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EVOLUCIÓN DE *MIMOMYS SAVINI* EN LA PENÍNSULA IBÉRICA DURANTE EL PLEISTOCENO INFERIOR; IMPLICACIONES BIOCRONOLÓGICAS Y PALEOAMBIENTALES EN EL ESTUDIO DE LAS PRIMERAS POBLACIONES HUMANAS DE EUROPA

Iván Lozano Fernández

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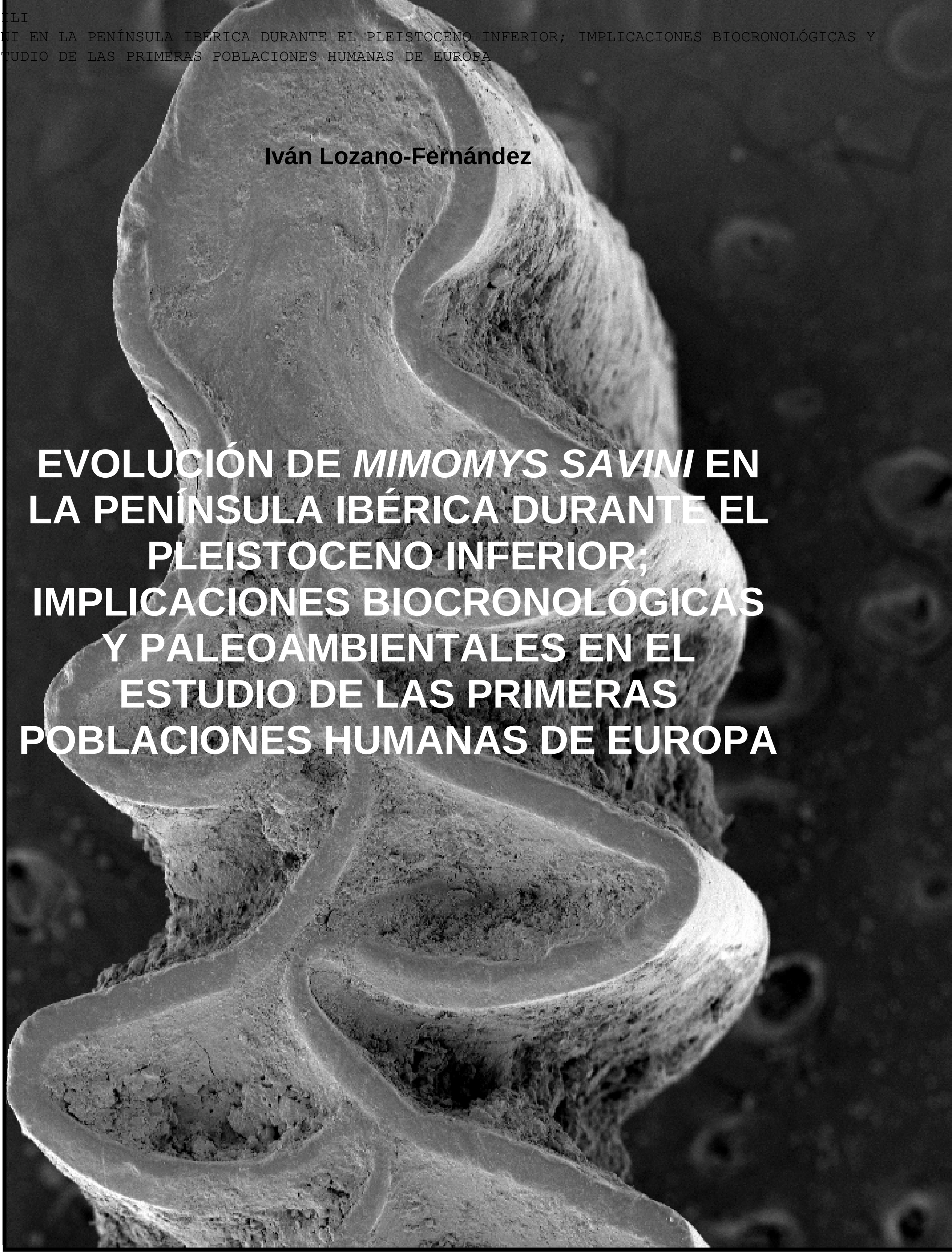

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el Dr. Jordi Agustí Ballester y la Dra. Gloria Cuenca-Bescós

Departamento de Historia e Historia del Arte

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"En la actualidad hay exploradores del tiempo como los hay del espacio geográfico. Los mundos desaparecidos son sus nuevos mundos y las especies extinguidas sus tribus preoriginales. Gran parte de la ciencia es exploración del tiempo."
(John Noble Wilford).

"En paleontología no hay una verdad definitiva. Cada nuevo observador aporta algo propio: una nueva técnica, una nueva inteligencia, incluso nuevos errores. El pasado se transforma. El científico se halla inmerso en un viaje perpetuo hacia un pasado que nunca podrá ser completamente conocido, y no hay final a la búsqueda de conocimientos."
(Richard Fortey).

"Si algo nos ha enseñado la historia de la evolución, es que la vida no puede contenerse. La vida se libera, se extiende a través de nuevos territorios y rompe las barreras dolorosamente, incluso peligrosamente. Pero así es [...]
Digo sencillamente que la vida se abre camino."
(Ian Malcom, Jurassic Park).

ÍNDICE

ESTRUCTURA DE LA TESIS

La presente tesis esta constituida como un compendio de artículos. Dos de ellos publicados y tres en proceso de publicación. Estos artículos corresponden a los capítulos del 1 al 5 de la tesis y equivalen a los apartados de **resultados** y **discusión** de las tesis clásicas. Se trata de capítulos autocontenidos, es decir que cada capítulo consta de introducción, metodología, resultados, discusión y conclusiones por si mismo. Además los capítulos enviados a revistas francesas (1 y 4), incluyen también un “résumé”. A efectos prácticos cada uno de estos capítulos puede constituir un trabajo independiente.

Previo a estos capítulos encontraremos en esta tesis los apartados de introducción y metodología y detrás de estos capítulos el apartado de conclusiones generales.

En la **introducción** se da una visión general sobre la especie *Mimomys savini* y el interés de su estudio tanto a nivel biocronológico como a nivel paleoecológico.

En la **metodología** se detallan los métodos y procesos generales utilizados para el estudió de microvertebrados. En los capítulos 1 al 6, en el apartado de metodología de cada uno de ellos se explican puntos más característicos de la metodología en función al problema que se aborda.

Los **capítulos 1** y **2** corresponden a un estudio de la evolución de *Mimomys savini* en la Península Ibérica. El **capítulo 1** de forma más genérica, sirvió para tener una idea general de los procesos evolutivos de *Mimomys savini* en la Península Ibérica. Mientras que el **capítulo 2** se centra en el yacimiento de Gran Dolina (Atapuerca, Burgos), que al ser una secuencia estratigráfica continua permitió estudiar de forma más detallada la evolución de esta especie.

Los **capítulos 3**, **4** y **5** corresponden a una revisión biocronológica de los yacimientos del Barranc de la Boella (Tarragona), Vallparadís (Barcelona) y Barranco León y Fuente Nueva 3 (Granada). Además, en los **capítulos 3** y **4** se realizó una interpretación paleoambiental de los yacimientos de Barranc de la Boella y Vallparadís, en base a su contenido en micromamíferos.

En el apartado de **conclusiones generales** se exponen el conjunto de conclusiones obtenidas en los capítulos del 1 al 5.

Las **referencias** en esta tesis se encuentran ordenadas de dos formas. Los capítulos del 1 al 5 tienen su propio apartado con las referencias de dichos capítulos (siguiendo el formato de la revista en la que se han publicado o se publicarán estos capítulos). Mientras que además, al final de la tesis hay un apartado de referencias que corresponden a las citas de la introducción, metodología y conclusiones generales.

Finalmente, en esta tesis encontramos el apartado de **anexos**. En este apartado se han incluido los capítulos publicados de esta tesis (capítulo 1 y 2) en el formato en que lo publico la revista correspondiente. Así como otros artículos de los yacimientos estudiados en esta tesis en los que el autor de dicha tesis ha participado durante el periodo de elaboración de la tesis.

INTRODUCCIÓN

En este trabajo se estudia la evolución de *Mimomys savini* (un roedor extinto emparentado con las actuales ratas de agua) y las posibles implicaciones biocronológicas y paleoambientales asociadas a sus cambios evolutivos y a su presencia en los yacimientos. El rango biocronológico de esta especie esta estimado entre 1.8 Ma (Topachevskij y Skorik, 1977; Jánossy, 1986; Rekovets, 1994; Fejfar et al., 1998) y 0.6 Ma (Fejfar et al., 1998), comprendiendo gran parte del Pleistoceno inferior y coincidiendo con las primeras ocupaciones humanas del continente europeo. Así, el estudio de este roedor puede aportarnos información tanto biocronológica como ambiental de estas primeras ocupaciones humanas durante el Pleistoceno Inferior.

Dentro de la Península Ibérica, los yacimientos con presencia humana más antiguos corresponden a Barranco León D (cuenca Guadix-Baza, Granada), Sima del Elefante (Complejo de yacimientos de Atapuerca, Burgos) y Gran Dolina (Complejo de yacimientos de Atapuerca, Burgos), y los yacimientos más antiguos con indicios de presencia humana corresponden a Fuente Nueva 3 (cuenca Guadix-Baza, Granada), Vallparadís (Barcelona) y los yacimientos del Barranc de la Boella, La Mina y El Forn (Tarragona). Entenderemos indicios de presencia humana como cualquier registro generado por acción antrópica, y presencia humana como los restos fósiles de estos humanos.

Estos yacimientos de la Península Ibérica son a su vez parte de los más antiguos de Europa.

Del conjunto de yacimientos anteriormente citados, todos se incluyen en esta tesis a excepción de Sima del Elefante que no presenta registro de *Mimomys savini*. Así pues, esta tesis aporta información tanto biocronológica como

paleoambiental sobre los primeros asentamientos humanos en la Península Ibérica y en Europa.

1 – MICROMAMÍFEROS

Los micromamíferos son mamíferos de talla pequeña, normalmente por debajo de 10 Kg de peso en su forma adulta. El término en si, “micromamífero”, no posee un valor taxonómico, pero es muy utilizado en la literatura científica para indicar a aquellos órdenes, familias o géneros de mamíferos en los que la mayor parte de las especies que los conforman son de tamaño reducido. No se incluyen las especies pequeñas o ejemplares infantiles de otros grupos de mamíferos en los que, en general, sus individuos son de mayor talla (carnívoros, primates, etc.). Bajo esta denominación suelen estar incluidos insectívoros, quirópteros, lagomorfos y roedores, aún cuando algunas especies de roedores sean de gran talla, como el capibara, el castor, el puercoespín o la marmota (Delany, 1981; Meléndez, 1986). Los roedores, grupo al que pertenece *Mimomys savini*, son especialmente importantes durante el Cuaternario europeo, debido a su gran diversificación y taxa de expansión geográfica. Algunos grupos de estos micromamíferos tuvieron una rápida evolución durante el Pleistoceno, lo que permite establecer con ellos una bioestratigrafía muy detallada (Chaline, 1982; Chaline, 1988; Andrews, 1990). Esto los convierte en una importante herramienta biocronológica.

Dentro de los roedores, el estudio de los cambios morfométricos de los molares de los arvicolinos (familia a la que pertenece *Mimomys savini*) ha sido utilizado por varios autores como posible herramienta biocronológica, como es el caso del linaje *Mimomys*-*Arvicola* o del linaje *Microtus* entre otros (Agustí, 1992;

Koenigswald y Kolfschoten, 1996; Lippi et al., 1998; Maul et al., 1998; Maul et al., 2007; Maul et al., 2013; entre otros), dando resultados fiables y coherentes con otros métodos cronológicos.

Los micromamíferos suelen ser muy sensibles a condiciones climáticas precisas, además de presentar una gran adaptabilidad a determinados biotopos, ya que los cambios climáticos les pueden obligar a migrar a otras zonas. Debido a sus necesidades energéticas y fisiológicas concretas y al gran número de especies existentes, que se traduce en unas complejas relaciones de competencia interespecífica, las especies de micromamíferos suelen tener unos rangos de distribución geográfica limitados, habitando un reducido número de biotopos. Esto convierte a estos animales en una herramienta muy útil para inferir características paleoambientales de los yacimientos en los que aparecen (Minwer-Barakat, 2005).

De este modo, el estudio de los micromamíferos tienen un valor doble en los yacimientos tanto arqueológicos como paleontológicos (Chaline y Alcalde, 1983). Por un lado, como indicadores bioestratigráficos: permitiendo establecer una cronología relativa, con un alto grado de resolución (sobre todo los roedores). Y por otro lado, también están adaptados a medios y condiciones climáticas precisas, de forma que su estudio en asociaciones fósiles da la posibilidad de reconstruir las fluctuaciones del clima y del paisaje.

Además, el estudio sobre roedores puede aportar datos de carácter paleoetnográfico, como la época de frecuentación del yacimiento por rapaces y la época de frecuentación del yacimiento por los humanos, o la diferenciación

espacial de la cueva como las zonas más frecuentadas y zonas más marginales para las rapaces y los humanos (Alcalde, 1988).

Por lo tanto, los micromamíferos permiten establecer en yacimientos dataciones relativas y reconstrucciones climáticas y paleoambientales.

2 – TIPOS DE YACIMIENTOS CON MICROMAMÍFEROS

Los restos fósiles de los micromamíferos generalmente aparecen en dos tipos de yacimientos, los cársticos y los fluvio-lacustres.

Los primeros, corresponden a rellenos de relieves cársticos, es decir, que se localizarán en fisuras o cuevas de rocas carbonatadas que ha sido rellenadas. Como ejemplo, el yacimiento de Gran Dolina estudiado en esta tesis corresponde a este tipo de yacimientos. En estos, el sedimento que rellena las fisuras puede ser tanto autóctono (del interior de la misma fisura), como alóctono (sedimento aportado desde el exterior de la fisura).

Los niveles sedimentarios de relleno de cuevas presentan unas características peculiares en cuanto a su formación. Estos se forman por los mismos mecanismos que los niveles en fisuras, pero a mayor escala. El mayor tamaño de las cuevas que las fisuras puede introducir mecanismos de acumulación y alteración de los restos de micromamíferos diferentes de los que se producen en las fisuras, como la intervención de predadores (en la acumulación), el “trampling” (pisoteo de los restos por parte de otros animales) o incluso la acción antrópica (Andrews, 1990).

Por su parte, los yacimientos fluvio-lacustres corresponden a acumulaciones al aire libre situadas en diversas partes de un sistema fluvial. En esta tesis los

yacimientos del Barranc de la Boella, Fuente Nueva 3, Barranco León y Vallparadís corresponden a este tipo de yacimientos.

Normalmente, los yacimientos de tipo fluvio-lacustre presentan menor acumulación de restos de micromamíferos debido a las características propias del medio sedimentario en que se forman.

Los yacimientos de este tipo más ricos en micromamíferos son aquellos en los que dominan los depósitos de margas (Badgley et al. 1995) como es el caso de los depósitos de la cuenca de Guadix-Baza en Granada (Agustí, 1985; Agustí y Martín Suárez, 1986; Agustí et al. 1987), donde se encuentran los yacimientos de Fuente Nueva 3 y Barranco León estudiados en esta tesis.

3 – ACUMULACIÓN DE RESTOS DE MICROMAMÍFEROS

El principal origen de las acumulaciones de micromamíferos responde a lo que se llama “hipótesis escatológica” (Mellet, 1974; Andrews, 1990). Ésta considera que la mayoría de los restos que componen las asociaciones de micromamíferos fueron ingeridos previamente por algún predador antes de producirse su deposición, en forma de excrementos o egagrópilas, en las proximidades de cursos de agua o en el interior de cuevas, donde posteriormente son cubiertos de sedimento. Este proceso recibe el nombre de “coprocenosis”.

Existen diversos grupos de predadores que incluyen micromamíferos en su dieta y, en función del modo de ingestión y digestión de sus presas, pueden contribuir a la formación de los yacimientos (Andrews, 1990).

Estos grupos de predadores se pueden dividir básicamente en tres:

- Las rapaces nocturnas:

Son las que contribuyen en mayor medida a la formación del registro fósil de micromamíferos. Estas, engullen sus presas enteras y una vez en el estómago y mediante los jugos gástricos disuelven las partes digestibles, mientras que las demás (pelos, plumas, huesos y dientes) son regurgitadas en forma de egagrópilas. La formación de estas egagrópilas es importante para el proceso tafonómico, ya que la baja acidez estomacal de las rapaces nocturnas, comparada con la de otros predadores, es la que contribuye a un alto grado de preservación de los huesos. Las rapaces producen rápidamente un gran número de egagrópilas que depositan principalmente en cuevas o estructuras humanas abandonadas. La lechuza común es uno de los más importantes agentes acumuladores de microvertebrados. Éste tiende a regurgitar los huesos de sus pequeñas presas intactos, proporcionando un registro completo de lo que ha comido y haciendo relativamente fácil la identificación de los elementos esqueléticos (Chaline y Alcalde, 1983; Chaline, 1988; Gosàlbez, 1987; Fernandez-Jalvo, 1988; Andrews, 1990; Pokines, 1998).

- Las rapaces diurnas:

Estas rapaces descarnan las presas y no las engullen con todos los huesos. Además su proceso digestivo es de gran capacidad destructora. De este modo, los dientes y huesos contenidos en sus egagrópilas presentan claros signos de digestión (pérdida de esmalte y epífisis dañadas).

- Los pequeños carnívoros:

Su ingestión y digestión es más destructiva que la de las aves. A pesar de ello, el comportamiento territorial de estos animales favorece a la concentración de restos, ya que frecuentemente depositan sus heces en lugares concretos.

Los restos depositados dentro de cavidades presentan una baja probabilidad de dispersión, mientras que los depositados cerca de cursos fluviales sufren más dispersión (Andrews, 1995).

En algunos casos, los restos de micromamíferos presentes en los yacimientos podrían haberse generado por muerte natural de estos mamíferos o incluso por acción antrópica (Chaline y Alcalde, 1983;; Andrews, 1990; Blasco, 1992).

En esta tesis, los restos estudiados se presentan aparentemente poco digeridos, se puede interpretar por tanto que el principal agente acumulador habrían sido las rapaces nocturnas. Al tratarse de depredadores oportunistas, los restos que acumulan se pueden considerar como representativos de las faunas del ambiente inmediato a los yacimientos en el momento de su deposición (Pokines, 1998). Esto nos permite realizar interpretaciones paleoambientales como las que se han realizado en los yacimientos de Vallparadís y el Barranc de la Boella en los capítulos 3 y 4 de esta tesis.

4 – ARVICOLINAE (ARVICOLINOS)

Como ya se ha dicho, los roedores son uno de los grupos de mamíferos más importantes a nivel estratigráfico del Cuaternario europeo. Su gran diversificación frente a otros grupos taxonómicos en este intervalo de tiempo los convierte en una útil herramienta biocronológica. Dentro de los roedores, los arvicolinos (topillos, lemmings y ratas de agua) son particularmente útiles para la biocronología debido a la abundancia de sus restos en el registro fósil y a sus rápidas tasas de evolución y expansión geográfica. La velocidad de sus migraciones y su extensa distribución geográfica (en al actualidad ocupan toda

la región holártica) permite utilizarlos para llevar a cabo correlaciones interregionales (Minwer-Barakat et al., 2011).

Por estas razones, los arvicolinos han sido utilizados para definir las subdivisiones bioestratigráficas del Cuaternario europeo (Chaline, 1972; van der Meulen, 1973; Agustí, 1986; Sala y Masini, 2007; Cuenca-Bescós et al., 2010b; entre otros).

La familia Arvicolinae incluye un total de 48 géneros distintos y 724 especies y subespecies (entre representantes actuales y extintos). En el registro fósil se identifican por sus molares y a nivel especifico por sus primeros molares inferiores (m1). Estos presentan una morfología compuesta por un lóbulo posterior (LB), varios prismas triangulares alternantes (a los que se llama triangulos; T) y un lóbulo anterior (LA). Son molares hipsodontos (con una corona elevada) y de crecimiento continuo. No tiene esmalte en la superficie oclusal (la parte superior de la corona) y existen géneros tanto con molares arrizodontos como rizodontos, es decir con raíces o sin raíces (figura 1.1). En algunas especies el tercer molar superior (M3) puede utilizarse también como diagnostico de la especie.

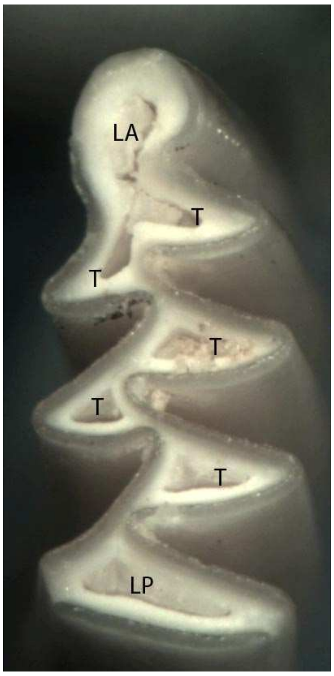


Figura 1.1. Vista oclusal de un primer molar inferior de arvicolino (en este caso un *Mimomys savini*). Se puede observar la superficie oclusal sin esmalte y las paredes de la corona con esmalte. **T**; prismas triangulares alternantes. **LP**; lóbulo posterior. **LA**; lóbulo anterior.

En la evolución de distintos géneros y linajes de arvicolinos se han observado tendencias evolutivas como la disminución en el índice de diferenciación de esmalte del género *Arvicola* (Heinrich, 1978; 1982; 1987), el aumento en la relación longitud/ancho del complejo anterocónido del género *Allophaiomys* en el primer molar inferior (Lippi et al., 1998), el aumento de hipsodoncia en todos los géneros (Chaline, 1987) o el aumento de tamaño en el linaje *Mimomys-Arvicola* (Viriot et al., 1990; Chaline et al., 1999; Maul et al., 2013), entre otras. Estas tendencias evolutivas se interpretan como una especialización de las distintas especies a los habitats que ocupan. Por ejemplo: el aumento de la relación longitud/anchura del complejo anterocónido del género *Allophaiomys* se interpreta como una mejora en la eficiencia de la dentición, o el aumento de tamaño en el linaje *Mimomys-Arvicola* como una adaptación a un medio de vida acuático (Maul et al., 2013).

