Well-developed mesial and distal marginal ridges (MMR and DMR). In some cases, the DMR exhibits small accessory cusps.
3. Smaller and less swollen lingual cusp, placed in a central position and differentiated by a fine cleft either from the MMR or from the DMR. In some cases both mesial and distal clefts are present.
4. The lower half of the buccal face is swollen, generally more pronounced at the mesial part.
5. The crown is almost symmetrical.
6. No signs of buccal cingulum.
7. Generally a single root, mesiodistally compressed.



Not to scale

### ACKNOWLEDGEMENTS

Grant sponsors: Dirección General de Investigación of the Spanish Ministerio de Educación y Ciencia (MEC), project number: CGL2015-65387-C3-3-P; Junta de Castilla y León; Grant numbers: BOCYL-D-30122013-33; BOCYL-D-20122012-38 and annual field seasons; Fundación Atapuerca; Leakey Foundation.

Fig. 1  
 Fig. 2  
 Fig. 3  
 Fig. 4  
 Fig. 5  
 Fig. 6  
 Fig. 7  
 Fig. 8  
 Fig. 9  
 Fig. 10  
 Fig. 11  
 Fig. 12

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### SOLUTION

Non-Neanderthal like:

a, b, c, d, e, f, g, h, i, j, k, l

Neanderthal like:

a, b, c, d, e, f, g, h, i, j, k, l



# Sexual Dimorphism of the HUMAN PERMANENT MANDIBULAR CANINE TISSUE PROPORTIONS

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## INTRODUCTION

Accurate sex estimation is one of the most important steps for the reconstruction of the biological profile of an individual both in a forensic and a paleoanthropological context. Due to their durability, teeth have increasingly been used in post-mortem identification procedures, especially when other elements are not available. Several researchers have corroborated that dental tissue proportions from permanent dentition have also differ significantly between males and females [1-5]. Among the different tooth classes, canines show the highest degree of dimorphism [3][6]. The aim of this study is to quantify the sexual dimorphism of mandibular canines tissue proportions from high-resolution micro-CT images in Spanish sample of known sex.

## CONCLUSIONS

Our results support the hypothesis that sexual dimorphism of dental tissue proportions are due to the male's greater amount of dentine, and that sex differences in enamel do not make a large contribution to overall tooth size dimorphism [1][5][7]. Even though it is unclear which is the exact mechanism by which the sexual hormones influence on dental tissues formation, there are a great number of evidences that support that hormones affect not only in the dentine original formation, but also in its subsequent deposition along the individual's life [2][8][9]. 3D measurements have end up being more appropriate to evaluate tissue proportions since it counteracts the effect of dimensional loss in classic 2D estimations, maximizing the biological information that can be obtained from teeth [5][10][11].



## METHODS



### Sample

The analytical sample consisted of a total of 22 mandibular permanent canines of known sex and age at death from the exhumation of two Spanish cemeteries from the Anthropological Collection of Escuela de Medicina Legal de Madrid.



### Micro-CT image acquisition and image processing

The teeth were scanned by X-ray microtomography (microCT). The following image processing was carried out using the Amira 6.0.0 software (Visage Imaging, Inc.). Each virtual record was reoriented to obtain crown buccolingual sections employing the method of Benazzi et al. (2014)[12] and crown reconstruction was carried out following the methodology described and validated by Saunders et al. in 2007[4]. 3D reconstructions were generated after the segmentation process.



### Dental tissue measurements

We recorded the variables described by Martín (1983)[10] from the cross sections in order to develop the 2D tissue proportions analysis. The three-dimensional metrics from the crown were measured following the protocols of Olejniczak et al. (2008)[13] and Feeney et al. (2010)[5]. To the whole tooth 3D measurements, the variables described by Bayle et al. (2009)[14] and Zanolli et al. (2013) [15] were considered. We also recorded the root volumes following the protocols describe by Le Cabec et al. (2012, 2013)[16][17]. T-Student test statistical analyses were then performed to compare the male and female means. This statistical evaluation was supplemented by means of a Principal Components analysis to provide additional information about of inter-sexual variability.