5 – GÉNERO *MIMOMYS*

Es un género descrito por Major en 1902 cuyo rango cronológico va desde hace 4 Ma (*Mimomys stehlini*) hasta hace 0.6 Ma (*Mimomys savini*) (Topachevskij y Skorik, 1977; Rekovets, 1994; Jánossy, 1986; Fejfar *et al.,* 1998).

Se trata de un género de gran importancia en la biozonación del Pleistoceno debido a su rápida evolución y a su abundancia en todos los niveles (Chaline y Michaux, 1969; 1971; Kretzoi, 1969). Este género apareció en Eurasia al final del Plioceno superior e incluye un total de 38 especies distintas conocidas hasta la fecha (*M. cappettai*, *M. dakotaensis*, *M. davakosi*, *M. gracilis*, *M. hajnackensis*, *M. hassiacus*, *M. hintoni*, *M. intermedius*, *M. ischus*, *M. magilli*,

M. medasensis, *M. minor*, *M. moldavicus*, *M. newtoni*, *M. occitanus*, *M. orientalis*, *M. ostramosensis*, *M. oswaldoreigi*, *M. panacaensis*, *M. peii*, *M. pitymyoides*, *M. pliocaenicus*, *M. polonicus*, *M. primus*, *M. pseudintermedius*, *M. pusillus*, *M. realensis*, *M. reidi*, *M. rex*, *M. rhabonensis*, *M. savini*, *M. sawrockensis*, *M. septimanus*, *M. stehlini*, *M. tanaitica*, *M. tornensis*, *M. virginianus*, *M. youhenicus*). Durante el Pleistoceno inferior esta representado por una gran diversidad de líneas distintas. Aparentemente, los representantes de este género ocuparon los nichos ecológicos de los actuales géneros *Arvicola*, *Microtus*, *Pitymys* y *Lagurus* (Chaline, 1982). En Europa, dos grandes líneas pueden servir paralelamente al establecimiento de la estratigrafía:

- La primer conduce, de *Mimomys stehlini* a *Mimomys savini*, por medio de las especies: *Mimomys polonicus* y *Mimomys pliocaenicus*, que representan estadios evolutivos de una misma línea de evolución. Para algunos autores existe en esta línea una laguna entre *Mimomys ostramosensis* y *Mimomys savini*, por tanto faltaría una especie intermedia (Viriot et al., 1990; Néreaudau et al., 1995).
- La segunda línea conduce de *Mimomys gracilis* a *Mimomys newtoni* y *Mimomys pusillus*.

Los primeros molares de las especies del género *Mimomys* se caracterizan por ser de talla media grande, aunque existen especies de talla pequeña como el caso de *Mimomys pusillus*. Tienen 5 prismas triangulares opuestos llamados triangulos, de los cuales el T4 y T5 (los adyacentes al lóbulo anterior) son los menos desarrollados y confluyentes entre si y con el lóbulo anterior. Presentan una diferenciación de esmalte del tipo llamado “mimomiano”, es decir que los triángulos presentan un esmalte más grueso en su cara posterior que en la

anterior. En el complejo anterocónido (formado por el T4, T5 y el lóbulo anterior), las especies de este género presentan islote de esmalte y pliegue mimomiano, aunque el ultimo representante del género (*Mimomys savini*) solo presenta estas características en sus estadios juveniles y los primeros representantes del género presentan el islote de esmalte unido a la pared de esmalte (*Mimomys stehlini* o *Mimomys occitanus* por ejemplo). El islote de esmalte es una característica que con el desgaste del diente desaparece en individuos de las especies más modernas (como es el caso de *Mimomys savini*). La evolución del género *Mimomys* conlleva la aparición y el incremento de cemento en los triángulos reentrantes de los molares de las especies que lo conforman. Sin embargo, esta característica puede verse afectada por procesos tafonómicos y por tanto podemos encontrar especies más modernas con poco cemento debido a su perdida.

Las especies de este género presentan raíces en sus molares (aunque la aparición de estas raíces es cada vez más tardía en especies más modernas)(figura 1.2)

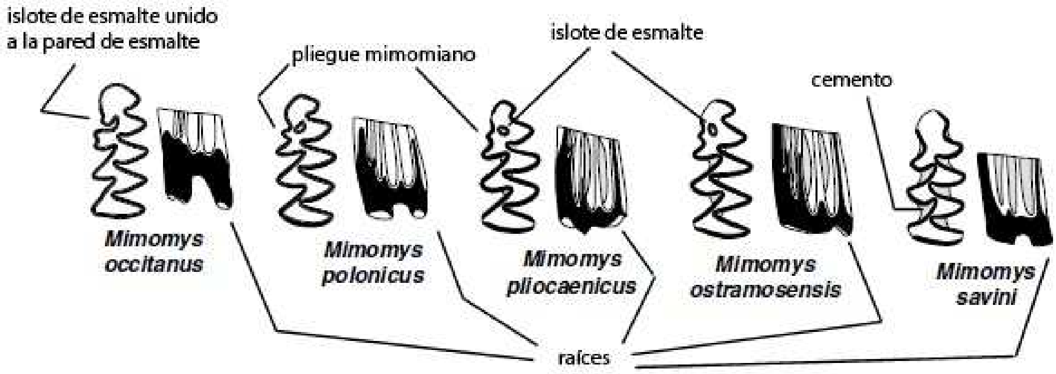


Figura 1.2. Características del género Mimomys en distintas especies de más antiguas (izquierda) a más modernas (derecha).

6 – *MIMOMYS SAVINI*

Family MURIDAE Illiger, 1811

Subfamily ARVICOLINAE Gray, 1821

Genus *MIMOMYS* Major, 1902

MIMOMYS SAVINI Hinton, 1910

Mimomys savini es el ultimo representante conocido del género *Mimomys* y esta considerado como el primero del linaje de las ratas de agua (*Mimomys savini*-*Arvicola sapidus/Arvicola terrestis*) y antecesor del género *Arvicola* (Chaline y Sevilla, 1990; Viriot et al., 1990; Chaline et al., 1999). Debido a esta relación filogenética, se estima que *Mimomys savini* ocupó un nicho ecológico similar a las actuales ratas de agua, un habitat acuático.

Los primeros restos descubiertos de esta especie fueron clasificados como *Mimomys intermedius* por Forsyth Major en 1902. En 1910 Hinton determinó que se trataba de una nueva especie a la que llamaría *Mimomys savini*.

Posteriormente, el mismo Hinton, presento una revisión en profundidad de la especie en 1926 en su obra “Monograph of the voles and Lemmings” (figura 1.3). El holotipo de la especie corresponde a un primer molar inferior derecho de la colección de A. C. Savin, que se encuentra depositado en el British Museum (con la referencia BM Nº M6986b). La primera representación gráfica de *Mimomys savini* corresponde a los dibujos de Forsyth Major de 1902 (aunque el lo identificara como *Mimomys intermedius*). El holotipo de la especie corresponde al nivel “Upper Freshwater Bed” del yacimiento de West Runton en Norfolk (Este de Inglaterra).

La distribución geográfica de *Mimomys savini* abarca Europa entre hace 1.8 Ma y 0.6 Ma (Topachevskij y Skorik, 1977; Jánossy, 1986; Rekovets, 1994; Fejfar et al., 1998). En la Península Ibérica el registro más antiguo que se tiene de esta especie esta situado en los yacimientos de la cuenca Guadix-Baza (Agustí, 1986; Agustí et al., 1987; 2010). El rango cronológico de *Mimomys savini* comprende las primeras ocupaciones humanas del continente europeo, de forma que su estudio puede aportar importante información sobre el momento y el ambiente en que sucedieron estas ocupaciones.

Los yacimientos más antiguos con presencia de este micrmamífero son: Tiligul (Topachevskij y Skorik, 1977) y Zhevakhova Gora en Ucraina (Rekovets, 1994), Villány 5 en Hungria (Jánossy, 1986), Fuente Nueva 3 y Barranco León en España (Agustí, 1986; Agustí et al., 1987; 2010), y los niveles TD 3-4 de Gran Dolina en España (Cuenca-Bescós et al., 1995; 1999; Cuenca-Bescós y García, 2007; Cuenca-Bescós et al., 2010b).

Las poblaciones más modernas de *Mimomys savini* corresponden al transito Pleistoceno inferior-Pleistoceno medio y han sido recuperadas de los yacimientos de Zapadnye Kairy en Ucraina (Markova, 1982, 2004), Kärlich E y F en Alemania (von Koenigswald y van Kolfschoten, 1996), Voigtstedt en Alemania (Maul, 2001; 2002), West Runton en Inglaterra (Stuart, 1981; Maul y Parfitt, 2010), y el nivel TD8 en Gran Dolina en España (Cuenca-Bescós et al., 2010b).

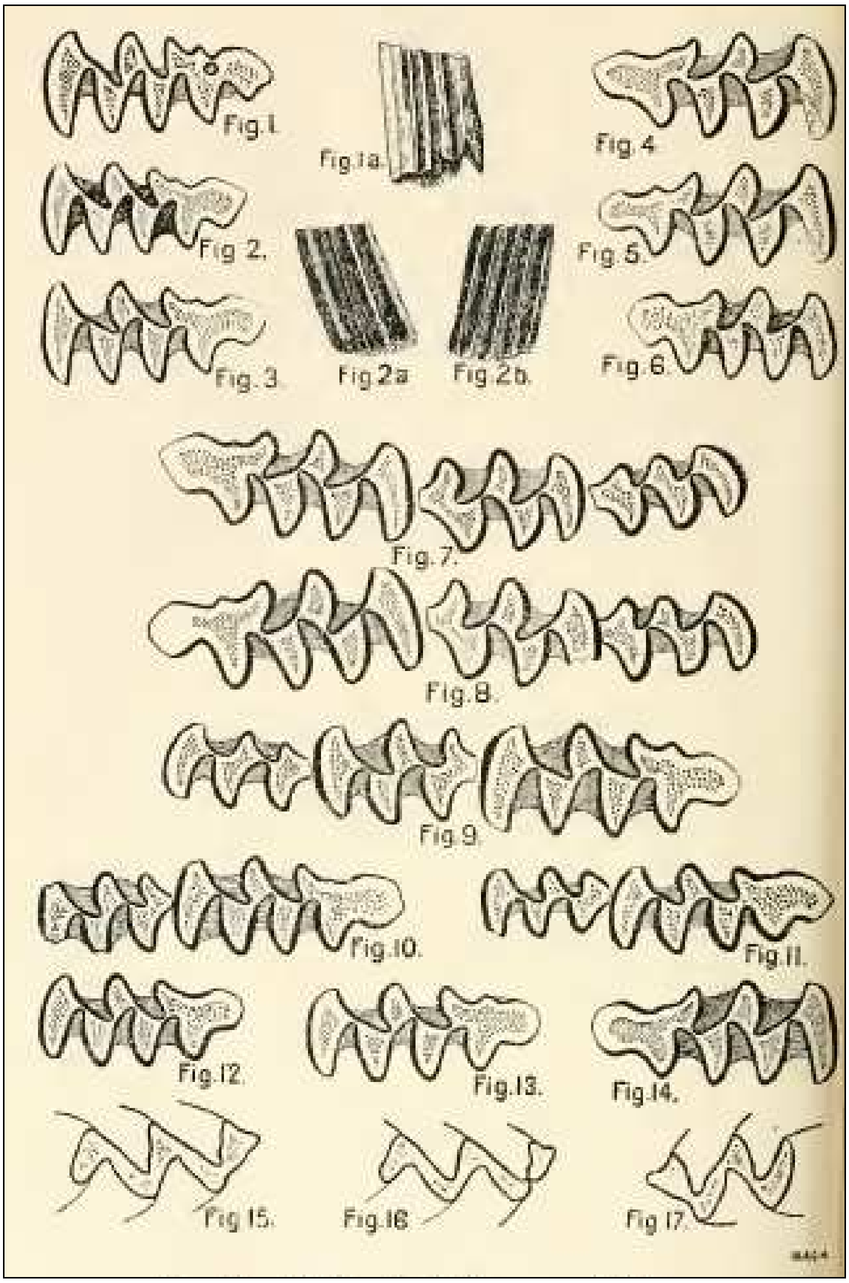


Figura 1.3. Dibujos originales de la revisión de *Mimomys savini* presentada por Hinton en 1926 en su obra "Monograph of voles and lemmings" (**página 366**). Todos son vistas oclusales excepto las **Fig 1a**, **2a** y **2b** que son vistas laterales. **Fig 1** y **1a**; m1 izquierdo juvenil con islote de esmalte. **Fig 2**, **2a** y **2b**; m1 izquierdo adulto, cerrándose los espacios del cemento (cerrándose las raíces). **Fig 3**; m1 izquiedo. **Fig 4**, **5** y **6**; m1 derecho. **Fig 7**, **8** y **9**; serie mandibular completa (m1, m2 y m3), **Fig 7** y **9** derechas y **Fig 8** izquieda. **Fig 10** y **11**; m1 y m2 izquierdos. Fig 12 y 13; m1 izquierdo con zonas de cemento cerradas. Fig 14; m1 derecho. **Fig 15** y **16**; molares derechos ligeramente desgastados. **Fig 17**; molar izquierdo ligeramente desgastado.

Además de los yacimientos anteriores, también se ha registrado presencia de *Mimomys savini* en los yacimientos de: Karaj Dubina en Ucraina (Markova, 1990), Huescar-1 en España (Maul et al., 2013), Port Katon en Russia (Markova, 1990), Gura Dobrogei 4 en Romania (Radulesco and Samson, 1993), Beftia 2 en Romania (Maul, 2001), Kozi Grzbiet en Polonia (Nadachowski, 1985), Monte Peglia A en Italia (Meulen, 1973), Castagnone en Italia (Siori and Sala, 2007), Tarkö capa 16 en Hungria (Jánossy, 1976), Untermassfeld en Alemania (Maul, 2001), Neuleiningen 5 y 15 en Alemania (Maul et al., 1998), Přezletice en Chechenia (Heinrich, 1987) y Koneprusy C718 en Chechenia (Heinrich, 1987).

Mimomys savini se caracteriza por ser un arvicolino de talla grande. Sus primeros molares inferiores presentan diferenciación de esmalte tipo mimomiano, los triangulos T4 y T5 confluyentes, cemento en los triangulo reentrantes, un angulo reentrante lingual 4 (LRA4) poco marcado y un angulo reentrante bucal 3 (BRA3) laxo. Los adultos presentan tres zonas libres de esmalte en el plano oclusal (dos en el lóbulo posterior y dos en el lóbulo anterior) y las formas juveniles no tienen zonas libres de esmalte y pueden presentar islote de esmalte y/o pliegue mimomiano. Los individuos juveniles no tienen raíces (raíces abiertas) mientras que los individuos adultos tienen las raíces completamente cerradas. Los m1 de adultos tienen dos raíces (figura 1.4). El paso de juvenil a adulto se marca con la aparición de las zonas libres de esmalte en el plano oclusal y en inicio del cierre de las raíces. Morfológicamente los m1 de las ultimas poblaciones de *Mimomys savini* son muy parecidos a los de las primeras de *Arvicola mosbachensis* con la única diferencia reseñable de la ausencia de raíces en *Arvicola*.

El tercer molar superior de *Mimomys savini* en algunos casos puede utilizarse para identificar la especie. Este consta de un lóbulo anterior, uno posterior y cuatro triángulos alternos, aunque el T4 esta muy poco desarrollado y puede no estar presente. Tiene una diferenciación de esmalte tipo mimomiano, las poblaciones más antiguas presentan islote de esmalte en el lóbulo posterior e igual que los m1, las formas adultas tienen dos raíces y tres zonas libres de esmalte en el plano oclusal (figura 1.4).

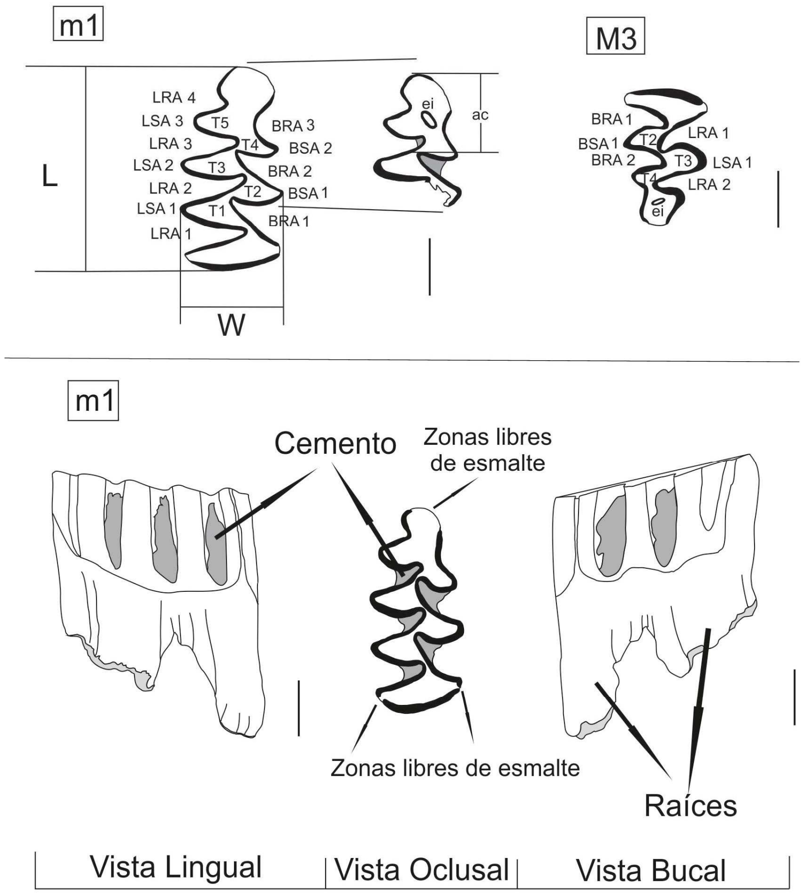


Figura 1.4. Figura superior: Nomenclatura utilizada (modificada de Meulen (1973), Heinrich (1978) y Rabeder (1981). **LRA**; Angulo reentrante lingual. **LSA**; Angulo saliente labial. **BRA**; Angulo reentrante bucal. **BSA**; Angulo saliente bucal. **ac**; Complejo anteroconido. **T**; Triángulos de dentina. **ei**; islote de esmalte.

Figura inferior: Distintas vistas de un primer molar de Mimomys savini y partes del molar. La escala gráfica corresponde a 1 milímetro.

7 OBJETIVOS DE ESTA TESIS

1) *Mimomys savini* esta considerado como el ancestro de las actuales ratas de agua; como el ancestro del género *Arvicola* (Chaline y Sevilla, 1990; Viriot et al., 1990; Chaline et al., 1999). Sin embargo, en el año 2010 se publicó el descubrimiento de una especie perteneciente al género *Arvicola* que había vivido hace 1.2 Ma, al rededor de 0.6 Ma antes que el siguiente representantes de este género (*Arvicola mosbachensis*). El descubrimiento de esta nueva especie, *Arvicola jacobaeus* (Cuenca-Bescós et al., 2010a), ponía en tela de juicio la relación filogenética preestablecida entre *Mimomys savini* y el *género Arvicola*.

Cual es el ancestro de *Arvicola jacobaeus* y de *Arvicola mosbachensis*? Como es que existen dos representantes de un género separados por 0.6 Ma sin más datos entre uno y otro?

Uno de los objetivos de esta tesis es plantear una hipótesis para explicar estas cuestiones.

2)La evolución de los arvicolinos se caracteriza por la existencia de un conjunto de tendencias evolutivas en los distintos grupos (Viriot et al., 1990; Chaline et al., 1987; 1999; Maul et al., 2013; Lippi et al., 1998). La línea evolutiva *Mimomys*-*Arvicola* presenta varias de estas tendencias con estadios claramente diferenciadas entre las distintas especies que la componen. Dentro de esta línea, *Mimomys savini* coincide cronológicamente con las primeras poblaciones humanas en la Península Ibérica y en Europa.

Uno de los objetivos de esta tesis es evaluar si en el periodo entre la aparición y la extinción de *Mimomys savini*, esta especie muestra alguna tendencia

evolutiva y si pueden utilizarse como herramienta biocronológica en el estudio de las primeras poblaciones humanas de la Península Ibérica y Europa.

3) El nicho ecológico definido para *Mimomys savini* es le mismo que ocupan las ratas de agua actuales. Esto se establece debido a su afinidad filogenética.

En esta tesis se ha realizado la interpretación paleoambiental del nivel EVT7 del yacimiento de Vallparadís (Terrassa, España) y del nivel 2 del Barranc de la Boella (Tarragona, España) en base al contenido en micromamíferos. Para ello, se ha utilizado el método del hábitat optimo (Chaline, 1982; Repenning, 2001, Cuenca-Bescós, 2003; 2008; Cuenca-Bescós et al., 2005) asignando a *Mimomys savini* un hábitat acuático. Una vez obtenida esta interpretación paleoambiental se han comparado los resultados con otros estudios similares a partir de otros indicadores (proxys) como sería la macrofauna, etc...

El objetivo de todo ello es comprobar si los resultados paleoambientales obtenidos asignando *Mimomys savini* a un hábitat acuático son coherentes con los obtenidos con otros “proxys” y, en caso afirmativo, aportar más información sobre el ambiente en que se formaron los yacimientos estudiados.

METODOLOGÍA

La recuperación de restos de micromamíferos fósiles requiere un conjunto de técnicas distintas a las utilizadas en otros grupos de mamíferos fósiles. Esto es debido fundamentalmente a su pequeño tamaño y a la baja densidad de restos que aparecen en los yacimientos de origen fluvio-lacustre. Así, en el estudio de micromamíferos no utilizaremos las técnicas de excavación y recolección utilizadas para la recuperación de mamíferos de mediana y gran talla. En este campo se utilizan técnicas de lavado-tamizado similares a las utilizadas en el campo de los invertebrados marinos o la paleobotánica, con la diferencia significativa que será necesario procesar una mayor cantidad de sedimento. Esto ha hecho que se hayan acabado desarrollando técnicas propias para un rápido y efectivo procesado de grandes cantidades de sedimento.

La técnica del lavado y tamizado del sedimento comenzó a ser utilizada por Lartet en el siglo XIX, pero no fue hasta la segunda mitad del siglo XX cuando se perfeccionó y generalizó su utilización gracias a Freudenthal y Damms (Freudenthal et al., 1976; Damms y Freudenthal, 1988) y a la mesa de lavado-tamizado conocida como mesa Freudenthal. Otro sistema de lavado-tamizado utilizado en la actualidad es una estructura en torre de tamices. La utilización de una estructura u otra dependerá de la concentración de restos de micromamíferos presentes en el sedimento y del volumen de sedimento que se deba lavar.