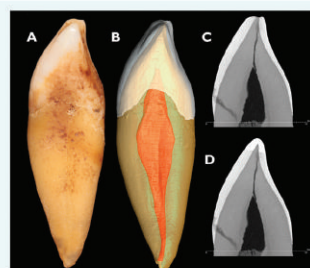
## RESULTS



- All the variables and rates considered in this study are described in detail in the Supplementary Information.
- Males canines have significantly greater mean dimensions, which have 35.19% more volume than female canines (Vt males: 552.93±70.37mm<sup>3</sup>; Vt females: 408.99±57.84mm<sup>3</sup>).
- The lower canines of both sexes possess equivalent amounts of enamel (Ve), though males have significantly more amount of dentine (Vcdp, Vcd, Vrd, Vd) even when tooth size is controlled (Vcdp/Vt).
- In the same way, EDJ dimensions (length and surface) are significantly greater in males, probably because of the bigger dentine volume.

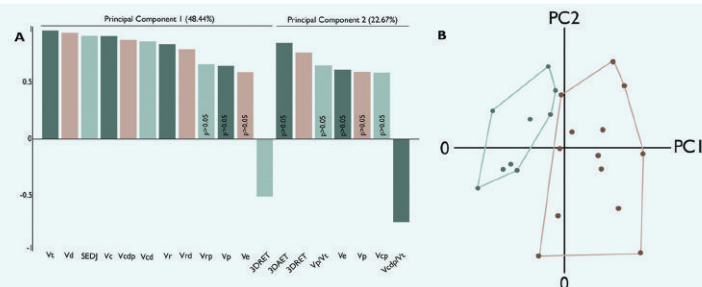
### Principal Component Analysis PCA

When we considered only the 2D variables from the crown there was a clear overlapping between both groups, which only differed along the first component. When we added a dimension, the overlapping substantially decreased. But only when we considered the coronal and the whole tooth 3D measurements, the PCA allowed us for clearly discriminating males from females.



**Tissue segmentation and cross-sections obtaining**

(A) Mesial surface of the individual UCM\_20 lower left canine. (B) After scanning, dental tissues (enamel, dentine and pulp) were semi-automatically segmented. (C) The virtual cross-sections were obtained following the method of Benazzi et al. (2014)[12], and the crown reconstruction was out applying the Saunders et al. in 2007[4] methodology (D).



**Results of the principal components analysis carried out with the three-dimensional measurements from the whole tooth.**

(A) Correlation coefficients between variables and canonical axes. Only the variables which have a coefficient higher than 0.5 are represented. We indicate in the graphic which variables are not significantly different between both groups when we employ T-Student test. (B) PC1 plotted against PC2. Brown circles: masculine individuals; green circles: feminine individuals. We could differentiate both sexes mainly due to the PC1, being females located at the negative quadrant and males more dispersed, but mainly in the positive one. The variables are described in the Supplementary Information.



## SUPPLEMENTARY INFORMATION

For more information about references, variables description and authors use the QR code



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# New methodology to reconstruct in 2D the enamel of human lower molars and its application to *Homo antecessor*

### Aim, Material & Method, Validation

- Aim:** statistical reconstruction of the enamel of lower molars
- Material** (unworn molars): 25 (*Homo sapiens*) + 2 (*H. antecessor*)
- Methodology:**
  - 3.1.) microCT reference plane [1] (Fig 1a)
  - 3.2.) 21 *H. sapiens* molars → polynomial regression (POL-PR) (Fig 1b,c)
  - 3.3.) 4 *H. sapiens* molars → digitally eroded (Fig. 1c)
- Validation:**
  - 4.1.) Interobserver error (4 co-authors)
  - 4.2.) Measure **crown heights** (4 eroded molars *H. sapiens*):
    - 4.2.1.) POL-PR (Video 1, QR code, bottom left corner)
    - 4.2.2.) Real values
    - 4.2.3.) Method 1 [2]
    - 4.2.4.) Method 2 [3]
  - 4.3.) Application of POL-PR to *Homo antecessor*.

### Results (Fig. 2)

**Homo sapiens**

Average = **-2.92%**  
 Lower 95% CL = **-4.79%**  
 Upper 95% CL = **-1.05%**

**H. antecessor**

ATD6-112 (M1, Fig. 3) = **+0.50%**  
 ATD6-5 (M3, Fig. 4) = **-2.90%**

### Percentage of error Crown Height (POL-PR vs. Real)

Fig. 2. Percentage of error between real and estimated values (using POL-PR, Method 1 and 2) of crown heights. 4 molars have been employed, and they were reconstructed by 4 co-authors.

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 Bermúdez de Castro, JM<sup>1,6</sup>

### Discussion and final remarks

- ✓ POL-PR confidently reconstructs the morphology of protoconids
- ✓ POL-PR is useful to estimate crown heights
- ✓ Associated errors with the estimations are known
- ✓ POL-PR can be used in fossil hominins (validation is required)
- ✓ POL-PR significantly improves previous methods

**Advantages of POL-PR applied to worn molars:**

- ★ Estimate the percentage of lost enamel
- ★ Estimate number of decidua that have been lost
- ★ Compensate perikymata counts in the decidua
- ★ Study of perikymata packaging distribution
- ★ Useful when measuring cuspal enamel thickness?

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### Affiliations, References, Acknowledgements

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**Acknowledgements**

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### How to reconstruct a worn molar using POL-PR

### Fig. 3. ATD6-112 (M1). Reconstruction of the protoconid using POL-PR

### Affiliations, References, Acknowledgements

### Fig. 4. ATD6-5 (M3). Reconstruction of the protoconid using POL-PR



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## Résultats préliminaires du récolement et de l'étude des fossiles humains des grottes de Montmaurin (Haute-Garonne, France)

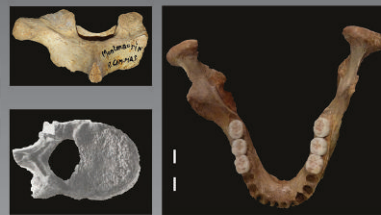
A. Vialet (MNHN, UMR7194, Paris, UPVD, CERP, Tautavel), M. Martínez de Pinillos (CENIEH, Burgos, UCL, Londres), M. Martínón-Torres (UCL, Londres, LEH, Burgos), J.-M. Bermúdez de Castro (CENIEH, Burgos, UCL, Londres), B. Bertrand (EA7367, IML, Univ. Lille), T. Colard (EA4490, PMOI, Univ. Lille)

### Récolement des restes humains

À la faveur de l'exploitation d'une carrière, plusieurs cavités ont été identifiées dans le massif karstique de Montmaurin (Saint-Gaudens, Haute-Garonne) déjà connu par les travaux de M. Boule au début du XXe s. De 1946 à 1961, L. Mèroc et R. Cammas entreprennent des fouilles, principalement dans les cavités du Coupe-Gorge et de La Niche. Parmi un matériel abondant (faune, industrie lithique), plusieurs fossiles humains ont été mis au jour (Baylac et al. 1950). L'ensemble du matériel archéologique est aujourd'hui dispersé voire difficile à localiser. Le premier objectif de ce projet vise donc à effectuer un récolement de ces collections.

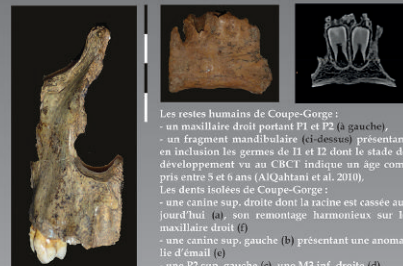
Pour les restes humains de La Niche : outre la célèbre mandibule (Billy et Vallois 1977), une vertèbre thoracique (signalée mais jamais étudiée) a été identifiée tandis que le tibia et une autre vertèbre thoracique, décrits par Cammas et Tavoso (1986), n'ont pas encore été localisés. Pour le Coupe-Gorge, tous les éléments décrits par Billy (1982, 1985) ont été retrouvés, authentifiés par leur numéro d'inventaire. Il s'agit de 4 dents isolées (C sup. droite, C sup. gauche, P2 sup. gauche, M3 inf. droite), un fragment de mandibule d'un individu immature et un maxillaire droit portant P1 et P2. Les études biochronologiques, effectuées sur la faune associée à ces restes humains, attribuent ceux de La Niche (Crégut-Bonnoure et al. 2010) au SI 7 et ceux de Coupe-Gorge (Guadelli 1990) au SI 5.