Las dimensiones de los restos fósiles de micromamíferos también requieren de un conjunto de técnicas específicas para su estudio y clasificación.

En este apartado se describen las técnicas utilizadas en los 5 capítulos autocontenidos de este trabajo para la recuperación, procesado y estudio de los restos de micromamíferos.

1 - RECOGIDA DE SEDIMENTO

Los pequeños mamíferos son una de las herramientas más útiles para correlacionar y datar los yacimientos. Esta correlación y datación, registro bioestratigráfico, precisa de un muestreo sistemático en la sucesión de niveles fosilíferos de un yacimiento. El muestreo estrato por estrato, por unidades, etc... vendrá determinado por los objetivos finales del trabajo, que puede ser la revisión sistemática de un taxón, su evolución, reconstrucciones paleoecológicas, paleoambientales, bioestratigrafía, dataciones relativas, etc...

Conseguir una muestra significativa, es decir con un número de restos mínimo para que su estudio sea fiable, supone recoger desde varios kilogramos hasta varias toneladas de sedimento dependiendo de la riqueza del estrato estudiado (es decir de la concentración de restos). Por ello, el objetivo principal cuando se realiza una prospección de micropaleontología de vertebrados, será calcular la cantidad de sedimento necesario para conseguir un volumen útil de restos. Esto nos ayudará a conocer la viabilidad del estudio de este yacimiento a nivel de micropaleontología.

En el caso particular del muestreo de yacimientos arqueológicos y paleontológicos cuya intención final es reconstruir el ambiente en que se desarrolló la vida de los primeros humanos, el muestreo de microvertebrados no estará solo diseñado para el estudio del micropaleontólogo, sino por el diseño y desarrollo de la excavación. Así, se recuperará más sedimento de las capas con un bajo contenido en fósiles de macrovertebrados y restos arqueológicos, mientras que en las capas con alto contenido en restos, se recuperará menos (hay menos matriz) y será importante conocer su relación espacial con los fósiles de macrovertebrados y con los restos arqueológicos.

Un caso especial son las excavaciones en rellenos de cuevas, donde la metodología es similar a la utilizada al aire libre, con la salvedad de que la continuidad lateral queda delimitada por las paredes, suelo y techo de la cueva. Este tipo de excavaciones presentan una gran ventaja ya que al no haber sufrido casi transporte, el material recuperado estará en mejor estado de conservación (Bennàsar, 2010).

La recogida del sedimento/muestras se lleva a cabo por el personal que esta realizando la excavación, es decir por el grupo de arqueólogos, paleontólogos, etc… que estén recuperando los restos arqueológicos y de macrofauna del yacimiento. Es importante, al igual que con todo el material recuperado de una excavación, mantener en todo momento un control de la procedencia y la situación en la vertical del sedimento. Para ello las muestras serán coordenadas, no de una forma tan estricta como con el material que se extrae del yacimiento, pero si que se deberá conocer en todo momento el cuadro del que procede la muestra (equivalente a X,Y) y la talla (Z). No cabe decir por supuesto, que en la misma etiqueta en la que figuren dichas coordenadas, figurará también el nombre del yacimiento y posibles datos relevantes (contacto entre estratos, etc…). Dependiendo del objetivo final y del tipo de yacimiento, también puede hacerse un lavado por capas en el que solo será importante la capa de procedencia de la muestra siendo indiferente la posición en la horizontal de la muestra. Este sistema se utiliza sobretodo en yacimientos generados por procesos sedimentarios fluviales, lacustres, eólicos, etc.. donde no parece haber zonas de acumulación preferente.

Para facilitar el transporte de las muestras, se colocan en sacos de 10-15 Kg. sin mezclar entre si y son recogidas por el equipo de lavado, que se encargará de llevarlas hasta la zona de lavado-tamizado.

Los restos utilizados en la presente tesis se lavaron por tallas y cuadricula en el yacimiento de Gran Dolina (Atapuerca, España), por niveles y cuadricula en el yacimiento de Vallparadís (Terrassa, España) y por niveles en los yacimientos de Fuente Nueva 3 y Barranco León D (Orce, España) y el Barranc de la Boella (Tarragona, España).

2 - LAVADO-TAMIZADO

Una vez concluida la recogida de muestras se pasa a la extracción de los microfósiles y para ello se utiliza la técnica del lavado-tamizado.

Siempre sin que se mezclen ni se confundan las etiquetas de las distintas muestras, estas serán repartidas en cubos (cada uno etiquetado como la muestra que contiene) y estos serán rellenados con agua (figura 2.1). Este proceso tiene como finalidad acabar de disolver, de disgregar, el sedimento de la muestra que aun mantenga algo de cohesión. Dependerá de esta cohesión inicial la duración de este proceso. A continuación se pasa las muestras a través de los distintos tamices, ya sea en una estructura en torre de tamices o en una mesa Freudenthal, con la ayuda de agua corriente proporcionada por un sistema de mangueras.

Figura 2.1. Muestras repartidas en cubetas con agua para disgregar el sedimento. En este caso, muestras de los yacimientos de Fuente Nueva 3 y Barranco León de la campaña de excavación de 2013.

En la recuperación de los restos de micromamíferos del yacimiento del Barranc de la Boella de esta tesis, el sedimento se lavo-tamizó utilizando una mesa Freudenthal (figura 2.2). En Gran Dolina se utilizó un sistema de torre de tamices para lavar el sedimento (figura 2.3) y en Orce ambos sistemas (el material utilizado en el capitulo 5 se recupero con mesa Freudenthal, mientras que en excavaciones posteriores se esta utilizando una estructura de torre de tamices).

Figura 2.2. Mesa Freudenthal instalada en los yacimientos del Barranc de la Boella durante la campaña de 2013. **Derecha**; esquema de la mesa Freudenthal para lavado de sedimentos en las excavaciones.

Figura 2.3. Esquema del montaje de tamices en torre. **Izquierda**: Estructura utilizada para el lavado-tamizado en Atapuerca (ideada por Gloria Cuenca-Bescós). **Derecha**: Estructuras utilizadas para el lavado-tamizado en los yacimientos de Orce y esquema del sistema de lavado con torre de tamices.

La base del sistema es el mismo tanto para la mesa Freudenthal como para la estructura en torre de tamices. Se pasa el sedimento a través de un conjunto de tamices de forma que cada vez la luz de maya es menor. Así la fracción más gruesa queda en el tamiz superior y la más fina en el inferior. Las distintas luces de maya empleadas son: 5 mm, 2 mm y 0,5 mm.

En el tamiz superior aparecen generalmente piedras que son desechadas y eventualmente algunos restos arqueológicos pequeños y fragmentos óseos, que son etiquetados y trasladados al laboratorio para su estudio por parte del personal responsable. Es en los otros dos tamices en los que aparecerán los restos de microvertebrados. Utilizar un sistema u otro dependerá de la cantidad de muestras ha procesar, de la densidad de restos fósiles en estas muestras, del tipo de estudios que se quieran llevar a cabo en los yacimientos y del tipo de yacimiento.

Finalmente, las dos fracciones más finas de cada muestra (concentrado final) se secarán (figura 2.4) y se guardarán debidamente etiquetadas para su posterior estudio en laboratorio. La fracción gruesa, dependiendo de las posibilidades de la excavación y del personal disponible, puede ser triada ya en el campo con la ayuda de un pequeño laboratorio de campo.

Figura 2.4. Concentrado después del lavado-tamizado secando-se en Atapuerca.

En los casos en que no se pueda disponer de agua se puede realizar un tamizado en seco (técnica de la criba en seco), aunque este método limita la recuperación de restos de menos de dos milímetros.

El resultado de un buen lavado-tamizado será un concentrado de huesos y piedras limpio de limos y arcillas.

3 - TRIADO

El triado consiste en la separación de los restos fósiles de la fracción mineral que constituye la mayor parte del residuo final. El triado de las fracciones más groseras (con tamaño de partícula de 2 mm o mayor) se realiza a simple vista, extendiendo el concentrado sobre una superficie plana y extrayendo los restos fósiles con ayuda de unas pinzas (figura 2.5). Para triar las fracciones de tamaño menor, es necesario el uso de la lupa binocular; se depositan pequeñas porciones de concentrado en una bandeja en cuyo fondo hay dibujado un retículo, y se examinan bajo la lupa, seleccionando los fósiles.

Durante el triado se extraen no sólo los dientes, sino también los huesos, enteros o fragmentados.

El proceso de triado se realiza en laboratorio, aunque como ya se ha dicho, dependiendo de las posibilidades de la excavación se puede realizar una parte en campo (figura 2.6). Para esta tesis, el material procedente de los yacimientos del Barranc de la Boella, Fuente Nueva 3 y Barranco León fue triado en el Iphes (Institut de Paleoecologia Humana i Evolució Social, Tarragona), el material procedente de Atapuerca se trió en el campo y en la Universidad de Zaragoza y el material de Vallparadís se trió en el ICP (Institut Català de Paleontologia)..

Figura 2.5. Triado con ayuda de pinzas.

Figura 2.6. Al fondo: estructura de lavado de torre de tamices utilizada en los yacimientos de Pinilla del Valle (Madrid). **En primer plano:** triado del concentrado final realizado en el campo.

En un principio se realiza un triado preliminar en el que se separan los restos paleontológicos del sedimento tamizado y se agrupan en restos craneales (mandíbulas, dientes, etc..) y post-craneales (húmeros, vértebras, falanges, etc...) (figura 2.7). Después estos restos se separan por grupos (roedores, insectívoros, quirópteros, etc...) y finalmente por familias y géneros.

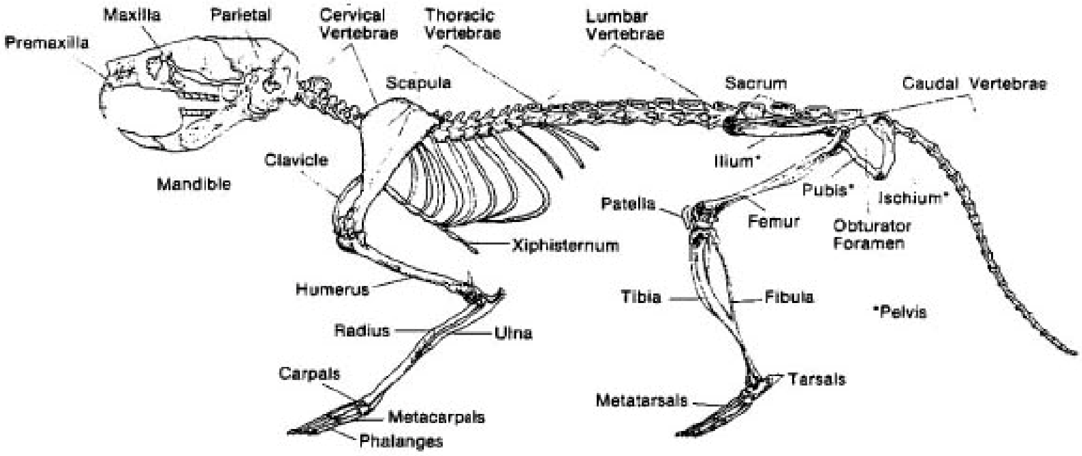


Figura 2.7. Esquema del esqueleto completo de un arvicolino. Los restos postcraneales corresponden a todos los restos que no proceden del cráneo (dibujo extraído de la guia “OWL PELLET KIT. Teacher's guide” publicado por Flinn scientific. Inc)

Una vez separado ya definitivamente el material para estudio, en algunos casos es necesario relavar alguna pieza en la que puedan quedar aun pequeñas partículas de sedimento adheridas. Para ello y a fin de evitar dañar el fósil, se utilizará una cubeta de ultra sonidos (figura 2.8).

Finalmente, los restos fósiles de microvertebrados se montan en cajitas de metraquilato sobre una superficie plana y de fácil manejo para su posterior estudio en el microscopio o lupabinocular. Esta superficie plana puede ser la propia tapa de la cajita de metraquilato o un soporte plano extraíble. Como ejemplo, el material del capitulo 5 de Barranco León y Fuente Nueva 3 se montó sobre fichas de un juego de construcción (lego) por uno de sus lados planos. Esto permite además de manipular con facilidad los restos fósiles, montar varias fichas si la muestra presenta una gran cantidad de restos a estudiar.

El montaje de los restos fósiles no se hace con pegamentos sino que se utiliza una pasta adhesiva no grasienta (tipo adhesivo TAC) por si es necesario modificar la posición en la que se han montado (figura 2.9).

Figura 2.8. Lavado de muestras con cubeta de ultrasonidos en la Univesidad de Zaragoza

Figura 2.9. Material fósil de micromamíferos montado sobre la tapa de una cajita de metraquilato con adhesivo TAC. Se aprecian varias hemimandíbulas y molares sueltos de arvicolinos.

4 - ANÁLISIS DEL MATERIAL

Para analizar el material, a diferencia de otros trabajos similares, las medidas no se tomaron mediante un sistema digital montado sobre una lupa binocular de forma instantánea, sino que se realizaron fotografías y fue sobre estas donde posteriormente con la ayuda de programas de edición de imagen se realizaron las mediciones (Adobe PhotoShop CS5). De esta forma, se conserva un registro fotográfico de cada muestra que permite repetir cualquier observación si fuese necesario y además se minimiza el tiempo de utilización de los sistemas de captura de imagen digitales. Se trabajó sobre fotografía digital y sobre fotografía de microscopio electrónico. En el caso de la fotografía digital, la preparación de la muestra solo requiere la fijación sobre una superficie plana como ya se ha dicho anteriormente. De esta forma, se consigue mantener la muestra inmóvil en la posición deseada para realizar la toma de fotografías digitales.

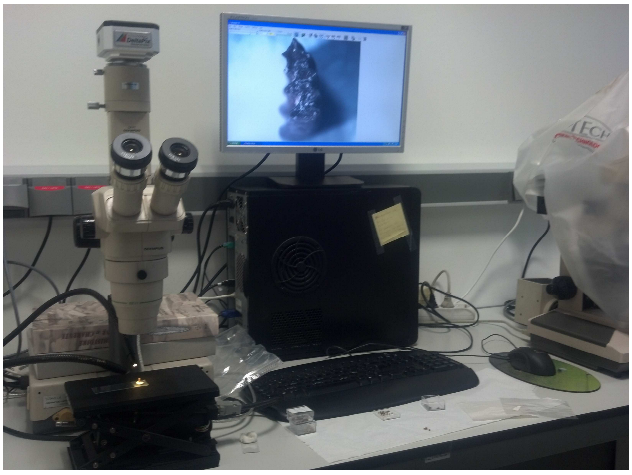
Para la realización de fotografías en microscopio electrónico (SEM) la muestra requiere una preparación previa, se fijará sobre un soporte especifico que permita trabajar en el microscopio electrónico (porta muestras) y se le aplicará un baño de grafito para asegurar su conductividad. En este trabajo se emplearon fotografías de microscopia electrónica en menor medida que las fotografías digitales, exclusivamente en los restos procedentes de Gran Dolina TD 4 (Atapuerca).

Las fotografías digitales fueron realizadas, en el caso de las muestras de Gran Dolina (Atapuerca) con el equipo de la Universidad de Zaragoza (figura 2.10). Para las muestras de Barranco León ,Fuente Nueva 3, el Barranc de la Boella y Vallparadís, se utilizó la lupa binocular (Olympus SZ-40) junto con la cámara (Infinty X) que se halla en las instalaciones del Iphes (figura 2.11).

Las fotografías realizadas con SEM se llevaron a cabo en los servicios científico técnicos de la Universidad de Zaragoza.

Figura 2.10. Lupa binocular conectada una cámara digital en la Universidad de Zaragoza utilizada para el estudio del material perteneciente a Atapuerca incluido en esta tesis.

Figura 2.11. Equipo utilizado para la toma de fotografías digitales en esta tesis, del Institut de Paleoecologia Humana i Evolució Social, en Tarragona.



Para la comparación entre las distintas poblaciones, se establecieron criterios de edad de las muestras con el fin evitar que los valores de individuos juveniles distorsionasen los resultados, debido a la variabilidad morfológica que estos pueden presentar. La comparación se realiza con datos relativos a individuos de edad adulta, con las zonas libres de esmalte del plano oclusal de los molares definidas y las raíces o bien cerradas o en proceso de cerrarse (figura 2.12).

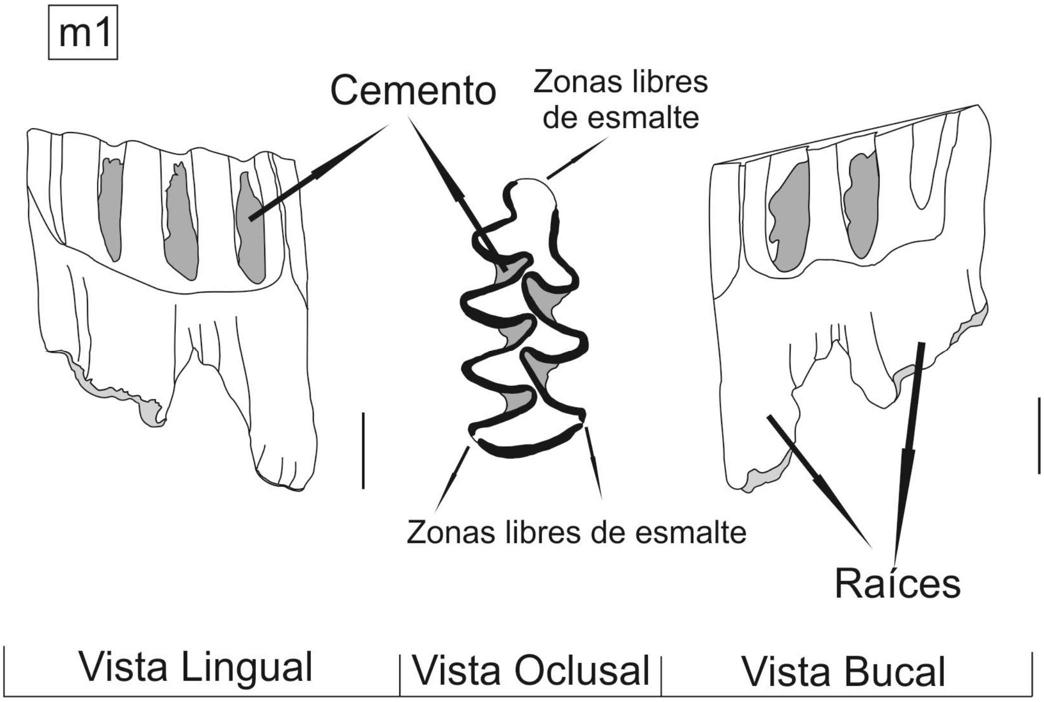


Figura 2.12. Distintas vistas de un primer molar de *Mimomys savini* y partes del molar. La escala gráfica corresponde a 1 milímetro.

5 - MEDIDAS Y NOMENCLATURA

Aunque en los capítulos 3 y 4 de esta tesis se han estudiado taxones distintos a *Mimomys savini* para realizar interpretaciones paleoambientales, en este apartado solamente se describe la nomenclatura y medidas de *Mimomys savini* (objeto central de esta tesis). Al tratarse de capítulos autocontenidos, en los apartados de metodología de los capítulos 3 y 4 ya se describe la nomenclatura y medidas utilizadas en el estudio de estos otros taxones.

Como ya se ha mencionado en la introducción de esta tesis, los elementos diagnósticos de la especie *Mimomys savini* son el primer molar inferior (m1) y el tercer molar superior (M3). Por tanto, la evolución de *Mimomys savini* durante el Pleistoceno inferior se ha estudiado en base a los cambios de determinados caracteres de estos molares.

En los m1 se ha medido la longitud (L), entendiendo esta como la distancia máxima entre la parte proximal y distal del diente. El ancho (W), determinado como la proyección sobre una recta perpendicular al eje de longitud entre los extremos más alejados del lado lingual y bucal del diente. La longitud del complejo anteroconido (A), distancia entre BSA 4 y el extremo del complejo anteroconido (figura 2.13). Por ultimo se midieron los diferentes gruesos del esmalte en los lados anterior y posterior del los triángulos salientes, para el posterior calculo del SDQ (Cociente de diferenciación del grueso de esmalte) (figura 2.14).

El SDQ se calcula según la formula;

$$\mathbf{SDQ = [\ \sum(teet \times 100/leet)]/N}$$

propuesta por Heinrich (1987) y Koenigswald y Kolfschoten (1996) modificada por Cuenca-Bescós et al., 2010a.

Donde teet corresponde al grueso de esmalte posterior del triangulo saliente y leet corresponde al grueso anterior del mismo triangulo (es decir, del mismo campo de dentina, figura 2.14) y N corresponde al numero de campos de dentina estudiados por diente. Se utilizó esta formula para facilitar la comparación futura con otros datos ya publicados.

En el caso de los M3 solo se midió longitud (L) y ancho (W) (figura 2.13).

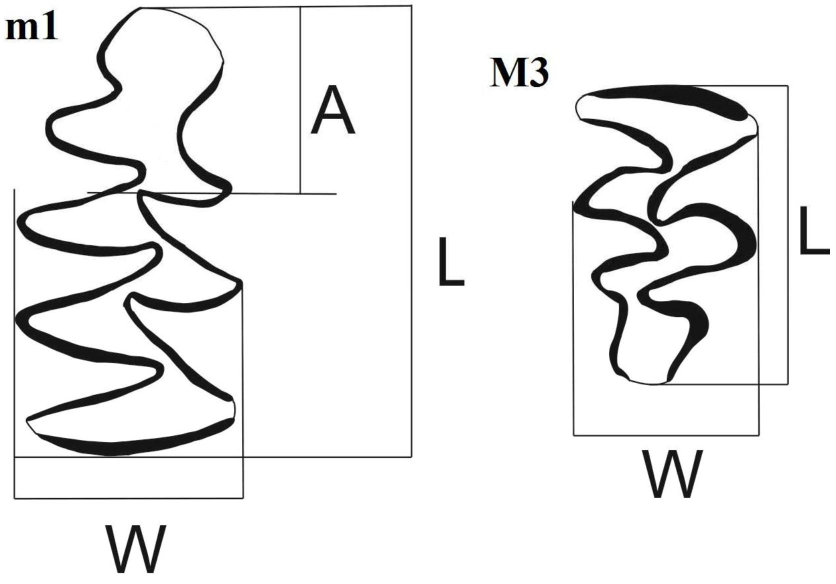


Figura 2.13. Esquema de las medidas estudiadas. **W**; Ancho de la pieza. **L**; Longitud de la pieza. **A**; Longitud del complejo anteroconido. **m1**; primer molar inferior. **M3**; Tercer molar superior.