### Resultats préliminaires

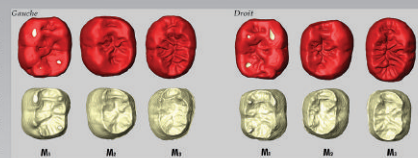
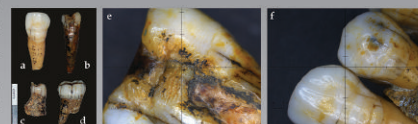


Les restes humains de La Niche : en noir et blanc, les ossements publiés par Cammas et Tavoso (1986) : un tibia gauche (vue postérieure) et une vertèbre thoracique (vue supérieure). En couleur : une vertèbre thoracique (vue postérieure), une mandibule (vue supérieure).

L'étude des caractères dentaires internes des molaires de la mandibule de La Niche a montré l'absence de crête distale trigonide continue à la jonction émail-dentine, comme sur les fossiles de la Caune de l'Arago (Tautavel), ce qui peut être interprété comme un caractère primitif par rapport à ce qui est observé sur les Néandertaliens et les individus de la Sima de los Huesos (Atapuerca), chez lesquels elle est plus fréquemment exprimée. Ainsi, le fossile le plus connu des sites de Montmaurin ne semble pas totalement engagé dans la lignée néandertalienne.



Les restes humains de Coupe-Gorge :  
- un maxillaire droit portant P1 et P2 (a gauche),  
- un fragment mandibulaire (ci-dessus) présentant en inclusion les germes de I1 et I2 dont le stade de développement vu au CBCT indique un âge compris entre 5 et 6 ans (AlQahtani et al. 2010).  
Les dents isolées de Coupe-Gorge :  
- une canine sup. droite dont la racine est cassée aujourd'hui (a) son remontage harmonieux sur le maxillaire droit (d)  
- une canine sup. gauche (b) présentant une anomalie d'émail (e)  
- une P2 sup. gauche (c) et une M3 inf. droite (d).



Reconstruction virtuelle des surfaces d'émail (en haut) et de dentine (en bas) des molaires de la mandibule de Montmaurin-La Niche.

### Références

AlQahtani et al. 2010 *AJPA* 142, Baylac et al. 1950 *L'Anthropologie* 54, Billy 1982 *BMSAP* 9, Billy 1985 *Z. Morph. Anthrop.* 75, Billy et Vallois 1977 *L'Anthropologie* 81, Cammas et Tavoso 1986 *CRAS* 302, Crégut-Bonnoure et al. 2010 *Préhistoires méditerranéennes* 1.

Remerciements à José Braga et Jean Dumoncel (AMIS, Toulouse) pour les données micro-CT de la mandibule de La Niche et à Pierre Marchandise (PMOI-IML, Lille) pour le support technique (CBCT et micro-CT des autres restes humains de La Niche et Coupe-Gorge).

# New methodology to reconstruct in 2-D the cuspal enamel of modern human lower molars

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**Abstract**

**Objectives:** In the last years different methodologies have been developed to reconstruct worn teeth. In this article, we propose a new 2-D methodology to reconstruct the worn enamel of lower molars. Our main goals are to reconstruct molars with a high level of accuracy when measuring relevant histological variables and to validate the methodology calculating the errors associated with the measurements.

**Methods:** This methodology is based on polynomial regression equations, and has been validated using two different dental variables: cuspal enamel thickness and crown height of the protoconid. In order to perform the validation process, simulated worn modern human molars were employed. The associated errors of the measurements were also estimated applying methodologies previously proposed by other authors.

**Results:** The mean percentage error estimated in reconstructed molars for these two variables in comparison with their own real values is -2.17% for the cuspal enamel thickness of the protoconid and -3.18% for the crown height of the protoconid. This error significantly improves the results of other methodologies, both in the interobserver error and in the accuracy of the measurements.