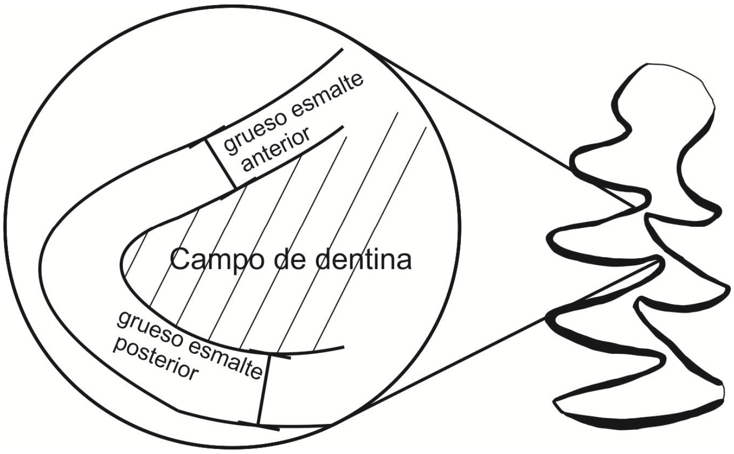


Figura 2.14. Esquema de la situación del campo de dentina (triángulos salientes) y el grueso de esmalte anterior y posterior.

La nomenclatura y terminología utilizada en esta tesis es la propuesta por Meulen (1973), Meulen y Zagwijn (1974), Heinrich (1978) y Rabeder (1981) (figura 2.15).

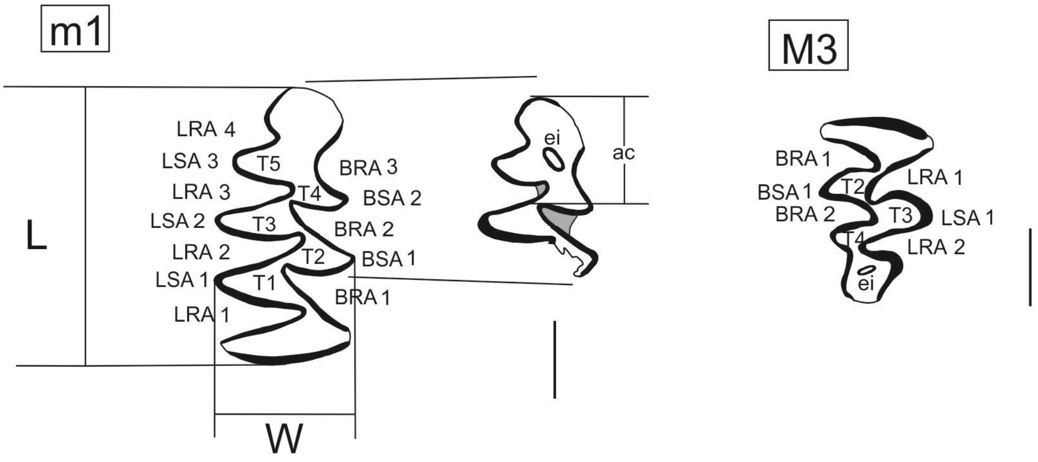


Figura 2.15. Nomenclatura utilizada (modificada de Meulen (1973), Heinrich (1978) y Rabeder (1981). **LRA**; Angulo reentrante lingual. **LSA**; Angulo saliente labial. **BRA**; Angulo reentrante bucal. **BSA**; Angulo saliente bucal. **ac**; Complejo anteroconido. **T**; Triángulos de dentina. **ei**; islote de esmalte. La escala gráfica corresponde a 1 milímetro.

6 – INTERPRETACIONES PALEOAMBIENTALES

En esta tesis las aproximaciones paleoambientales se han realizado mediante el método del hábitat óptimo. Para ello, lo primero que se debe hacer es conocer el peso cuantitativo de cada taxón de una asociación de micromamíferos dentro de esta asociación. Existen diversas maneras de estimar la composición cuantitativa de las asociaciones de micromamíferos. Una de ellas es el cálculo del Número Mínimo de Individuos (NMI) por taxón, que viene dado por el elemento esquelético o dentario diagnóstico en la asociación para cada taxón más representado (Daams y Freudenthal, 1988; Andrews, 1990).

El cálculo del NMI permite conocer las proporciones de individuos que hay de las especies, con tal de ver la diversidad específica existente.

Este cálculo es apropiado para las acumulaciones de micromamíferos en los que los procesos tafonómicos tienden a concentrar los restos, como las producidas por trampas naturales, por muertes masivas sin o con escaso transporte, o por la acción directa de predadores, en la que los restos se acumulan originalmente articulados.

Una vez calculado el numero mínimo de individuos, la composición cuantitativa de una asociación faunística consiste en calcular la abundancia relativa de cada taxón. Es decir, el porcentaje que representa un taxón dentro de la asociación. Esto se calcula tomando como 100% la suma de numero mínimo de individuos de todos los taxónes.

El análisis de la abundancia relativa de especies es de ayuda para la inferencia de los distintos hábitats. El dominio de una o dos especies sobre las demás es un indicador de inestabilidad climática, mientras que la complejidad en la asociación de las distintas especies se encuentra en relación a un hábitat más complejo, y por lo tanto a una mayor estabilidad climática. Además, la distribución de las especies en el pasado y el presente puede indicar preferencias de hábitat y clima (Brunet-Lecomte y Delibes, 1984; Montuire et al. 1997; Pokines, 1998; Repenning, 2001).

En esta tesis, se ha realizado una clasificación de las especies en función a su hábitat óptimo (Prado Seco, Prado Húmedo, Bosque, Roquedos y Agua) En base a los trabajos de Chaline (1982), Repenning (2001), Cuenca-Bescós (2003), Cuenca-Bescós et al. (2005) y Cuenca-Bescós (2008).

El límite de este método, como sucede con otros procedimientos válidos para observar el tipo de hábitat que representan las especies en un yacimiento, como el Taxonomic Habitat Index (Andrews, 1990; Fernandez-Jalvo et al., 1998) o el Climatic Restrinction Index (Hernández Fernández, 2001), radica en

el intento de extrapolación de la ecología de especies actuales a especies fósiles que no tienen representantes en la actualidad. Por lo tanto, el método de la asociación de pequeños mamíferos por hábitat será efectivo, siempre y cuando las especies que encontramos en nuestros yacimientos tengan representantes actuales.

CAPÍTULO 1

TENDENCIAS EVOLUTIVAS EN LA MORFOLOGÍA DENTAL DE *MIMOMYS SAVINI* (RODENTIA, MAMMALIA) DEL PLEISTOCENO EN LA PENÍNSULA IBÉRICA Y DISCUSIÓN SOBRE EL ORIGEN DEL GÉNERO *ARVICOLA*

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PLEISTOCENE EVOLUTIONARY TRENDS IN DENTAL MORPHOLOGY OF *MIMOMYS SAVINI* (RODENTIA, MAMMALIA) FROM IBERIAN PENINSULA AND DISCUSSION ABOUT THE ORIGIN OF THE GENUS *ARVICOLA*

Iván Lozano-Fernández[1,2], Jordi Agustí[2,3], Gloria Cuenca-Bescós[4], Hugues-Alexandre Blain[1,2], Juan Manuel López-García[5] & Josep Vallverdú[1,2]

[1] IPHES, Institut Català de Paleoecologia Humana i Evolució Social, C/ Escorxador s/n, E-3003 TARRAGONA. *Emails:* ilozano@iphes.cat, hblain@iphes.cat

[2] Area de Prehistoria, Universitat Rovira i Virgili (URV), Avinguda de Catalunya 35, E-43002 TARRAGONA.

[3] ICREA, IPHES, Institut Català de Paleoecologia Humana i Evolució Social, C/ Escorxador s/n, E-43003 TARRAGONA. *Email:* jordi.agusti@icrea.cat

[4] Área de Paleontología, Departamento de Ciencias de la Tierra, Facultad de Ciencias, Universidad de Zaragoza, E-50009 ZARAGOZA. *Email:* cuencag@unizar.es

[5] Gruppo di Ricerca di Paleobiologia e Preistoria, Dipartimento di Studi Umanistiche, Università degli Studi di Ferrara, C.so Ercole I d'Este 32, I-44121 FERRARA. *Email:* jlopezgarcia1980@gmail.com

ABSTRACT

The study of *Mimomys savini* material from the Spanish sites of Barranco León and Fuente Nueva 3 (Granada), Gran Dolina (Atapuerca), Vallparadis (Barcelona) and La Boella (Tarragona) shows evolutionary trends in the dental morphology of this species within the Lower and early Middle Pleistocene. The data obtained from each site were ordered on the basis of absolute datings available for the ~1.46-0.7 Ma time interval. Clearly detected trends are the size increase and a successive reduction in enamel islets on both the upper third and lower first molar, and in the *Mimomys* ridge on the lower first molar. However, the SDQ (enamel differentiation index) values of the lower first molar show no clearly directed tendency within the considered time range.

On the basis of these evolutionary tendencies observed on *Mimomys savini* in the Iberian Peninsula, the phylogenetic relationship between *Mimomys savini* and the genus *Arvicola* is discussed.

Keywords: Lower Pleistocene, Middle Pleistocene, *Mimomys savini*, Iberian Peninsula, evolutionary trends

RÉSUMÉ

TENDANCES ÉVOLUTIVES DE LA MORPHOLOGIE DENTAIRE DE *MIMOMYS SAVINI* (RODENTIA, MAMMALIA) DANS LA PÉNINSULE IBÉRIQUE DURANT LE PLÉISTOCÈNE ET DISCUSSION SUR L'ORIGINE DU GENRE *ARVICOLA*

L'étude du matériel de *Mimomys savini* des sites espagnols de Barranco León et Fuente Nueva 3 (Grenade), Gran Dolina (Atapuerca), Vallparadis (Barcelone) et La Boella (Tarragone) montre des tendances évolutives dans la morphologie dentaire de cette espèce durant le Pléistocène inférieur et le début du Pléistocène moyen. Les données obtenues pour chaque gisement ont été ordonnées selon les datations absolues disponibles pour l'intervalle temporel ~1,46-0,7 Ma. Les tendances évidentes détectées sont une augmentation de la taille et une réduction progressive des îlots d'émail aussi bien sur la troisième molaire supérieure que sur la première molaire inférieure, et du pli mimomyen sur cette dernière. Toutefois, les valeurs du rapport SDQ (indice de différenciation de l'émail) de la première molaire inférieure ne montrent aucune tendance claire pour la période considérée.

Sur la base de ces tendances évolutives observées chez *Mimomys savini* dans la péninsule Ibérique, la relation phylogénétique entre *Mimomys savini* et le genre *Arvicola* est discutée.

Mots-clés : Pléistocène inférieur, Pléistocène moyen, *Mimomys savini*, péninsule Ibérique, tendances évolutives

1 - INTRODUCTION

The first appearance data (FAD) for *Mimomys savini* in Europe date to ca. 1.8 Ma (Topachevskij & Skorik, 1977; Jánossy, 1986; Rekovets, 1994; Fejfar *et al.,* 1998), and the species survived until 0.6 Ma (Fejfar *et al.,* 1998). In the Iberian Peninsula this taxon was documented for the first time around 1.6 Ma in the Guadix-Baza Basin (Agustí, 1986; Agustí *et al*., 1987; 2010). Its earliest record coincides approximately with the first presence of hominids on the European continent, i.e. with the *Homo antecessor* remains found at Gran Dolina, Atapuerca (Bermúdez *et al.,* 1997; Carbonell *et al*., 2008), and with the lithic industries and cut-marks at the sites in the Orce region in the Guadix-Baza Basin (Martínez-Navarro *et al*., 1997; Oms *et al*., 2000; Toro *et al.,* 2010).

Mimomys savini is the oldest known representative of the so-called water vole lineage, all the members of which are characterized by rather large m1 teeth. Lower first molars of extant *Arvicola* species, which are descendants of, or at least forms closely related to, *Mimomys savini* (see discussion below), can reach lengths of as much as 4 mm.

To date, *Mimomys savini* is the last known representative of the genus *Mimomys*. The evolution of this genus shows a tendency that brings its molar morphology successively closer to that of the genus *Arvicola*. *Mimomys savini* is considered by many authors to be the ancestor of *Arvicola* (Chaline & Sevilla, 1990; Viriot *et al*., 1990; Chaline *et al.,* 1999).

Due to their rapid evolutionary changes and dispersal, rodents have become a particularly useful tool in worldwide biozonation (arvicolines in the Holarctic region), separating the Pleistocene into the Villanyian, the Biharian and the

Toringian stages (in the sense of Fejfar and Heinrich, 1980, 1987, among others). The Biharian, which corresponds to the *Microtus-Mimomys* superzone (characterized by the coexistence of these two genera), is subdivided into two rodent zones: the lower is the *Mimomys savini* + *Mimomys pusillus* zone, and the upper is the *Mimomys savini* zone (fig. 1) (Fejfar *et al.,* 1998). In the biochronological subdivision defined for the Iberian Peninsula, *Mimomys savini* is present in the *Iberomys brecciensis* biozone, the *Allophaiomys chalinei* biozone, the *Allophaiomys lavocati* biozone and the *Allophaiomys pliocaenicus* biozone (Cuenca-Bescós *et al*., 2010b).

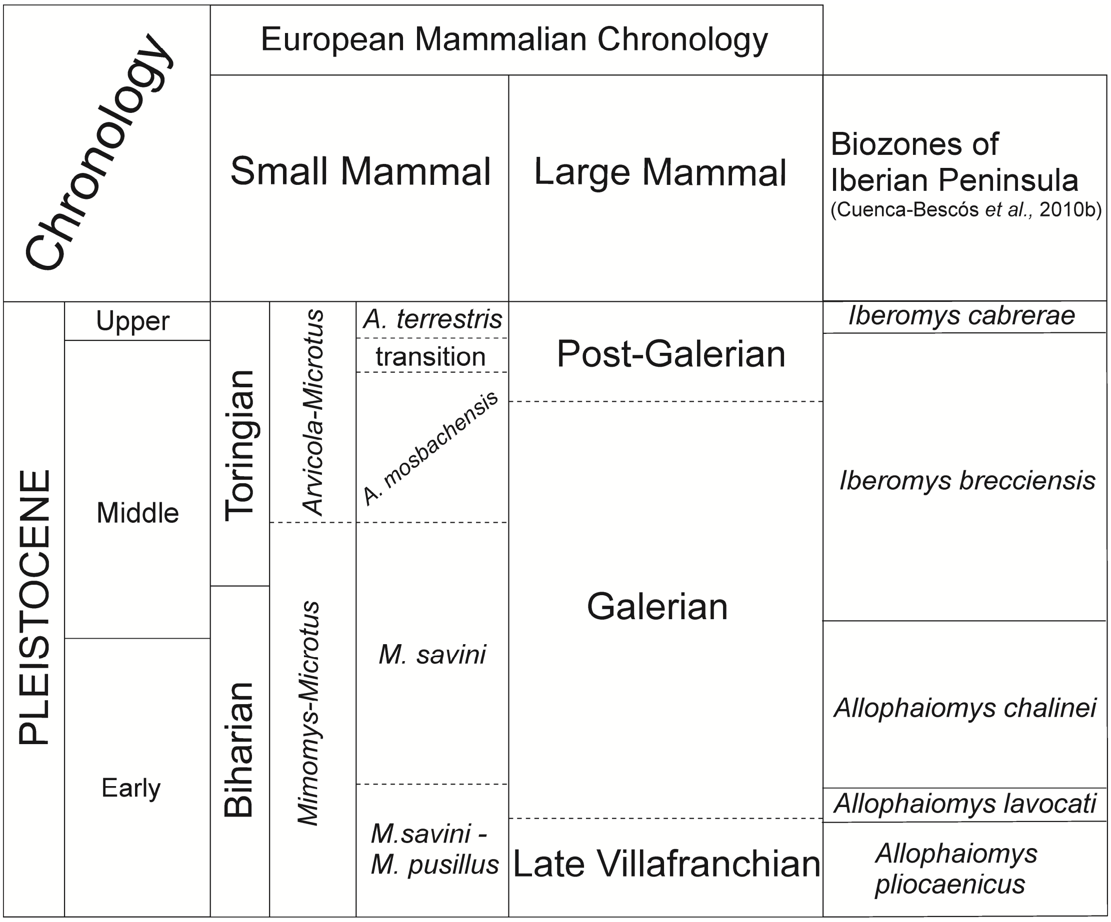

Figure 1. European biozones (modified from Masini & Sala, 2007) and biozones of Iberian Peninsula (Cuenca-Bescós *et al.,* 2010b).

The oldest known populations of *Mimomys savini* in Europe date to the Early Pleistocene period and have been recorded at Tiligul (Topachevskij & Skorik, 1977) and Zhevakhova Gora in the Ukraine (Rekovets, 1994), Villány 5 in Hungary (Jánossy, 1986), Fuente Nueva 3 and Barranco León in Spain (Agustí, 1986; Agustí *et al*., 1987; 2010), and levels TD 3-4 (the current TD 4 was divided into TD 3 and TD 4 in the earliest papers) of Gran Dolina in Spain (Cuenca-Bescós *et al*., 1995; 1999; Cuenca-Bescós & García, 2007; Cuenca-Bescós *et al*., 2010b). The most recent populations correspond to the Early-Middle Pleistocene transition and have been recorded at several sites such as Zapadnye Kairy in the Ukraine (Markova, 1982, 2004), Kärlich E and F in Germany (von Koenigswald & van Kolfschoten, 1996), Voigtstedt in Germany (Maul, 2002), West Runton in England (Stuart, 1981), and level TD 8 of Gran Dolina in Spain (Cuenca-Bescós *et al*., 2010b).

In this article we present the results of our studies on the evolution of the molar morphology of *Mimomys savini* from the Iberian Peninsula. On the basis of these results, we discuss the phylogenetic relationship between *Mimomys savini* and the genus *Arvicola*.

2 - GEOGRAPHICAL, GEOLOGICAL AND CHRONOLOGICAL BACKGROUND

This paper is based on the data obtained from *Mimomys savini* remains from Barranco León (level D), Fuente Nueva 3, Gran Dolina (levels TD 4B, TD 5b, TD 5a, TD 6-3, TD 6-2 and TD 6-1), Vallparadis (layer 10) and La Boella (level 2) sites (fig. 2).

2.1 - FUENTE NUEVA 3 AND BARRANCO LEÓN

Fuente Nueva 3 (FN-3) and Barranco León (BL) are located within the Guadix-Baza Basin, which forms part of the Betic Mountain Range in the northern part of the province of Granada (Spain) (fig. 2). These sites fall within the *Allophaiomys lavocati* biozone for the Iberian Peninsula (Agustí *et al*., 2010; Cuenca-Bescós *et al*., 2010b; Oms *et al*., 2011), which corresponds to the upper part of the Early Pleistocene.

The first data on the rodent fauna of Barranco León were published by Agustí *et al*. (1987); the first on Fuente Nueva 3 by Martínez-Navarro *et al*. (1997).

The section at Fuente Nueva 3 presents a sedimentary record of some 20 meters of thickness, and the studied section of Barranco León presents a 25-m-thick sedimentary record. Both consist of a single stratigraphic unit that is Early Pleistocene in age. The samples analyzed for this article come from the layers of red and white clays of Fuente Nueva 3 and from level D of Barranco León (known in the first excavations as level 5) (fig. 2) (Toro *et al*., 2010).

Palaeomagnetic data have revealed that these two sites date back to before the Jaramillo event (Oms *et al*., 2000), while ESR dating has shown that level D of Barranco León dates back to 1.46 ± 0.38 Ma, and Fuente Nueva 3 to a period between 1.34 and 1.67 Ma (Duval, 2008). Recently, however, a new dating result of 1.19 ± 0.21 Ma was published for Fuente Nueva 3 (Duval *et al*., 2011), thus giving a new chronological range between 1.46 ± 0.38 Ma and 1.19 ± 0.21 Ma for these sites.

2.2 - GRAN DOLINA

Gran Dolina is one of the sites that form part of the archaeo-palaeontological complex of Atapuerca. It is located in a cave formed as a continuation of one of the fracture planes of the Upper Cretaceous layers of the Sierra de Atapuerca. Broadly speaking, this sierra, situated approximately 15 km to the east of the city of Burgos (Spain), is a small rocky promontory situated at the north-eastern limit of the hydrographic basin of the River Duero.

The sedimentary filling of Gran Dolina is divided into 11 levels (from TD 1 to TD 11). The Matuyama-Brunhes magnetic polarity reversal has been located in level TD 7 (fig. 2). The material under study in this paper corresponds to the section between the top of TD 4 (TD 4B) and the top of TD 6 (Parés & Pérez-González, 1995).

Levels TD 5 and TD 6 are subdivided into various sublevels, of which TD 5b, TD 5a, TD 6-3, TD 6-2 and TD 6-1 provided remains of *Mimomys savini*.

Chronologically, studied levels encompass a period extending from approximately 1 Ma to 0.78 Ma (Falguères *et al*., 1999; Berger *et al*., 2008; Cuenca-Bescós *et al*., 2010b).

2.3 - VALLPARADIS

The site of Vallparadis is located in the north-east of the Iberian Peninsula in the province of Barcelona (Spain). It displays a faunal association characteristic of the Lower Pleistocene. The sedimentary sequence is divided into two parts separated by an erosive discontinuity (unit 5) and is formed by the intercalation of fluvial and alluvial sedimentation (fig. 2). The palaeontological and

archaeological remains are found in almost all the sequence (Madurell-Malapeira *et al*., 2010; Martínez *et al*., 2010; Minwer-Barakat *et al*., 2011). The archaeological excavation focused mainly on the richest unit, unit 7 (Martínez *et al*., 2010).

Unit 7 presents two archaeological layers: layer 10 and layer 10c.

Layer 10c has been interpreted as an accumulation produced by massive transport due to a high-density fluid with erosive capacity, whereas layer 10 has been interpreted as flood muds deposited above the previous layer (fig. 2) (Madurell-Malapeira *et al*., 2010; Martínez *et al*., 2010).

US-ESR dating carried out on layer 10 yielded a chronology of 0.83 ± 0.07 Ma (Martínez *et al*., 2010).