**Conclusions:** The new methodology based on polynomial regressions can be confidently applied to the reconstruction of cuspal enamel of lower molars, as it improves the accuracy of the measurements and reduces the interobserver error. The present study shows that it is important to validate all methodologies in order to know the associated errors. This new methodology can be easily exportable to other modern human populations, the human fossil record and forensic sciences.

**KEYWORDS**

molar reconstruction, polynomial regression, cuspal enamel thickness, crown height

**1 | INTRODUCTION**

Unworn teeth are important to assess crown formation times and enamel extension rates with a high degree of accuracy. Especially, an intact protoconid is of particular interest in developmental studies because it is the first cusp to start forming and the cusp that normally

takes the longest time to finish its growth in molars (Mahoney, 2008). Unfortunately, the presence of unworn teeth in the fossil record is relatively scarce. The present study proposes a new methodology to reconstruct the protoconid of slightly worn lower molars, in order to increase of the number of samples where developmental variables could be evaluated. We employed the computerized microtomography

## XX CONGRESO DE LA SOCIEDAD ESPAÑOLA DE ANTROPOLOGÍA FÍSICA

## Contribution of dental tissues to sex determination in modern human populations

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**Introduction:** Sex determination is an essential step in the post-mortem identification of skeletal remains. Given their overall greater resistance compared to that of other parts of the skeleton, teeth are considered useful elements in the study of mass fatalities or catastrophic events since there is a great probability to recover them intact. Among teeth, canines have shown the greatest sexual dimorphism. Through Discriminant Function Analysis, we have explored the potential for reliable sex estimation of volumetric and surface measurements from mandibular canine dental tissues.

**Material and methods:** The teeth included in this study (n=69) were selected from anthropological collections from Spain, South Africa and Sudan. In all cases, the sex of the individuals samples was known. The teeth were scanned and three-dimensional measurements were subsequently obtained. Discriminant function accuracy was tested on the original sample, using a cross validation and a hold-out sample.

**Results:** Our results showed that sexual dimorphism in canine size is due to males having greater amounts of dentine, whereas enamel volume does not overall contribute significantly to tooth size dimorphism. Classification accuracy of the multi-variable equations tested on slightly worn teeth ranged from 78% to 90.2% for the cross-validation, and from 71.43% to 84.62% for the hold-out sample validation. When we applied all of the functions together we obtained a 92.30% of correct assignments.

**Conclusions:** Our results suggest that the three-dimensional variables from mandibular canine dental tissues are highly useful for sex determination and their application should be considered as a supplemental method to others. 3D measurements counteract the effect of the dimension loss of classic 2D estimations, reflecting the dental morphology and the patterns of dental tissues distribution more accurately.



Poster Presentation Number 97, Th (12:15-14:15)

### *Homo antecessor* lower molars at a glance.

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Since the recovery of about a hundred human fossil remains from the TD6 level of the Gran Dolina cave (Burgos, Spain) in 1994, the paradigm on human evolution in Europe has considerably changed. These fossils were dated to the Early Pleistocene and attributed to a new species, *Homo antecessor* [1]. Furthermore, the increasing number of human fossil remains found in Africa and Eurasia has allowed new phylogenetic interpretations for *Homo antecessor* hominins as well as alternative hypotheses about the settlement of Europe [2].

To date, the Gran Dolina-TD6 human remains are the oldest and most representative human fossils from Europe. The unique combination of primitive and derived cranial and postcranial traits provides important data to understand the first settlement of this continent [3]. The trigonid crest pattern has an extraordinary utility for taxonomic and phylogenetic studies [4,5]. The main aim of this study is to characterize the pattern of trigonid crest expression at the internal and external surfaces of the lower permanent (n = 11) and deciduous (n = 3) molars from *Homo antecessor* by means of micro-computed tomography (microCT). In order to explore the evolutionary meaning of this feature, *Homo antecessor* specimens will be compared against the outer enamel surface (OES) and enamel dentine junction (EDJ) of modern humans and other Pleistocene *Homo* in Eurasia.

The results of our analysis show that *Homo antecessor* present continuous mid-trigonid crests, although in lower frequencies than in other Middle and Upper Pleistocene hominins from Eurasia. This finding suggests that this feature cannot be considered a Neanderthal apomorphy as it is not exclusive to this species. In addition, our study also explores the evolutionary status of this species and its relationship with the Middle Pleistocene populations of Europe. Overall, evidence points to a less linear settlement of Europe and the possibility of *Homo antecessor* representing one of the successive hominin waves into Europe, possibly from Western Eurasia.