2.4 - LA BOELLA

The site of La Boella (Barranco de la Boella, La Boella Ravine) is situated in the north-east of the Iberian Peninsula in the province of Tarragona, near the municipality of La Canonja. Two sites are currently being excavated within the ravine of La Boella, El Forn and La Mina, the first of which yielded the remains under study in this paper. The stratigraphy of the ravine is divided into 4 units (fig. 2). The material under study comes from level 2 at the top of unit 3.

The studies carried out on this site date it to roughly 0.7 Ma (Saladié *et al*., 2008; Vallverdú *et al*., 2008).

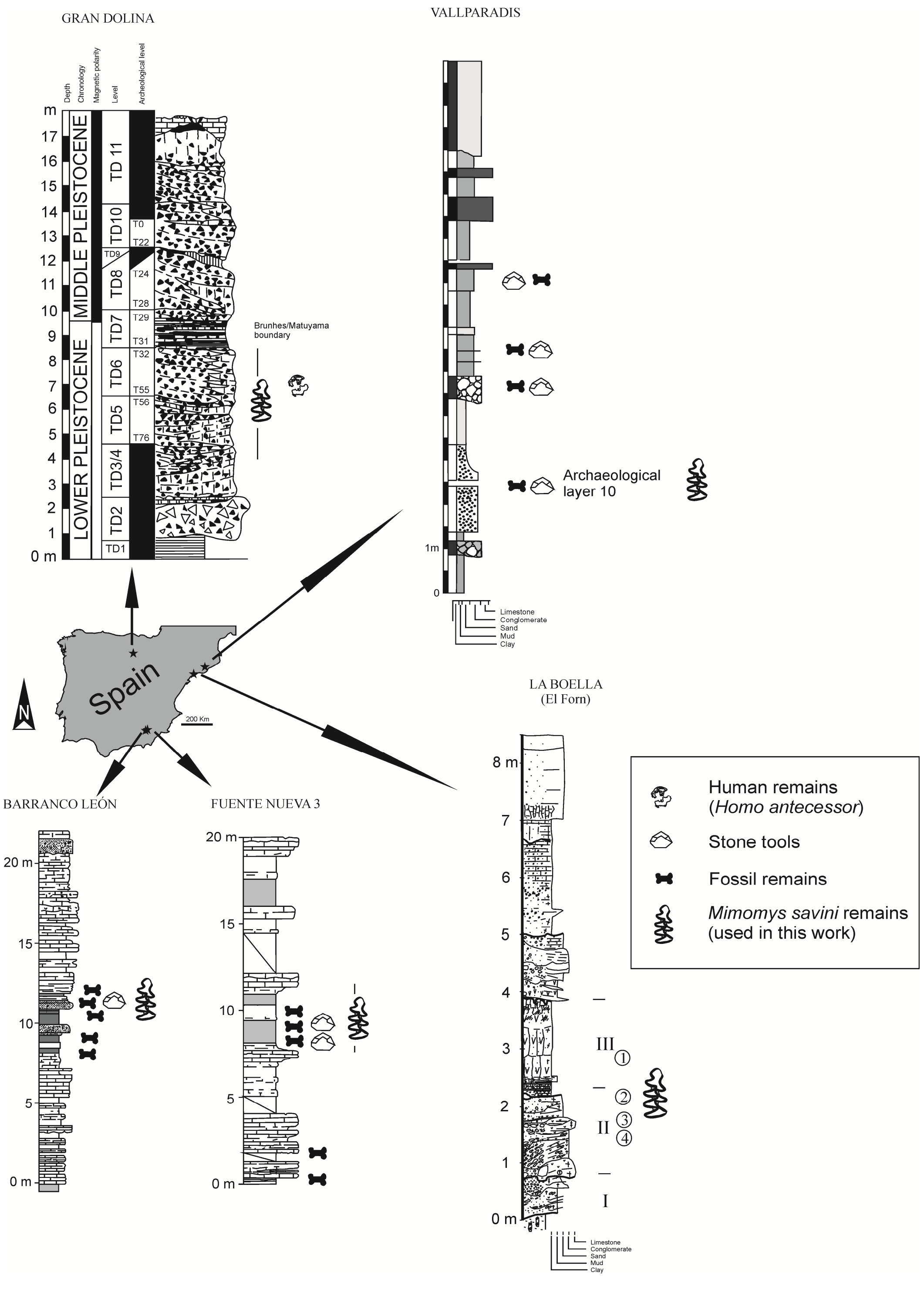

Figure 2. Geographical location and stratigraphic columns of sites that yielded studied remains. Gran Dolina (Parés & Pérez-González, 1995), Vallparadis (Garcia *et al*., 2011), Fuente Nueva 3 and Barranco León (Toro *et al.,* 2010) and El Forn (stratigraphic column by Josep Vallverdú). For La Boella, Roman numerals refer to units, and circled numbers to archaeological levels.

3 - METHODOLOGY

The remains were recovered by water-screening the sediment with both Freudenthal tables (Daams & Freudenthal, 1988) and a tower of sieves. Which equipment was used depended on the richness of the sediment. The sediment from sites very rich in remains, such as Gran Dolina, was processed using the tower of sieves. For sediments with few remains we used the Freudenthal table, which makes it possible to wash larger samples in less time. For the washing tables, mesh sizes of 5 mm (concentrate did not contain microfaunal remains), 2 mm and 0.5 mm were used.

Remains of *Mimomys savini* were extracted from the 2-mm concentrate. Lower first molars (m1) and upper third molars (M3), from adult specimens only, were used for the study in order to prevent the high morphological variability of juvenile forms from biasing the results. We regarded m1 and M3 as belonging to adult animals when enamel-free areas were visible at the occlusal surface and roots were closed or in the process of closing (fig. 3).

On these teeth, the presence or absence of enamel islets was recorded for m1 and M3, and of the *Mimomys* ridge for m1. Measurements were taken of the length (L) and the width (W) of m1 and of the enamel thickness, as shown in figure 3. The SDQ (enamel differentiation index) was calculated as:

$$\mathrm{SDQ} = [\ \Sigma\ (\mathrm{teet} \times 100/\mathrm{leet})\ ]\ /\ N$$

where N refers to the number of dentine fields of the studied tooth; teet (trailing edge enamel thickness) refers to the maximum thickness of the posterior enamel band; and leet (leading edge enamel thickness) refers to the maximum thickness of the anterior enamel band of each dentine field (Heinrich, 1978, 1987; Koenigswald & Kolfschoten, 1996; Cuenca-Bescós *et al*., 2010a).

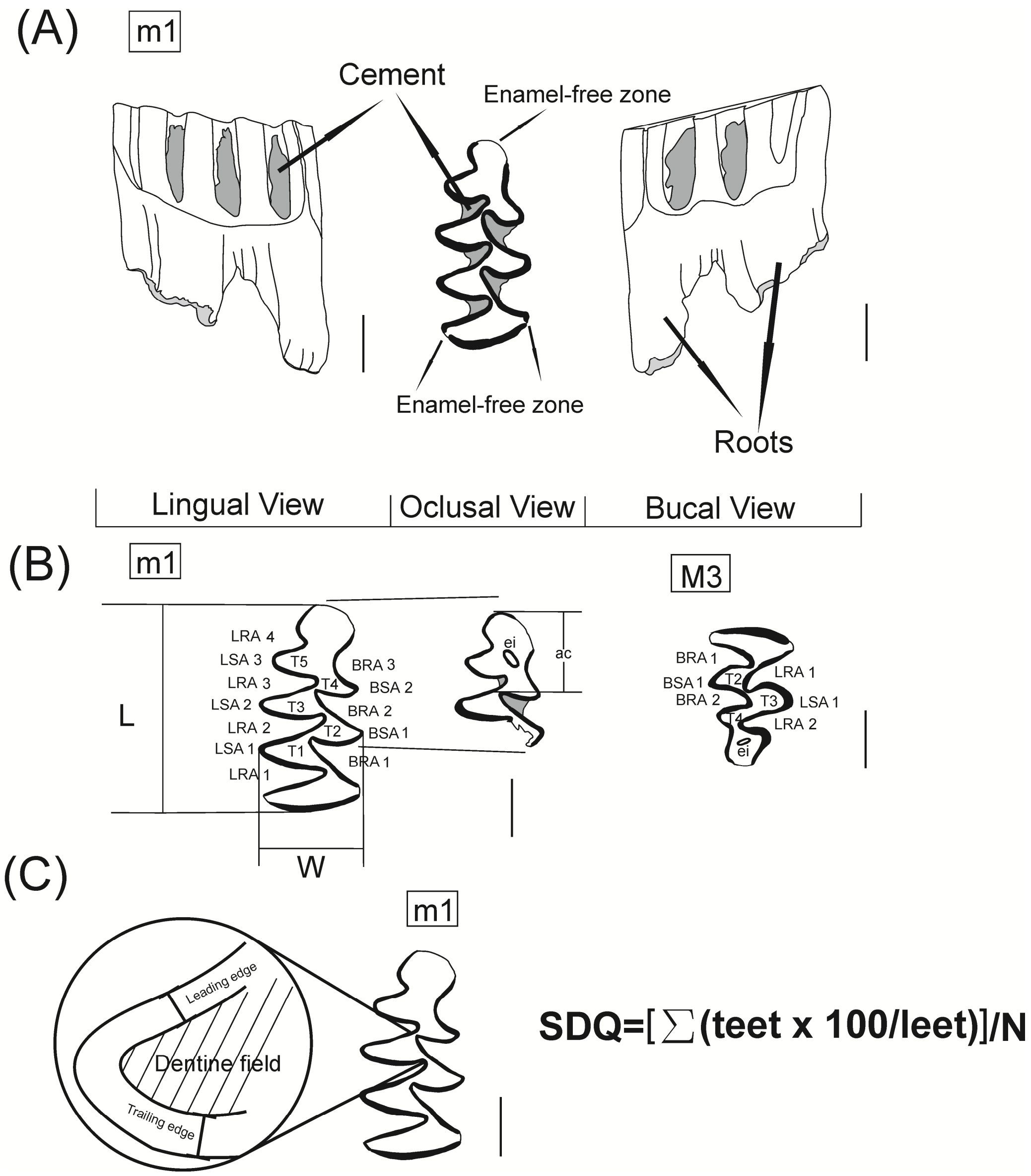

Figure 3. **(A)** Different views and general characters of a m1 from *Mimomys savini*. **(B)** Nomenclature of the parts distinguished in the occlusal plane of a m1 and of a M3, and measurements used in this study. **(C)** Parts of triangles and formula for the **SDQ** calculation of each type of tooth. **L**: length; **W**: width; **T1**, **T2**, **T3**, **T4** and **T5**: triangles composing the tooth; **LRA**: lingual re-entrant angles; **BRA**: buccal re-entrant angles; **LSA**: lingual salient angles; **BSA**: buccal salient angles; **ac**: anteroconid complex; **ei**: enamel islet (modified from van der Meulen, 1973; Heinrich, 1978; Rabeder, 1981). Formula variables: **teet**: trailing edge; **leet**: leading edge; **N**: total number of triangles. Scale bars = 1 mm.

All the measurements were taken on the occlusal plane of the molars with the image-treatment software Adobe PhotoShop CS5, using photographs from an Infinity X camera coupled to an Olympus SZ-40 binocular microscope. This software ensures highly reliable measurements made on flat surfaces.

4 - MATERIAL

The characters of *Mimomys savini* m1 are:

- an occlusal surface with a posterior lobe,
- five alternating triangles and an anteroconid complex,
- the presence of roots (except in the earliest stages of life),
- enamel with *Mimomys*-type differentiation (Heinrich, 1978, 1987; von Koenigswald *et al*., 1994; von Koenigswald & van Kolfschoten, 1996),
- cement in the re-entrant angles,
- T4 and T5 widely confluent,
- depending on the age of the populations, a shallow or absent BRA3; and the neck of the head of the anteroconid complex tends to be narrow (fig. 3).

Most of the remains from Barranco León and Fuente Nueva 3 show dark coloration, and in many cases they are fractured and relatively fragile. In the absence of a detailed taphonomic study, this is interpreted as being a consequence of diagenetic processes in acid environments. It is significant that the remains come from layers showing the dark coloration characteristic of high organic matter content, which would have been responsible for the acidification of the environment. The sample from Fuente Nueva 3 and Barranco León consists of 132 m1 and 32 M3.

The material under study from Gran Dolina was recovered in the course of a drilling carried out at the site during the 1990s (Cuenca-Bescós *et al.,* 1995, 1999). Material from more than one level of Gran Dolina was studied (TD 4B, TD 5b, TD 5a, TD 6-3, TD 6-2 and TD 6-1). The total number of remains from Gran Dolina is 364 m1 and 28 M3.

The sample from Vallparadis used in this study is made up of 22 m1. It corresponds to remains recovered between 2005 and 2007 (Martinez *et al*., 2010).

Finally, as regards the remains studied from La Boella, the sediment is very poor in microfaunal remains, and the few remains that are recovered tend to be highly fractured. Normally only remnants of enamel are recovered. For this reason, the sample used in this study was restricted to just two complete m1 recovered during the 2010 campaign.

5 - RESULTS

As the chronology of Fuente Nueva 3 includes that of Barranco León and in the light of the fact that they occur within the same geological context, the samples from these two sites were grouped together.

The data were arranged in accordance with the available physical datings, from oldest to youngest: Barranco León and Fuente Nueva 3, Gran Dolina TD 4B, Gran Dolina TD 5b, Gran Dolina TD 5a, Gran Dolina TD 6-3, Vallparadis, Gran Dolina TD 6-2, Gran Dolina TD 6-1 and La Boella.

The results show a reduction in the percentage of individuals with the *Mimomys* ridge over the evolution of the species and changing values for the percentage of the population with the enamel islet, with the maximum values associated with the oldest sites (Barranco León and Fuente Nueva 3). The enamel islet on M3 only occurs in populations older than 1 Ma (Barranco León and Fuente Nueva 3), whereas the enamel islet on m1 and the *Mimomys* ridge are retained until at least 0.78 Ma (fig. 4 and tab. 1).

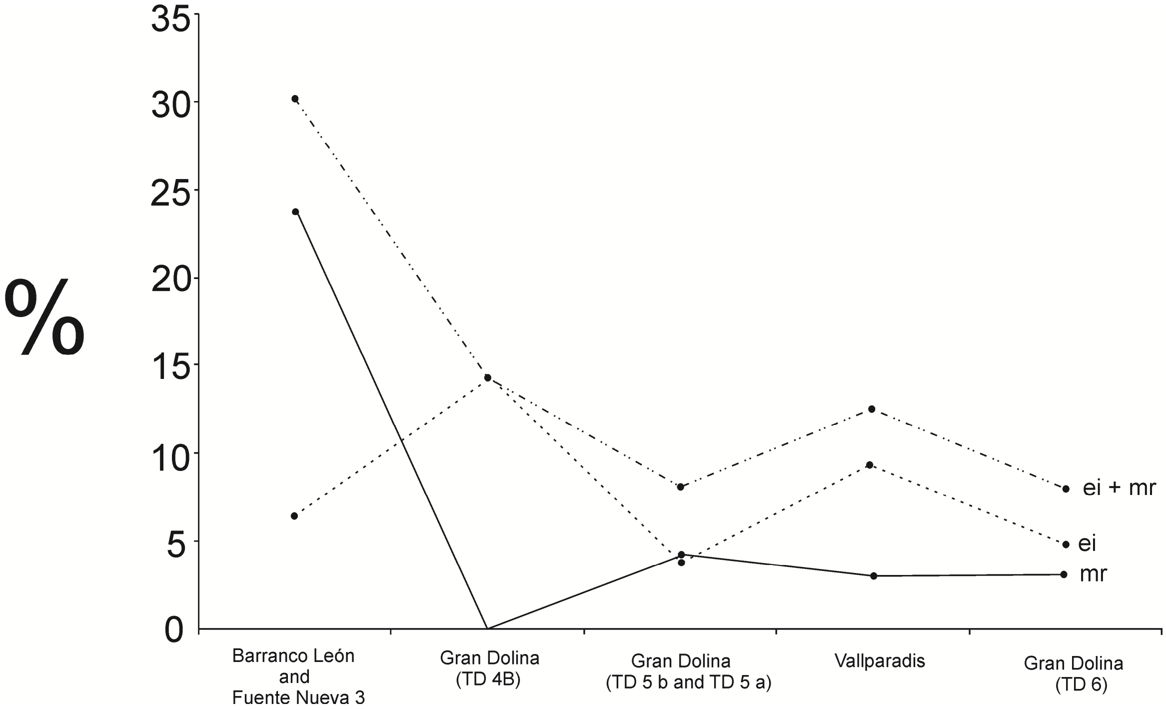

Figure 4. Percentage of the population with m1 ancestral characters. **ei**: enamel islet; **mr**: *Mimomys* ridge.

	Barranco León and Fuente Nueva 3	Gran Dolina (TD 4B)	Gran Dolina (TD 5b and TD 5a)	Vallparadis	Gran Dolina (TD 6)	La Boella
% ei	6.3	14.2	3.86	9.37	4.8	50
% Mr	23.8	0	4.24	3.12	3.2	50
% ei + Mr	30.15	14.2	8.1	12.5	8	100
M3 with ei	Yes	No	No	No	No	No

Table 1. Percentages of the population with an enamel islet (**ei**), a *Mimomys* ridge (**mr**), archaic characters (**ei + mr**) and the presence of enamel islet in M3 (**M3 with ei**) at the various sites. Gran Dolina encompassing a broad time interval, it is represented separately.

The SDQ index of the species for this period does not show a clear trend. It oscillates between values of 160 and 140 (fig. 5 and tab. 2).

The length and the width of m1 show a clear tendency to increase during this period, with the exception of the L values obtained from La Boella (fig. 6 and tab. 2).

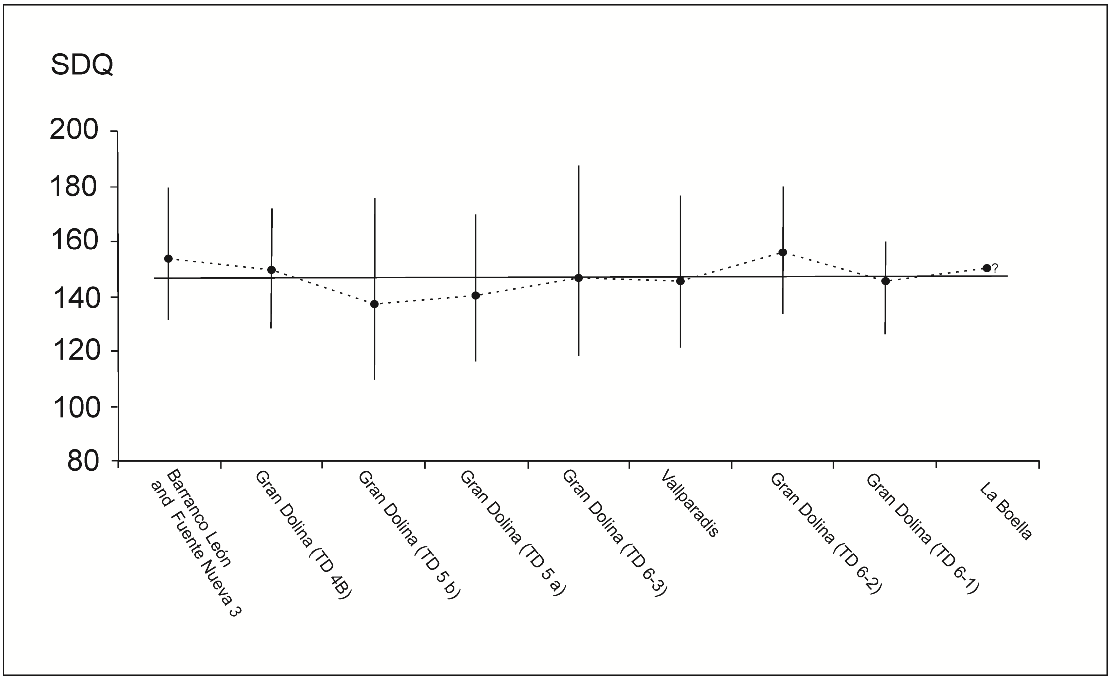

Figure 5. Variation over time of the enamel differentiation index (**SDQ**) for studied Iberian populations of *Mimomys savini*.

	Barranco León and Fuente Nueva 3	Gran Dolina (TD 4B)	Gran Dolina (TD 5b)	Gran Dolina (TD 5a)	Gran Dolina (TD 6-3)	Vallparadis	Gran Dolina (TD 6-2)	Gran Dolina (TD 6-1)	La Boella
L mean	3.23	3.34	3.46	3.48	3.43	3.48	3.58	3.61	3.31
L max	3.4	3.6	3.78	3.82	3.96	3.81	3.8	3.82	3.34
L min	2.92	3.25	3.04	3.11	2.87	3.14	3.36	3.26	3.29
W mean	1.41	1.44	1.46	1.49	1.49	1.53	1.55	1.51	1.55
W max	1.6	1.52	1.67	1.67	1.63	1.69	1.69	1.64	1.63
W min	1.26	1.31	1.27	1.26	1.23	1.46	1.41	1.38	1.48
SDQ	153.4	149.6	137.34	140.2	146.3	145.2	156.1	145.3	151.9
n	132	10	137	103	102	22	4	9	2

Table 2. Values of m1 length (**L**), m1 width (**W**) and enamel differentiation index (**SDQ**), and number of m1 (**n**) obtained for each site.