This research has been supported by the Dirección General de Investigación of the Spanish Ministerio de Economía y Competitividad (MINECO) (Proyect CGL2015-65387-C3-3-P), the Consejería de Cultura y Turismo of the Junta de Castilla y León, and the Fundación Atapuerca. One of the authors (MM-P) has the benefit of a predoctoral contract of the Junta de Castilla y León co-financed by European Social Funds through the Consejería de Educación (BOCYL-D-20122012-38). We also acknowledge The Leakey Foundation through the personal support of Dub Crook and Gordon Getty to one of the authors (MM-T).

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Podium Presentation: Session 9, Sa (10:20)

**New dental remains from Atapuerca-Gran Dolina TD6 level: *Homo antecessor* revisited.**

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*Homo antecessor* species was named in 1997 based on the fossil hominin collection recovered at the Gran Dolina-TD6 level of Atapuerca [1]. At that time, *H. antecessor* was proposed as the best candidate to represent the last common ancestor of *H. sapiens* and *H. neanderthalensis*. However, the suggestion that the modern human-Neanderthal split occurred during the late Middle Pleistocene was an important handicap for the acceptance of this hypothesis [2]. Recently, new molecular data points to an earlier split for both lineages [3] and calls for a reconsideration of the evolutionary meaning of this hominin population under a new light [4, 5]. Here, we describe for the first time the outer enamel (OES) and dentine (EDJ) surfaces of 15 permanent teeth attributed to *H. antecessor*. We compare the new teeth against a large sample of African, European and Asian hominins from the Early to the Late Pleistocene. Some of the new dental specimens have been unearthed in the excavations held during the last decade. Other specimens have been virtually extracted by means of micro-CT from inside an immature maxilla discovered more than 20 years ago. Overall, *H. antecessor* presents a primitive dentition in common with most of the Early and Middle Pleistocene hominins from Africa such as *H. habilis*, *H. ergaster* and the Buia and Tighenif specimens. However, TD6 teeth present a suite of traits that are present in Asian *H. erectus* and absent in their African counterparts. The identification of this Eurasian dental pattern suggests an early differentiation of the Eurasian Early Pleistocene groups from the African groups. *H. antecessor* does not display any dental synapomorphy with *Homo sapiens* but presents a few traits exclusively shared with Neanderthals. Overall, the new data supports the taxonomic validity of *H. antecessor* by presenting a mosaic of dental traits that is unique to this group. Our data is also compatible with a position close to the node of divergence of *H. sapiens* and *H. neanderthalensis* but warns about the complexity of the interactions and dispersals during the Early to Middle Pleistocene transition in Europe.

This work has been supported by the grants from Chinese Academy of Sciences (132311KYSB20160004), National Natural Science Foundation of China (41630102, 41302016), British Academy (International Partnership and Mobility Scheme, grant PM160019), LM-F is beneficiary of a Fundación Atapuerca Post-Doctoral Research Grant, whereas, MM-P, CG-C and MM-M have Predoctoral contracts of the Junta de Castilla y León financed by European Social Funds through the Consejería de Educación and the Leakey Foundation through the personal support of Dub Crook (2014, 2015, 2016) and Gordon Getty (2013) to one of the authors (M.M.-T)

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## 2D Enamel thickness in Early Pleistocene *Homo antecessor* (Atapuerca, Spain)

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Teeth possess a strong genetic expression used for taxonomic and phylogenetic inferences in hominins [1]. Despite being widely investigated, the taxonomic signal of enamel thickness in the genus *Homo* remains unclear due to the scarcity and preservation of the fossil remains. Genus *Homo* is known to possess thicker relative enamel compared to living African Great apes. Within the genus *Homo*, different trends in enamel thickness were observed between older and younger taxa as well as among geographic groups [2]. In particular, molar tissue proportions have been useful to distinguish between Neanderthals and modern humans [3]. However, little is known about the polarity of this feature. In this context the addition of new data will contribute to the discussion of this trait within the genus *Homo*. In this study we provide for the first time the characterization of the 2D enamel thickness in the Gran Dolina (TD6) molar sample. Early Pleistocene *Homo antecessor*, dated ca. 0.86 Ma, is defined by a unique mosaic of primitive traits of the *Homo* clade, and derived traits shared with Neanderthals and modern humans. The skeletal and dental remains have been associated to eight individuals [4]. In this study we calculate the 2D molar tissue proportions in *H. antecessor* to: i) characterize the molar enamel thickness in this population; ii) provide new insights about the polarity of the enamel thickness within the genus *Homo*; iii) assess how different is *H. antecessor* population in relation to Neanderthals and modern humans. We applied mCT imaging to Early Pleistocene *H. antecessor* molar collection (n=17). Following Olejniczak and colleagues methodology [3] we calculated the relative enamel thickness and average enamel thickness, and compared the results with fossil hominins and modern humans. Our results indicate that the relative enamel thickness of *H. antecessor* molars is generally greater than in Neanderthals and closer to *H. sapiens* values, except for the upper first molar. The polarity of the enamel thickness in the genus *Homo* is discussed to the light of these results. Future studies in other Early Pleistocene hominins may shed further light on the evolutionary meaning of this feature.

This research has been supported by the Dirección General de Investigación of the Spanish Ministerio de Economía y Competitividad (MINECO) (Proyect CGL2015-65387-C3-3-P). We acknowledge The Leakey Foundation through the personal support of Gordon Getty (2013) and Dub Crook (2014, 2015, 2016) to one of the authors (MM-T). LM-F is beneficiary of a Fundación Atapuerca Post-Doctoral Research Grant, whereas, MM-P, CG-C and MM-M have Predoctoral contracts of the Junta de Castilla y Leon financed by European Social Funds through the Consejería de Educación.

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Poster Presentation Number 118, Fr (12:15-14:15)

### **A comparative study of the Late Middle European Pleistocene Montmaurin-La-Niche (MLN). Preliminary results.**

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Among several caves settled in the limestone mountain shaped by the Save and Seygouade rivers near Montmaurin, 75km south-west of Toulouse (France), La Niche is the one, with Coupe-Gorge, which has yielded human remains collected by Raoul Cammas in 1949 (one cervical vertebra, one well-preserved mandible bearing its 6 molars) and recognized among the fauna by Cammas and André Tavoos in 1986 (one dorsal vertebra, one fragmentary left tibia). Work done by Crégut-Bonnouere and colleagues [1] on the faunal assemblage has attributed the level bearing hominins to the OIS 7 placing the Montmaurin-La-Niche (MLN) in an intermediate location between Middle Pleistocene fossils such as those from Arago (Tautavel, France) and Sima de los Huesos (Atapuerca, Spain), in the one hand, and Neandertals, in the other hand. Here we have made a morphological comparative study using some selected features with a taxonomical signal. In order to cluster the specimens we have used the correspondence analysis using the R package "ca". Moreover, a metrical and morphological study was carried out on the teeth, including an analysis of the dental inner features by means of micro-computed tomography (microCT). Results highlight the primitiveness of the MLN mandible whereas a more fully Neandertal morphology was expected regarding the time range of the fossil. Although a geochronological study of La Niche cave is pending, it will be an interesting exercise to confront the predominant primitive morphology of this mandible with the quantitative results of a future geochronological analysis. Thus, it is possible to test these anthropological results against the different models, like the accretion [2] and two-phases model [3], to explain the variability of the European Middle Pleistocene hominins. It will be also tested the evolutionary scenario proposing a settlement of Europe by some waves of population sharing a common ancestor [4], as well as a complex history of wipe-outs and new occupations, as well as genetic mechanisms, like drift, founder effect, directional adaptation and hybridization [5].

For the access to the MLN mandible, the authors thank Dominique Grimaud-Hervé, Liliانا Huet, Stéphanie Renault from the Musée de l'Homme. They are grateful to José Braga and Jean Dumonceil for the micro-CT data that they provided and to Patricia Wils (USM2700, MNHN, Paris) for her technical support.

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