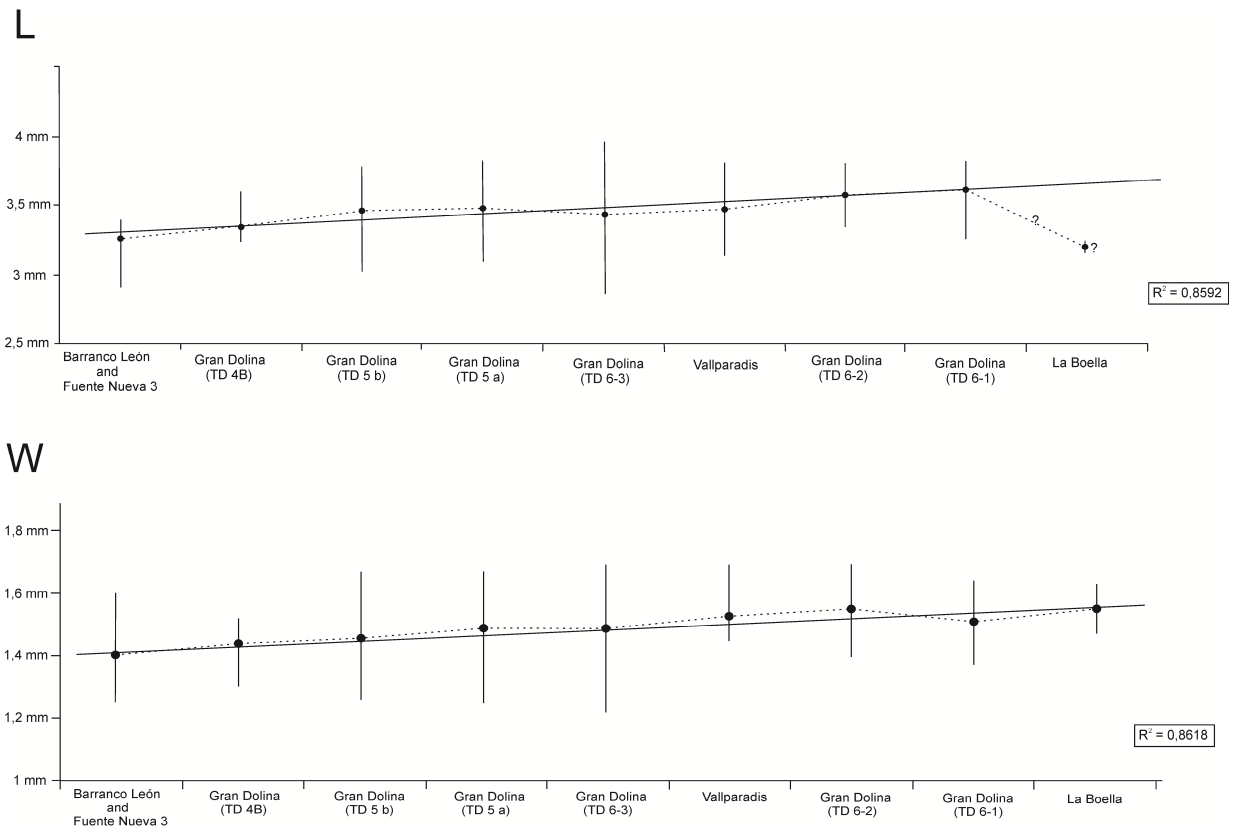

Figure 6. Trend in evolution of size. **L**: length of m1; **W**: width of m1. Both characters show increasing trends over time.

6 - DISCUSSION

6.1 - EVOLUTION OF *MIMOMYS SAVINI* IN THE IBERIAN PENINSULA

This study shows that the evolution of *Mimomys savini* in the Iberian Peninsula is characterized by a gradual disappearance of ancestral characters in the m1 (*Mimomys* ridge and enamel islet) and M3 (enamel islet) and an increase in size. The specimens from La Boella have not been taken into account for the conclusions of this paper because the sample was not large enough for the statistics to be considered reliable.

The enamel islet in M3 is not present in populations dating to less than 1 Ma, while percentage of individuals with the enamel islet in m1 shows a gradual decrease in populations. This evolutionary decrease had previously been noted for this species by Cuenca-Bescós *et al.* (1999), who ascertained that in Lower Pleistocene populations of the percentage of individuals with the enamel islet on m1 is greater than 14%, whereas it is lower in Middle Pleistocene populations. In our study these percentages are not attained, which could be due to the different size of the sample or to the inclusion of juvenile individuals in Cuenca-Bescós *et al.* (1999). Nevertheless, the tendency towards a decrease in the number of individuals with the enamel islet on m1 could be clearly made out in both cases: i.e. both the study by Cuenca-Bescos *et al.* (1999) and the present investigation. Both characteristics, the enamel islet and the *Mimomys* ridge, are lost during the individual’s life (due to wear). The reduction in the population with these characteristics indicates the gradual disappearance of these characters in the evolution of the species (given that the palaeontological population is a reflection of the original biological population).

These changes constitute a progressive process over the whole stratigraphic range of *M*. *savini* and represent an evolution from an archaic m1 (showing similarities to the m1 of *Mimomys ostramosensis*) to a m1 which - except for the presence of roots - is very similar to the first populations of *Arvicola* (*Arvicola cantianus*) studied at Meisenheim I (van Kolfschoten, 1990) and at a number of localities of the Holsteinian, Eemian, Saalian and Weichselian of central Europe and the Pannonian Basin (Heinrich, 1982). The set of evolutionary changes undergone by *Mimomys savini* represents a clear evolutionary tendency, a phenomenon noted in other arvicoline genera such as *Ondatra* (Martin, 1979), *Kislangia* and the theridomyids (Vianey-Liaud, 1972; Chaline & Sevilla, 1990; Agustí *et al.,* 1993; Chaline *et al.,* 1993).

6.2 - RELATIONSHIP BETWEEN THE GENUS *ARVICOLA* AND *MIMOMYS SAVINI*

In arvicolines the increase in size at the lineage level has been studied for *Kislangia cappetai* - *Kislangia gusii* and *Mimomys occitanus* - *Mimomys pliocaenicus* (Agustí *et al*., 1993), as well as for *Mimomys occitanus* - *Mimomys savini* (Viriot *et al.,* 1990; Néraudeau *et al*., 1995; Chaline *et al*., 1999). As the evolution of *Mimomys savini* molars involves a loss of *Mimomys*-type characters and an increase in size that brings it closer to the size and molar morphology of the earliest populations of *Arvicola*, an evolutionary relationship between these taxa (*Mimomys savini*-*Arvicola cantianus*) seems to be clear. It is corroborated by the chronology of the records and the fact that the evolution of the genus *Arvicola* also shows an increase in size. This relationship has already been suggested by many authors (e.g. Viriot *et al*., 1990; Chaline *et al*., 1999), However, the discovery of the new species *Arvicola jacobaeus* dated to approx 1.2 Ma (Cuenca-Bescós *et al*., 2010a) raises a number of doubts regarding this evolutionary relationship (fig. 7). This record showed that the first representatives of *Arvicola* are similar in age to *Mimomys savini*. As this article reveals, the dental morphological characters (SDQ index, the presence of an enamel islet and *Mimomys* ridge) and size of *M. savini* are different from those of *Arvicola jacobaeus* during this period. Among *M. savini* populations, a higher percentage of individuals than in modern ones possess an enamel islet (*Arvicola jacobaeus* does not have an enamel islet), and their average length is approximately 3.2 mm, whereas in *Arvicola jacobaeus* smallest length values are 3.48 mm (Cuenca-Bescós *et al*., 2010a). The data obtained in this study, together with the classification

of *A. jacobaeus*, thus force us to reconsider the evolutionary relationship between *Mimomys savini* and *Arvicola*.

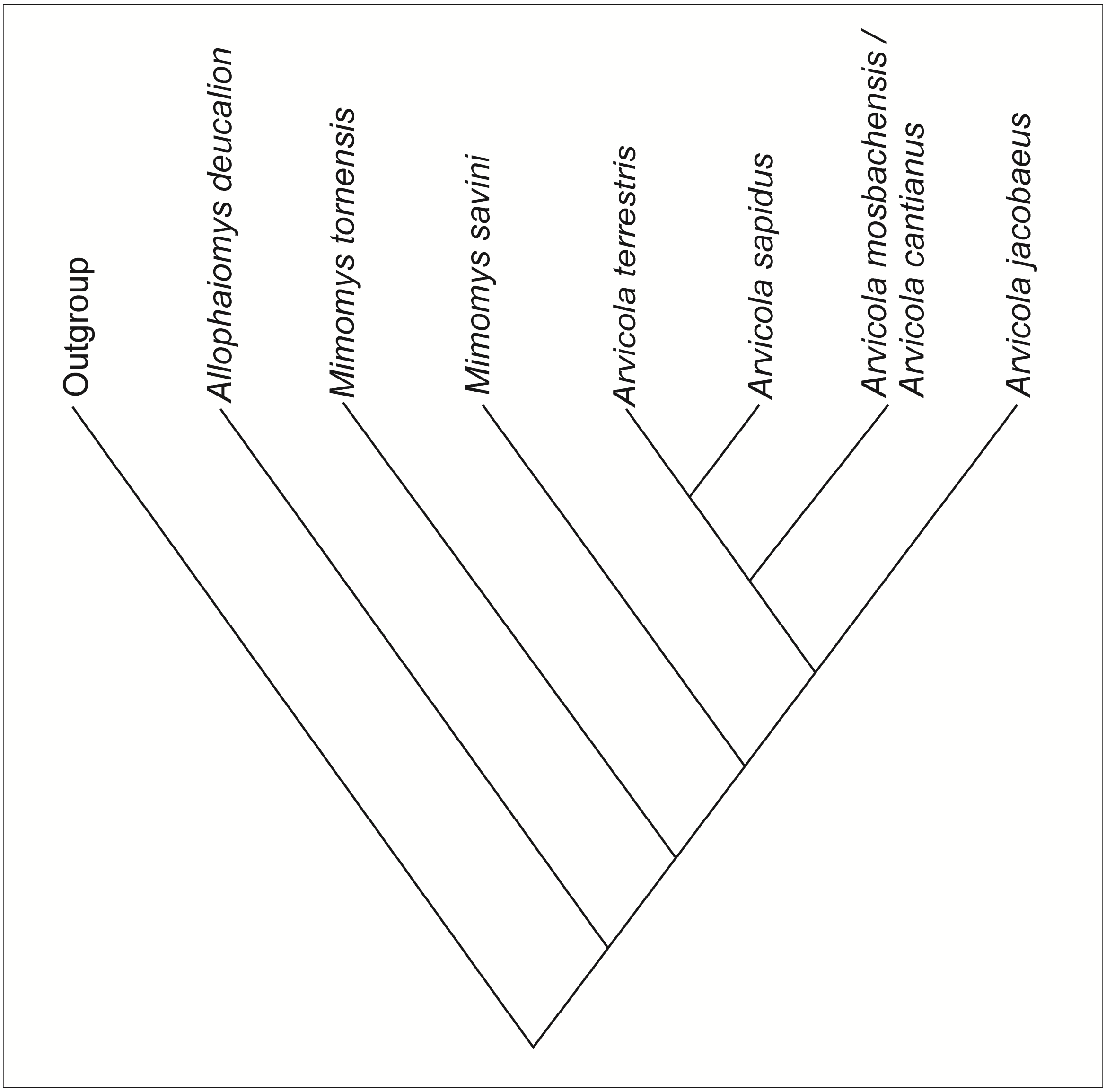

Figure 7. Cladogram of the *Mimomys-Arvicola* relationship proposed by Cuenca-Bescós *et al*. (2010a) *.*

Various alternatives explaining the relation between *Mimomys* and *Arvicola* have been proposed. Chaline & Sevilla (1990) and Horàcek (1990) argue that *Mimomys savini* gave rise to *Arvicola terrestris*. Rabeder (1981) proposes that the origin of *Arvicola sapidus* can be traced to *Mimomys savini*, whereas *Arvicola terrestris* would be the evolutionary descendant of *Mimomys milleri*. By contrast, Ruiz Bustos (1999) proposes the existence at 1.6 Ma of the species *Arvicola deucalion*, an ancestor of *Mimomys tornensis*. This theory raises a problem, because *Arvicola deucalion* is considered as a synonym of *Allophaiomys deucalion* by most authors who also uphold the phylogenetic relationship between these two species, *Mimomys tornensis* - *Allophaiomys deucalion* (Rabeder, 1981; Garapich & Nadachowski, 1996; Chaline *et al*., 1999), or at least between *Mimomys* sp. and *Allophaiomys deucalion*. This phylogenetic relationship between *Mimomys tornensis* and *Allophaiomys deucalion* is defended by Chaline & Sevilla (1990), who also suggest that *Mimomys savini* is the ancestor of *Arvicola*.

As mentioned above, the increase in size during the evolution of *Mimomys savini* also occurs in *Arvicola*. Additionally, the morphological similarities between the two taxa would imply a phylogenetic relationship between them.

When the SDQ values obtained in this study are compared with those from various populations of *Arvicola* throughout Europe (fig. 8), both *Arvicola jacobaeus* and the oldest populations of *Arvicola cantianus* display similar values to those of *Mimomys savini*. Moreover, the most modern populations of *Mimomys savini* (Gran Dolina TD 6-2, TD 6-1 and Voigtstedt) show a tendency towards a reduction in this index, which is continued in *Arvicola* populations up to recent times.

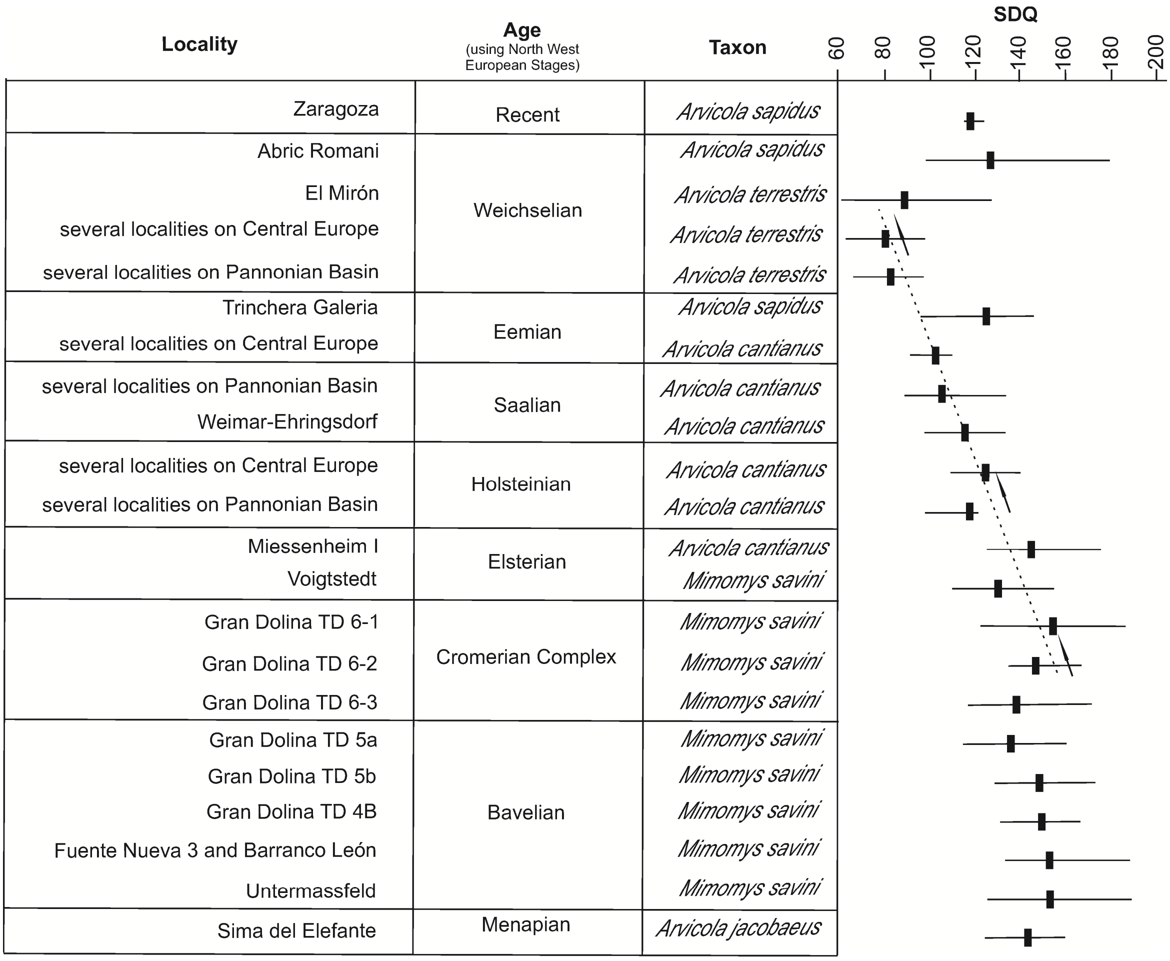

Figure 8. Comparison of various populations of *Mimomys savini*, *Arvicola cantianus*, *Arvicola sapidus*, *Arvicola terrestris* and *Arvicola jacobaeus***.** Sima del Elefante (Cuenca-Bescós *et al.*, 2010a), Untermassfeld (Maul *et al.*, 1998), Fuente Nueva 3, Barranco León, Gran Dolina TD 4B, TD 5b, TD 5a, TD 6-3, TD 6-2 and TD 6-1 (this study), Voigtstedt (Maul *et al.*, 1998), Meisenheim I (Kolfschoten, 1990), localities in the Pannonian Basin, Central Europe and Weimar-Ehringsdorf (Heinrich, 1982), Trinchera Galeria (Atapuerca) (Cuenca-Bescós *et. al.*, 2010a), El Mirón (Cantabria), Abric Romani (Tarragona), and finally current data from populations in Zaragoza (Cuenca-Bescós *et. al.*, 2010a). A decreasing trend in SDQ starts in late populations of *Mimomys savini* and continues in *Arvicola* ones.

The continuous evolution of this character would be an indicator that *Mimomys savini* is the ancestor of *Arvicola cantianus*, as proposed by Chaline *et al.* (1999). Taking into account that the youngest populations of *M. savini* have length and SDQ values similar to the earliest *A. cantianus* populations, both species follow the same evolutionary tendency for these characters (Abbassi & Desclaux, 1996; Escudé *et al*., 2008a, 2008b), the morphology of their m1 is similar, and they are only clearly distinguished by the absence of roots.

7 - CONCLUSIONS

In the Iberian Peninsula, *Mimomys savini* displays clear evolutionary tendencies: the successive reduction or loss of archaic characters in stratigraphically consecutive samples, such as the enamel islet on M3, which is only present in populations older than 1 Ma, and the enamel islet and the *Mimomys* ridge on m1.

In the course of its evolution, this species also undergoes an increase in size. The only character that seems not to follow a clearly directed evolutionary tendency in *M*. *savini* is the SDQ value, which only shows oscillatory variations.

The occurrence of *Arvicola jacobaeus* during similar periods to *Mimomys savini* requires the assumption of a common ancestor shared by *Mimomys savini* and the genus *Arvicola*, as already argued by Cuenca-Bescós *et al.* (2010a). However, this paper has demonstrated that the youngest populations of *Mimomys savini* show a tendency towards a decrease in the SDQ index, which is continued by the oldest *Arvicola* populations. The evolution of this character supports *Mimomys savini* as a possible ancestor of the *Arvicola* genus, as proposed by Chaline *et al*. (1999), or at least of *Arvicola cantianus*. However, the origin of *Arvicola jacobaeus* still remains unexplained.

Everything seems to indicate that two groups with different origins have been classified as *Arvicola*: on the one hand *Arvicola jacobaeus*, which shares a common ancestor with *Mimomys savini*, and on the other hand *Arvicola cantianus* and descendants, whose ancestor would be *Mimomys savini*.

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REFERENCES

Abbassi, M., Desclaux, E., 1996. *Arvicola* Lacépède, 1799 (*Rodentia, Mammalia*) de quatre sequences du sud-est de la France et de Ligurie datant de la fin du Pléistocène moyen et du début du Pléistocène supérieur. *Quaternaire*, 7 (1), 29-37.

Agustí, J., 1986. Synthèse biostratigraphique du plio-pleistocène de Guadix-Baza (Province de Granada, Sud-Est de l'Espagne). *Geobios*, 19 (4), 505-510.

Agustí, J., Arbiol, S., Martín Suárez, E., 1987. Roedores y Lagomorfos (Mammalia) del Pleistoceno inferior de Venta Micena (depresión de Guadix-Baza, Granada). *Paleontologia i Evolució, Memòria especial*, 1, 95-107.

Agustí, J., Castillo, C., Galobart, A., 1993. Heterochronic evolution in the late pliocene-early pleistocene arvicolids of the Mediterranean area. *Quaternary International*, 19, 51-56.

Agustí, J., Blain, H.-A., Furió, M., De Marfá, R., Santos-Cubedo, A., 2010. The early Pleistocene small vertebrate succession from the Orce region (Guadix-Baza Basin, SE Spain) and its bearing on the first human occupation of Europe. *Quaternary International*, 223-224,162-169.

Berger, G.W., Pérez-González, E., Carbonell, E., Arsuaga, J.L., Bermúdez De Castro, J.-M., Ku, T.-L., 2008. Luminescence chronology of cave sediments at the Atapuerca paleoanthropological site, Spain. *Journal of Human Evolution*, 55 (2), 300-311.

Bermúdez De Castro, J.M., Arsuaga, J.L., Carbonell, E., Rosas, A., Martinez, I., Mosquera, M., 1997. A hominid from lower Pleistocene of Atapuerca, Spain: Possible ancestor to Neanderthals and modern humans. *Science*, 276 (5317), 1392-1395.

Carbonell, E., Bermúdez De Castro, J.M., Parés, J.M., Pérez- González, A., Cuenca-Bescós, G., Ollé, A., Mosquera, M., Huguet, R., Van der Made, J., Rosas, A., Sala, R., Vallverdú, J., García, N., Granger, D.E., Martinón-Torres, M., Rodríguez, X.P., Stock, G.M., Vergès, J.M., Allué, E., Burjachs, F., Cáceres, I., Canals, A., Benito, A., Díez, C., Lozano, M., Mateos, A., Navazo, M., Rodríguez, J., Rosell, J., Arsuaga, J.L., 2008. The first hominin of Europe. *Nature*, 452 (7186), 465-469.

Chaline, J., Sevilla, P., 1990. Phyletic gradualism and developmental heterochronies in a European Plio-Pleistocene *Mimomys* linage (Arvicolidae, Rodentia). *In* O. Fejfar & W.-D. Heinrich (eds.), *International Symposium on the Evolution, Phylogeny and Biostratigraphy of Arvicolids, Rohanov, May 1987*. Geological Survey, Prague, 85-98.

Chaline, J., Laurin, B., Brunet-Lecomte, P., Viriot, L., 1993. Morphological trends and rates of evolution in arvicolids (Arvicolidae, Rodentia): Towards a punctuated equilibria/disequilibria model. *Quaternary International*, 19, 27-39.

Chaline, J., Brunet-Lecomte, P., Montuire, S., Viriot, L., Courant, F., 1999. Anatomy of the arvicoline radiation (Rodentia): palaeogeographical, palaecoecological history and evolutionary data. *Annales Zoologici Fennici*, 36 , 239-267.

Cuenca-Bescós, G., Laplana, C., Canudo J.I., 1995. Los Arvicólidos (Rodentia, Mammalia) de los niveles inferiores de Gran Dolina (Pleistoceno Inferior, Atapuerca, Burgos, España). *Revista Española de Paleontología*, 10 (2), 202-218.

Cuenca-Bescós, G., Laplana, C., Canudo, J.I., 1999. Biochronological implications of the Arvicolidae (Rodentia, Mammalia) from the Lower Pleistocene hominid-bearing level of Trinchera Dolina 6 (TD6, Atapuerca, Spain). *Journal of Human Evolution*, 37 (3-4), 353-373.

Cuenca-Bescós, G., García, N., 2007. Biostratigraphic succession on the Early and Middle Pleistocene mammal faunas of the Atapuerca cave sites (Burgos, Spain). *Courier Forschungsinstitut Senckenberg*, 259, 99-110.

Cuenca-Bescós, G., Agustí, J., Lira, J., Melero, M., Rofes, J., 2010a. A new species of water vole from the Early Pleistocene of Southern Europe. *Acta Palaeontologica Polonica*, 55 (4), 565-580.

Cuenca-Bescós, G., Rofes, J., López-García, J.M., Blain, H.-A., De Marfá, R.J., Galindo-Pellicena, M.A., Bennásar-Serra, M.L., Melero-Rubio, M., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2010b. Biochronology of Spanish Quaternary small vertebrate faunas. *Quaternary International*, 212 (2), 109-119.

Daams, R., Freudenthal, M., 1988. Synopsis of the Dutch-Spanish collaboration program in the Neogene of Calatayud-Teruel Basin. 1976-1986. *Scripta Geologica, Special Issue*, 1, 3-18.

Duval, M., 2008. *Evaluation du potentiel de la méthode de datation par Résonance de Spin Electronique (ESR) appliquée aux gisements du Pléistocène inférieur : étude des gisements d'Orce (bassin de Guadix-Baza, Espagne) et contribution à la connaissance des premiers peuplements de l'Europe*. Thèse de Doctorat, Muséum national d'Histoire naturelle, Paris, 522 p.

Duval, M., Aubert, M., Hellstrom, J., Grün, R., 2011. High resolution LA-ICP-MS mapping of U and Th isotopes in an Early Pleistocene equid tooth from Fuente Nueva-3 (Orce, Andalusia, Spain). *Quaternary Geochronology*, 6 (5), 458-467.

Escudé, E., Montuire, S., Desclaux, E., 2008a. Variabilité morphologique de l'espècie *Arvicola cantiana* (Arvicolinae, Rodentia) du Pléistocène moyen au Pléistocène Supérieur de France et de Liguire (Italie). *Quaternaire*, 19 (1), 31-41.

Escudé, E., Montuire, S., Desclaux, E., Quéré, J.-P., Renvoisé, E., Jeannet, M., 2008b. Reappraisal of 'chronospecies' and the use of *Arvicola* (Rodentia, Mammalia) for biochronology. *Journal of Archaelogical Science*, 35 (7), 1867-1879.

Falguères, C., Bahain, J.-J., Yokoyama, Y., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., Bischoff, J.L., Dolo, J.M., 1999. Earliest humans in Europe: the age of TD6 Gran Dolina, Atapuerca, Spain. *Journal of Human Evolution*, 37 (3-4), 343-352.

Fejfar, O., Heinrich, W.-D., 1980. Zur biostratigraphischen Abgrenzung und Gliederung des kontinentalen Quartärs in Europa anhand von Arvicoliden (Mammalia, Rodentia). Časopis pro Mineralogii a Geologii, 25(2), 185−189.

Fejfar, O., Heinrich, W.-D., Lindsay, E.H., 1998. Updating the Neogene Rodent biochronology in Europe. *Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen Toegepast Natuurwetenschappelijk Onderzoek*, 60, 533-554.

Garapich, A., Nadachowski, A., 1996. A contribution to the origin of *Allophaiomys* (Arvicolidae, Rodentia) in Central Europe: the relationship between *Mimomys* and *Allophaiomys* from Kamyk (Poland). *Acta Zoologica Cracoviensia*, 39 (1), 179-184.

Garcia, J., Martínez, K., Carbonell, E., 2011. Continuity of the first human occupation in the Iberian Peninsula: Closing the archaeological gap. *Comptes Rendus Palevol*, 10 (4), 279-282.

Heinrich, W.-D., 1978. Zur biometrischen Erfassung eines Evolutiontrends bei *Arvicola* (Rodentia, Mammalia) aus dem Pleistozän Thüringens. *Säugetierkundliche Informationen*, 1(2), 3-21.

Heinrich, W.-D., 1982. Zur Evolution und Biostratigraphie von *Arvicola* (Rodentia, Mammalia) im Pleistozän Europas. *Zeitschrift für Geologische Wissenschaften*, 10, 683-735.

Heinrich, W.-D., 1987. Neue Ergebnisse zur Evolution und Biostratigraphie von *Arvicola* (Rodentia, Mammalia) im Quartär Europas. *Zeitschrift für Geologische Wissenschaften*, 15, 389-406.

Horàcek, I., 1990. On the context of Quaternary arvicolid evolution: changes in community development. *In* O. Fejfar & W.-D. Heinrich (eds.), *International Symposium on the Evolution, Phylogeny and Biostratigraphy of Arvicolids, Rohanov, May 1987*. Geological Survey, Prague, 201-222.

Jánossy, D., 1986. *Pleistocene vertebrate faunas of Hungary*. Akadémiai Kiadó, Budapest, 208 p.

Madurell-Malapeira, J., Minwer-Barakat, R., Alba, D.M., Garces, M., Gomez, M., Aurell-Garrido, J., Ros-Montoya, S., Moya-Sola, S., Berastegui, X., 2010. The Vallparadís section (Terrassa, Iberian Peninsula) and the latest Villafranchian faunas of Europe. *Quaternary Science Reviews*, 29 (27-28), 3972-3982.

Markova, A.K., 1982. *Pleistotsenovye gryzuny Russkoi ravniny* [Pleistocene Rodents of the Russian Plain]. Nauka, Moscow, 184 p. [in Russian]

Markova, A.K., 2004. Pleistocene mammal faunas of Eastern Europe. *In* V.N. Konishchev & G.A Safyanov (eds.), *Structure, dynamics and evolution of natural geosystems*. Gorodets, Moscow, 583-597.

Martin, L.D., 1979. The biostratigraphy of arvicoline rodents in North America. *Transactions of the Nebraska Academy of Sciences*, 7, 91-100.

Martínez, K., Garcia, J., Carbonell, E., Agustí, J., Bahain, J.-J., Blain, H.-A., Burjachs, F., Cáceres, I., Duval, M., Falguères, C., Gómez, M., Huguet, R., 2010. A new Lower Pleistocene archeological site in Europe (Vallparadís, Barcelona, Spain). *Proceeding of the National Academy of Sciences*, 107 (13), 5762-5767.

Martínez-Navarro, B., Turq, A., Agustí, J., Oms, O., 1997. Fuente Nueva 3 (Orce, Granada, Spain) and the first human occupation of Europe. *Journal of Human Evolution*, 33 (5), 611-620.

Masini, F., Sala, B., 2007. Large and small mammal distribution patterns and chronostratigraphic boundaries from the Late Pliocene to the Middle Pleistocene of the Italian peninsula. *Quaternary International*, 160 (1), 43-56.

Maul, L., Masini, F., Abbazzi, L., Turner, A., 1998. The use of different morphometric data for absolute age calibration of some South and Middle European arvicolid populations. *Palaeontographia Italica*, 85, 111-151.

Maul, L.C., 2002. The Quaternary small mammal faunas of Thuringia (Central Germany). *In* R.A. Meyrick, D.C. Schreve (eds.), *The Quaternary of Central Germany (Thuringia and surroundings)*. Quaternary Research Association, London, 79-96.

Minwer-Barakat, R., Madurell-Malapeira, J., Alba, D., Aurell-Garrido, J., Esteban-Trivigno, S., Moyà-Solà S., 2011. Pleistocene rodents from the torrent de Vallparadis section (Terrassa, northeastern Spain) and biochronological implications. *Journal of Vertebrate Paleontology*, 31 (4), 849-865.

Néraudeau, D., Viriot, L., Chaline, J., Laurin, B., Van Kolfschoten, T., 1995. Discontinuity in the Plio-Pleistocene Eurasian water vole lineage. *Palaentology*, 38 (1), 77-85.

Oms, O., Parés, J.M., Martínez-Navarro, B., Agustí, J., Toro, I., Martínez Fernández, G., Turq, A., 2000. Early human occupation of Western Europe: Paleomagnetic dates of two paleolithic sites in Spain. *Proceeding of the National Academy of Sciences*, 97 (19), 10666-10670.

Oms, O., Anadón, P., Agustí, J., Julià, R., 2011. Geology and chronology of the continental Pleistocene archeological and paleontological sites of the Orce area (Baza basin, Spain). *Quaternary International*, 243 (1), 33-43.

Parés, J.M., Pérez-González, A., 1995. Paleomagnetic age for hominid fossils at Atapuerca archaeological site, Spain. *Science*, 269 (5225), 830-832.

Rabeder, G., 1981. Die Arvicoliden (Rodentia, Mammalia) aus dem Pliozän und dem älteren Pleistozän von Niederösterreich. *Beiträge zur Paläontologie von Österreich*, 8, 1-373.

Rekovets, L., 1994. *Melkie mlekopitayushchie Antropogena yuzhnoy chaste vostochnoi Evropy* [Small mammals from the Anthropogene of the southern part of East Europe]. Naukova Dumka, Kiev, 371 p. [in Russian]

Ruiz Bustos, A., 1999. The role of the water voles (*Arvicola*, Rodentia) in the Quatenary. *Estudios Geologicos*, 55 (1-2), 89-95.

Saladié, P., Vallverdú, J., Bennàsar, L.L., Cabanes, D., Mancha, E., Menéndez, L., Blain, H.-A., Ollé, A., Mosquera, M., Vilalta, J., Cáceres, I., Exposito, I., Esteban, M., Huguet, R., Rosas, A., Solé, A., López-Polín, L., Garcia, A.B., Martínez, B., Carbonell, E., Capdevila, R., 2008. Resultats preliminars del nivell 2 del sondeig al Centre de Convencions del barranc de la Boella. *Cota Zero*, 23, 13-19.

Stuart, A.J., 1981. A comparison of the Middle Pleistocene Mammal Faunas of Voigstedt (Thuringia, GDR) and West Runton (Norfolk, England). *Quartärpaläontologie*, 4, 155-163.

Topachevskij, V.A., Skorik, A.F., 1977. *Gryzuny rannetamanskoj fauny tiligul'skogo razreza* [Rodents of Early Tamanian faunas of the Tiligul section]. Naukovo Dumka, Kiev, 250 p. [in Russian]

Toro, I., Martínez-Navarro, B., Agustí, J. (eds.), 2010 - *Ocupaciones Humanas en el Pleistoceno inferior y medio de la Cuenca de Guadix-Baza* Arqueología. Serie Monografías, .Junta de Andalucía & Consejería de Cultura, Seville, 582 p.

Vallverdú, J., Saladié, P., Bennàsar, L.L., Cabanes, D., Mancha, E., Menéndez, L., Blain, H.-A., Ollé, A., Vilalta, J., Mosquera, M., Cáceres, I., Exposito, I., Esteban, M., Huguet, R., Rosas, A., Solé, A., López-Polin, L., Martinell, J., Barbo, A., Martínez-Navarro, B., Agustí, J., Ros, S., Carbonell, E., Capdevila, R., 2008. El barranc de la Boella de la Canonja (Tarragonès) revisitat en la intervenció arqueològica preventiva de l’any 2007. *Tribuna d’Arqueologia*, 2008-2009, 7-28.

Van der Meulen, A.J., 1973. Middle Pleistocene smaller mammals from the Monte Peglia (Orvieto, Italy), with special reference to the phylogeny of Microtus (Arvicolidae, Rodentia). *Quaternaria*, 17, 1-144.

Van Kolfschoten, T., 1990. The evolution of the mammal fauna in the Netherlands and the Middle Rhine area (Western Germany) during the late Middle Pleistocene. *Mededelingen Rijks Geologische Dienst*, 43 (3), 1-69.

Vianey-Liaud, M., 1972. Un cas de parallélisme intragénérique : l’évolution du genre *Therydomys* (Rodentia, Theridomyidae) à l’Oligocène moyen. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences. Série D, Sciences Naturelles*, 174 (1), 1007-1010.

Viriot, L., Chaline, J., Schaaf, A., 1990. Quantification du gradualisme phylétique de *Mimomys occitanus* à *Mimomys ostramosensis* (Arvicolidae, Rodentia) à l'aide de l'analyse d'images. *Comptes Rendus de l'Académie des Sciences. Série 2, Mécanique, Physique, Chimie, Sciences de l'Univers, Sciences de la Terre*, 310 (II), 1755-1760.

Von Koenigswald, W., Sander, M.P., Leite, M.B., Mörs, T., Santel, W., 1994. Functional symmetries in the schmelzmuster and morphology of rootless rodent molars. *Zoological Journal of the Linnean Society*, 110 (2), 141-179.

Von Koenigswald, W., Van Kolfschoten, T., 1996. The *Mimomys*-*Arvicola* boundary and the enamel thickness quotient (SDQ) of Arvicola as stratigraphic markers in the Middle Pleistocene. *In* C. Turner (ed.), *The early Middle Pleistocene in Europe: proceedings of the SEQS Cromer Symposium, Norwich, 3-7 September 1990*. A.A. Balkema, Rotterdam, 211-226.

CAPÍTULO 2

EVOLUCIÓN DEL TAMAÑO DE *MIMOMYS SAVINI* EN EL PLEISTOCENO INFERIOR DEL SUROESTE DE EUROPA Y POSIBLES IMPLICACIONES BIOCRONOLÓGICAS

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MIMOMYS SAVINI SIZE EVOLUTION IN THE EARLY PLEISTOCENE OF SOUTH-WESTERN EUROPE AND POSSIBLE BIOCHRONOLOGICAL IMPLICATIONS

Iván Lozano-Fernández [a, *], Gloria Cuenca-Bescós [b], Hugues-Alexandre Blain [a], Juan Manuel López-García [c] and Jordi Agustí [d]

[a] IPHES, Institut Català de Paleoecologia Humana i Evolució Social, C/ Escorxador s/n, E-43003 Tarragona, Spain, and Area de Prehistoria, Universitat Rovira i Virgili (URV), Avinguda de Catalunya 35, E-43002 Tarragona, Spain.

[b] Área de Paleontología-EIA-IUCA, Dpto. Ciencias de la Tierra, Facultad de Ciencias, Universidad de Zaragoza, E-50009 Zaragoza, Spain.

[c] Gruppo di Ricerca di Paleobiologia e Preistoria, Dipartimento di Studi Umanistiche, Università degli Studi di Ferrara, C.so Ercole I d'Este 32, I-44121 Ferrara, Italy.

[d] ICREA. IPHES, Institut Català de Paleoecologia Humana i Evolució Social, C/ Escorxador s/n, E-43003 Tarragona, Spain.

[*] Corresponding author E-mail address: ilozano@iphes.cat

ABSTRACT

Over the course of their evolutionary history, some species of mammals have undergone variations in size, with a general trend towards increased morphometry. This effect can be seen very clearly in the fossil record of rodents because their high rate of reproduction that generates a high fossil record, which allows this phenomenon to be studied in detail. Furthermore, the rapid geographic distribution of rodents means that their evolution can be studied on a continental scale.

If a relationship can be established between the size of individuals and their chronology, and the trend that governs a species' increase in size can be determined, then the chronologies of different sites can be estimated based on the size of the individuals of that species recovered at those particular sites. The correlation between morphometric data of micromammal fossils and age was already used by other authors.

This article studies the rate at which the length of the first lower molar (m1) of *Mimomys savini* (a species of Palearctic arvicoline present in Europe between approximately 1.8 and 0.6 Ma ago) increased over the course of its evolution in Iberian Peninsula (south-western Europe). Because this increase in length occurred at a constant rate, a direct relationship can be established between average length of m1 and chronology, which allows us to set numerical dates to Pleistocene sites containing *Mimomys savini* remains.

Keywords: Biochronology, Early Pleistocene, Iberian Peninsula

1- INTRODUCTION

The existence of evolutionary trends has held the interest of the scientific community ever since the theory of evolution was first put forward (Darwin, 1859). An evolutionary trend is essentially a directional change within a single lineage or parallel changes in several lineages or, in other words, a situation in which several lineages undergo the same types of changes. To be considered an evolutionary trend, this directional change has to be maintained over time and may affect one or more taxa within the lineages in which it occurs.

The origin of these evolutionary trends in nature or their causes remains a topic of debate for which there have classically been two different schools of thought: orthogenesis (a biological hypothesis according to which life has an innate tendency to evolve in a unilinear fashion due to some ‘guiding force’, whether it be internal or external [Marsh, 1874]) and directional selection or orthoselection (a particular modality of natural selection [Simpson, 1944]). In any case, starting from the basic assumption that species evolve in a chain-like fashion and are constantly changing, the existence of evolutionary trends is a completely logical consequence of evolution, and is patently obvious in the fossil record (Simpson, 1944).

The genus *Mimomys* was present in Europe during the Pliocene that disappeared at the beginning of the Middle Pleistocene (about 4 to 0.6 Ma ago [Chaline and Laurin, 1986; Chaline and Sevilla, 1990; Chaline et al., 1993; Agustí, 1995]). The first representative of this genus in Europe was *Mimomys occitanus* and the last was *Mimomys savini* (Chaline and Laurin, 1986; Agustí, 1995). Features of the evolution of the lineage include an increase in size, the

appearance of cement in the re-entrant angles in molars and a progressive increase in crown height (Agustí, 1995). The last representative of the genus *Mimomys* (*Mimomys savini*) lived from about 1.8 to about 0.6 Ma ago (Fejfar et al., 1998) and exhibits a series of evolutionary trends such as a progressive increase in size (Viriot et al., 1990; Chaline et al., 1999; Lozano-Fernández et al., 2013), a gradual loss of 'mimomyian' traits (mimomys-ridge and enamel islet in m1) and variations in tooth enamel thickness (Koenigswald, 1973; 1982; Heinrich, 1978; Koenigswald and Kolfschoten, 1996; Cuenca-Bescós et al., 1999; Lozano-Fernández et al., 2013).

This work investigates the correlation between size and age of *Mimomys savini* at the Gran Dolina site in order to ascertain whether this trend followed a linear pattern over time and, if so, to evaluate its use as a method for the numerical dating of archaeological sites. If validated, this method would constitute yet another tool with which to study the first human populations in Europe on the Iberian Peninsula (Bermúdez et al., 1997; Martínez-Navarro et al., 1997; Oms et al., 2000; Carbonell et al., 2008 Toro et al., 2010) during the late Early Pleistocene.

2 - GEOLOGICAL AND CHRONOLOGICAL SETTING

This study was conducted based on data obtained from the *Mimomys savini* remains recovered during the excavation carried out at the Gran Dolina site (Atapuerca, Spain) between levels TD4 and TD6 in the 1990's.

The Sierra de Atapuerca is ~1080 m above sea level, dominating the now-flat landscape of the Castilian grain-growing plains irrigated by the River Arlanzón near the village of Ibeas de Juarros, located 14 km east of the city of Burgos (Fig. 1).

The Gran Dolina is one of the caves of the Railway Trench of the Atapuerca Hill. The Trinchera Dolina represents one of the longest stratigraphic sequences at Atapuerca. It comprises 18–19 m of surface filling which is divided into 11 stratigraphic levels. Nine of these levels (TD3–TD11, numbered from bottom to top) are rich in faunal remains and artefacts (Carbonell et al., 1995, 1999; Bermúdez de Castro et al., 1997, Cuenca-Bescós et al., 2005, Rodríguez et al., 2011).

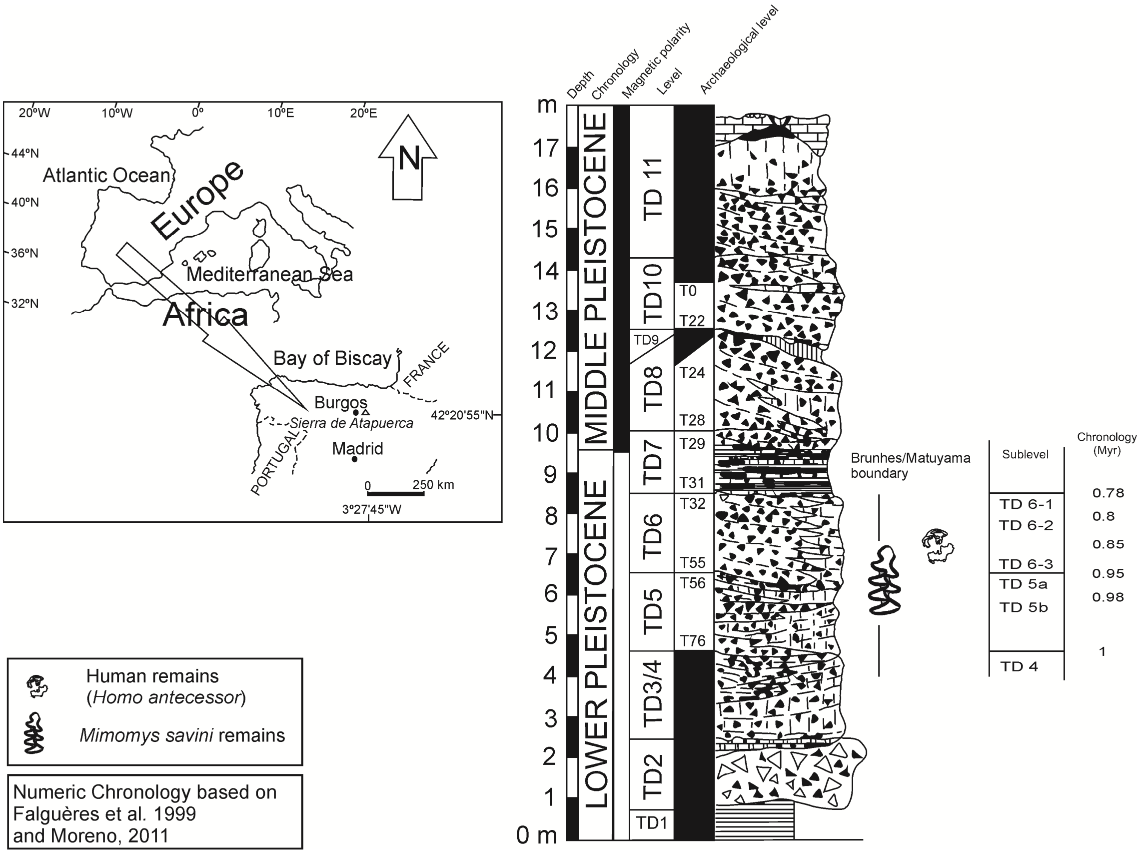

Figure 1. Geographical location of the Sierra de Atapuerca archaeological sites complex, and Stratigraphic log of Gran Dolina (Modified from Parés and Pérez-González, 1999).

The archaeological and paleontological excavations in Gran Dolina, or Trinchera Dolina (TD), cave have been conducted every year since 1976, and have revealed a long, culturally and paleontologically rich sequence dated at between ca. 1 Ma and 250 Ka ago by means of biostratigraphy, electron spin resonance, electron spin resonance on optically bleached quartz dating, U-series, thermoluminescence, infrared-stimulated-luminescence analysis, and paleomagnetic dating (Cuenca-Bescós et al., 2011; Moreno, 2011 [Fig. 1]).

3 - MATERIAL AND METHODS

We studied 372 lower first molars (m1), all of them from adult individuals (Table 1). In other words, these molars all had defined areas free of enamel on the occlusal plane and fully developed roots (Fig. 2). In other published works, both variations in the length and the width of the occlusal plane of the m1 have been used as a reflection of size-related changes among individuals from different paleontological populations (Viriot et al.,1990; Chaline et al., 1999; Lozano-Fernández et al., 2013). The size of the individuals in this study was interpreted based on the length (L) of the occlusal plane (Fig. 2).

Once these data were recorded, the average length and the standard deviation were calculated to define the populations of the different sublevels of TD4 and TD6 containing m1s of *Mimomys savini*. This allowed us to characterize each population by a point (average length) and by the associated dispersal. Finally, the populations were put in order and arranged chronologically for each sublevel and each population was assigned to the average chronology between the bottom and the top of the sublevels in order to detect any possible patterns

in how these animals evolved in terms of size. We assumed a maximum error in chronology of ± 120 ka, corresponding to the error in the dating at the top of TD6-1 and an average error of ± 110 ka based on the datings performed by Falguères et al. (1999) and Moreno (2011).

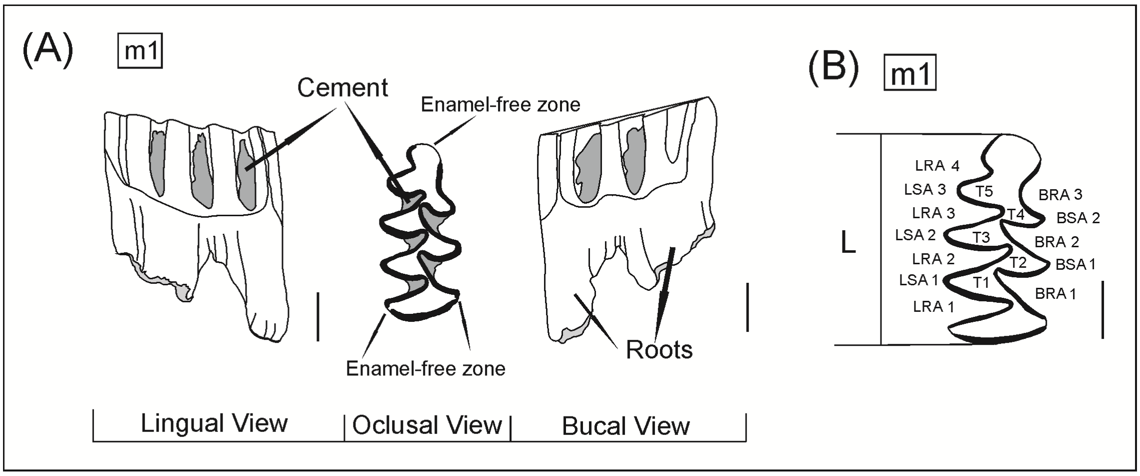

Figure 2. A: Schema of the buccal, labial and occlusal views of a right inferior, first lower molar of *Mimomys savini* and its different parts. The characteristics defining adult specimens are indicated (enamel-free zones and presence of roots). Scale = 1 mm.

B: Nomenclature of the parts distinguished in the occlusal plane of an m1, and the measurement used in this study: **L** refers to the length; **T1**, **T2**, **T3**, **T4** and **T5** are the various triangles that make up the tooth; **LRA** refers to the various lingual re-entrant angles, and **BRA** to the buccal re-entrant angles; **LSA** refers to the lingual salient angles, and **BSA** to the buccal salient angles (modified from Meulen, 1973; Heinrich, 1978; Rabeder, 1981).

4 - RESULTS

Of the various sublevels in the sequence between TD4 and TD6, m1s of *Mimomys savini* were only found at the top of TD4, in TD5a, TD5b, TD6-3, TD6-2 and TD6-1. Although remains from *M. savini* were recovered from sublevels TD5c and TD5d, m1s from adult individuals were not among them.

The first relevant piece of data we found is that the standard deviation of the different populations always ranges between 0.14 and 0.17. In other words, the distribution values are similar for the populations and therefore the populations are comparable (Table 1).

Sublevel	Age (Myr)	Length m1 (mm)				
			Min	Mean	Max	sd
TD6-1	0.8	9	3,26	3,62	3,82	0,17
TD6-2	0.83	10	3,36	3,59	3,81	0,17
TD6-3	0.86 (Mean error	101	2,87	3,43	3,96	0,17
TD5a	0.96 ±120 kyr)	103	3,11	3,49	3,82	0,14
TD5b	0.99	137	3,04	3,46	3,78	0,14
TD4	1.01	12	3,22	3,43	3,68	0,14

Table 1. Measurements for the first lower molar of *Mimomys savini* in the different sublevels of Gran Dolina cave. The age of the levels corresponds to the mean between the upper and lower ages of each level given by Falguères et al. (1999) and Moreno (2011). Abbreviations: **n**: number of remains per level; **sd**: standard deviation.

The relationship between size and chronology can only be approximated by means of a linear, logarithmic or exponential trend. When the populations are put in chronological order, a clear increase in size can be seen over time. However there is no constant acceleration or deceleration in this increase, which rules out exponential and logarithmic models as possible approaches to the evolutionary trend of this trait. That leaves the linear trend model (linear regression) as the best fit for approximating the reality of the situation.

Using all of the data from the TD4–TD6 sequence, the trend towards size increase over the course of time is governed by the equation:

$$Y = 838.86X – 3847.6$$

(where X corresponds to the length of the occlusal plane of the m1s in millimetres and Y to the chronology in ka).

The correlation coefficient and the determination coefficient for this relationship are not statistically representative ($r = 0.7555$; $R^2 = 0.5708$) due to the value obtained in level TD6-3 (Fig. 3). Level TD6-3 contains a higher diversity of microvertebrate species as well as central European fauna input (Cuenca-Bescós et al., 2011; Cuenca-Bescós and García, 2007) and a possible mixture of *M. savini* populations from Iberian Peninsula with populations from Central Europe, which may be responsible for this anomalous value.

Obviating this value, the trend towards size increase over the course of time is governed by the equation:

$$Y= 1178.6X – 5064.3$$

(where X corresponds to the length of the occlusal plane of the m1s in millimetres and Y to the chronology in ka).

In this case, both the correlation coefficient and the determination coefficient are statistically representative ($r = 0.9958$; $R^2 = 0.9917$), which allows us to conclude that the trend towards an increase in size among *Mimomys savini* is linear and governed by the equation $Y= 1178.6X – 5064.3$ (figure 3)**.**

Therefore, using this equation allows us to assign numerical dates based on the size of the *M. savini* remains recovered as long as the standard deviation of individual size in the population is equal to or less than 0.17. We assume a margin of error of ± 120 ka for these dates because this is the maximum error for the datings of the sequence used to obtain the relationship between size and chronology for this species, as well as the margin at which the error generated by the regression analysis is less than 1%, thereby encompassing everything within ± 120 ka.

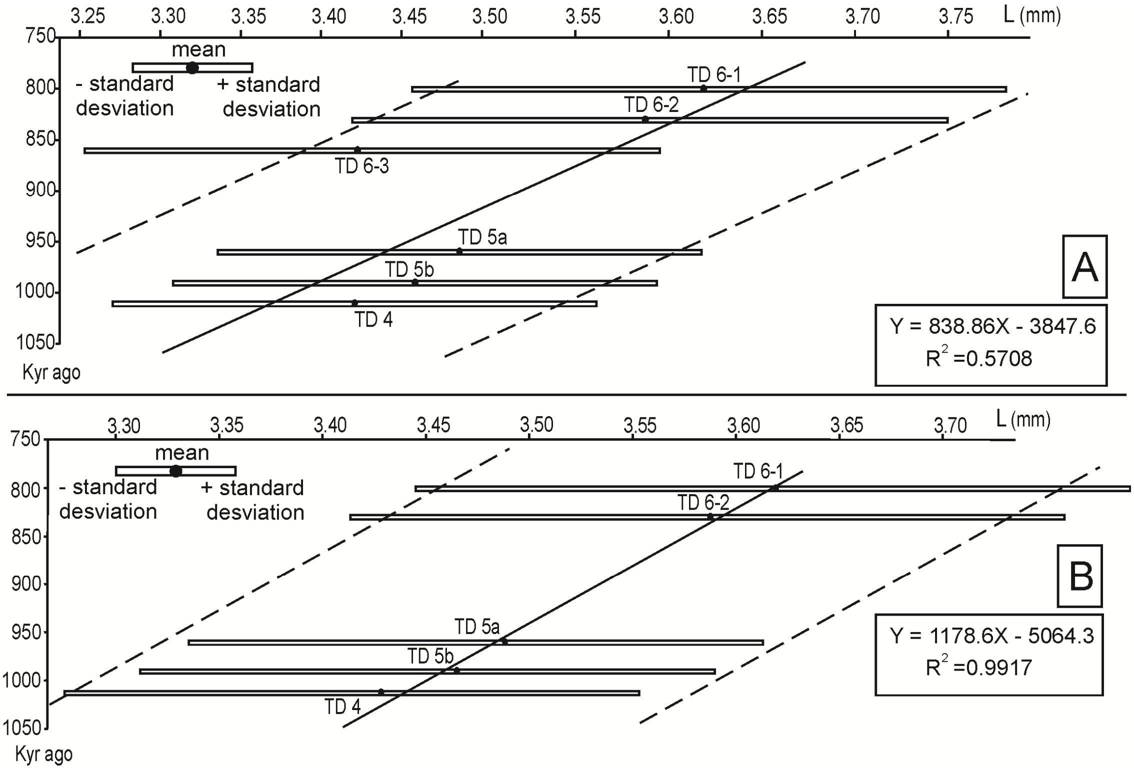

Figure 3. Relationship between the length of the m1 of *Mimomys savini* from Gran Dolina cave and the chronology according to the age of each level given by Falguères et al. (1999) and Moreno (2011).

In graph **A** we observe the presence of one population with values deviating significantly from the tendency line (TD 6-3) and resulting in a relatively low determination coefficient (R^2=0.5708). In graph **B** we observe that when TD 6-3 is removed, we obtain a tendency with a very good determination coefficient (R^2=0.9917).

The populations of each level are characterized by the mean length (**L**) and its associated standard deviation.

In populations with a standard deviation in individual size of more than 0.17, because they are outside of the range used in this study, the difference may

affect the central size trend in the sample. To correct this possible uncertainty, the margin of error was governed by the formula:

$$\pm (120+(f(x+\sigma)-f(x)) \text{ kyr with } f(x)= 1178.6X - 5064.3$$

(where X corresponds to the average length of the occlusal plane of the m1s of the population in millimetres and σ to the standard deviation).

5 - DISCUSSION

Both in central Europe and on the Iberian Peninsula, *M. savini* exhibits the same evolutionary trends, including an increase in size (Maul, 1990; Viriot et al., 1990; Maul et al., 1998 a,b; Chaline et al., 1999; Lozano-Fernández et al., 2013). However, the Iberian individuals (those studied here) are systematically larger (as seen in the comparison of values obtained in this work with those previously published (Maul, 1990; Maul et al., 1998 a,b). This is explained by a separate evolution of the populations of Iberian Peninsula and Central Europe. This phenomenon would have been similar to what was seen in islands where different to the evolutive rhythms of the continents is observed (Millien, 2006).

Foster (1964) found that in island systems the body size of micromammals tends to be larger. This is due to their isolation from the continent, which means there are fewer predators and less interspecies competition (Heaney, 1978; Sondaar, 1991; Damuth, 1993; Dayan and Simberloff, 1998). Lister (1996), Sondaar (1991) and Millien (2006, 2011) observed that what actually caused these characteristics of less competition and less predation was first of all the acceleration of the trend towards a larger size and subsequently the stability of the rate of growth, which resulted in larger individuals on islands than on the continents.

It is possible that the size difference of the individuals observed within Central Europe and Iberian Peninsula was also due to the issue that the populations of the Iberian Peninsula have suffered the acceleration-stabilization process of evolutive tendency when separating from the central European populations.

The evolutive tendency of the size increase is also observed in the *Arvicola* genus (Agadzhanyan, 2012; Maul et al., 2000), descendent of *M. savini* [Chaline and Sevilla, 1990; Viriot et al., 1990; Chaline et al., 1999]). If we compare the data published on *Arvicola* of the Iberian Peninsula with the data of Central Europe, it can be observed that the individuals of Iberian Peninsula are bigger for the similar chronologies of Central Europe (Sesé and Villa, 2008; López-García, 2008; López-García et al., 2011; Agadzhanyan, 2012; Maul et al., 2000) as it occurs with *M.savini*.

The specific characteristic of the islands which facilitates this acceleration in the evolutionary trends of micromammal species is isolation from the rest of the continent. In our case, the Iberian Peninsula is isolated to a certain extent by the biogeographical barrier of the Pyrenees. This mountain chain that separates the peninsula from the rest of the continent certainly also separated the continental populations of *M. savini* from the Iberian populations of the species. Therefore, a phenomenon similar to the island-effect phenomenon occurred on the Iberian Peninsula.

Putting the Atapuerca data in order by numerical datings (Falguères et al., 1999; Cuenca-Bescós et al., 2011; Moreno, 2011) reveals that all of the levels except TD6-3 show a highly pronounced linear trend in size increase. In other

words, if it were not for TD6-3, the conclusion could be drawn that there is a direct relationship between the size of the individuals and their chronology. Millien and Damuth (2004) found that the island effect has a more marked impact than climatic variations on the evolution of rodents and therefore on their increase in size. Because the incidence of the island effect does not change over time, what we have here is a highly pronounced linear evolutionary trend in size increase, or in other words, a direct relationship between the size of the individual animals of a population and their chronology.

Upon studying level TD6-3 in detail in an attempt to understand this apparently anomalous result, it became clear that in TD6-3 the evolutionary trend of the species would have been affected by environmental circumstances: an increase in the biodiversity of micromammals (Cuenca-Bescós et al., 2011) and lower average annual temperatures (Blain et al., 2009, 2012). The increase in biodiversity would have meant an increase in interspecies competition and the resulting deceleration in the pace of evolutionary changes (Heaney, 1978; Sondaar, 1991; Damuth, 1993; Dayan and Simberloff, 1998), but would not have changed the evolutionary trend itself. Meanwhile, lower temperatures may have favoured an increase in size (Bergman, 1847) or, on the other hand, they may have slowed down the evolution of the size of individual animals due to a reduction in trophic resources, which would have affected the pace of growth. But in no case would the evolutionary trends have been reversed. Therefore, the explanation for this decrease in size in the individuals recovered from TD6-3 must lie in a combination of these two factors.

As seen with large mammals, in the period corresponding to the transition between TD5 and TD6-3 the Iberian Peninsula was affected by the addition of new European fauna to the pre-existing fauna on the peninsula (Cuenca-Bescós and García, 2007; Cuenca-Bescós et al., 2011), which was very likely due to the decrease in temperatures experienced in the region at the time. This is reflected in the increased biodiversity of micromammals in level TD6-3. The appearance of more northern species also meant the arrival of populations of *M. savini* from central Europe, where individuals were smaller (Maul, 1990 and Maul et al., 1998 a, b). So, the decrease in size of the individuals in TD6-3 may be the result of the mixing of populations. Subsequently, the system returned to species diversity values similar to those found in TD5a and TD5b, going back to the evolutionary trend seen prior to TD6-3. This process of reacceleration and return to a stable pace in evolutionary trends would have happened relatively quickly, as in island effect processes (Sondar, 1991; Lister, 1996), which is why we see the values for TD6-2 return to fit within the theoretical trend.

6 - CONCLUSIONS

The significance of conducting this study using data from the Gran Dolina stratigraphic sequence lies in the fact that this is a relatively continuous, well-dated sequence in which ecological and climatic variations have been exhaustively studied (Cuenca-Bescós et al., 1999, 2001, 2005, 2011; Blain et al., 2008, 2009, 2012). This allows us to determine whether external factors may have had an influence on the evolutionary trends documented in this species.

The stratigraphic sequence studied here, TD4-TD-6 of Gran Dolina (Atapuerca, Spain), has yielded evidence of the existence of an evolutionary trend towards increased size in the species *M. savini* in south-western Europe. This trend is very close to a linear model with very good correlation and determination coefficients and can therefore be defined as linear. This means that this characteristic can be used to extrapolate chronologies outside of the TD4–TD6 range using the size of individuals to provide datings in the chronological framework between the FAD and LAD of *M. savini*.

The application of this method can provide clarity in the dating of the sites that have diverse opinions about the chronologies as it is the case for the sites of Orce (Cuenca Guadix-Baza, Granada, Spain).

This chronological tool yields results with error ranges similar to radiometric methods, but it is relatively faster and less destructive to the sample. Furthermore, it can be used as a complement to radiometric methods to increase the precision of datings.

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REFERENCES

Agadzhanyan, A. K., 2012. Timing of the *Mimomys-Arvicola* transition on the Russian Plain. Quaternary international 271, 38-49.

Agustí, J., 1995. Ritmo y modalidades de la evolución. Innovación y Ciencia 4, 70-79.

Bergmann, C., 1847. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. Göttinger Studien 3, 595-708.

Bermúdez de Castro, J. M., Arsuaga, J.L., Carbonell, E., Rosas, A., Martínez, I., Mosquera, M., 1997. A homínid from Lower Pleistocene of Atapuerca, Spain: possible ancestor to Neanderthals and modern humans. Science 276, 1392-1395.

Blain, H. -A., Bailon, S., Cuenca-Bescós, G., 2008. The Early-Middle Pleistocene palaeoenvironmental change based on the squamate reptile and amphibian proxies at the Gran Dolina site, Atapuerca , Spain. Palaeogeography, Palaeoclimatology, Palaeoecology 261, 172-192.

Blain, H. -A., Bailon, S., Cuenca-Bescos, G., Arsuaga, J. L., Bermudez de Castro, J.M., Carbonell, E., 2009. Long-term climate record inferred from early-middle Pleistocene amphibian and squamate reptile assemblages at the Gran Dolina Cave, Atapuerca, Spain. Journal of Human Evolution 56, 55-65.

Blain, H. -A., Cuenca-Bescós, G., Lozano-Fernández, I., López-García, J.M., Ollé, A., Rosell, J., Rodríguez, J., 2012. Investigating the Mid-Brunhes Event in the Spanish terrestrial sequence. Geology 40, 1051-1054.

Carbonell, E., Bermúdez de Castro, J.M., Arsuaga, J.L., Díez, J.C., Rosas, A., Cuenca, G., Sala, R., Mosquera, M., Rodríguez, J., 1995. Lower Pleistocene hominids and artifacts from Atapuerca-TD6 (Spain). Science 269, 826-830.

Carbonell, E., Esteban, M., Nájera, A. M., Mosquera, M., Rodríguez, X. P., Ollé, A., Sala, R., Vergès, J. M., Bermúdez de Castro, J. M., Ortega, A. I., 1999. The Pleistocene site of Gran Dolina, Sierra de Atapuerca, Spain: a history of the archaeological investigations. Journal of Human Evolution 37, 313-324.

Carbonell, E., Bermúdez de Castro, J. M., Parés, J.M., Pérez-González, A., Cuenca-Bescós, G., Ollé, A., Mosquera, M., Huguet, R., van der Made, J., Rosas, A., Sala, R., Vallverdú, J., García, N., Granger, D.E., Martinón-Torres, M., Rodríguez, X.P., Stock, G.M., Vergés, J.M., Allué, E., Burjachs, F., Cáceres, I., Canals, A., Benito, A., Díez, C., Lozano, M., Mateos, A., Navazo, M., Rodriguez, J., Rosell, J., Arsuaga, J.L., 2008. The first Hominin of Europe. Nature 452, 465-469.

Chaline, J., Brunet-Lecomte, P., Montuire, S., Viriot, L., Courant, F., 1999. Anatomy of the arvicoline radiation (Rodentia): palaeogeographical, palaecoecological history and evolutionary data. Annales zoologici fennici 36, 239-267.

Chaline, J., Laurin, B., 1986. Phyletic gradualism in a European Plio-Pleistocene *Mimomys* lineage (Arvicolidae, Rodentia). Paleobiology 12, 203-216.

Chaline, J., Laurin, B., Brunet-Lecomte, P., Viriot, L., 1993. Morphological trends and rates of evolution in arvicolids (Arvicolidae, Rodentia): Towards a punctuated equilibria/disequilibria model. Quaternary International 19, 27-39.

Chaline, J., Sevilla, P., 1990. Phyletic gradualism and developmental heterochronies in a European Plio-Pleistocene *Mimomys* linage (Arvicolidae, Rodentia): International Symposium on the Evolution, Phylogeny and Biostratigraphy of Arvicolids, p. 85-98.

Cuenca-Bescós, G., García, N., 2007. Biostratigraphic sucession of the early and middle Pleistocene mammal faunas of the Atapuerca cave sites (Burgos, Spain). Courier Forschunginstitut Senckenberg 259, 99-100.

Cuenca-Bescós, G., Canudo, J.I., Laplana. C., 2001. La séquence des rongeurs (Mammalia) des sites du Plèistocen infèrieur et moyen d'Atapuerca (Burgos, Espagne). L'Antropologie 105, 115-130.

Cuenca-Bescós, G., Laplana, C., Canudo, J.I., 1999. Biochronological implications of the Arvicolidae (Rodentia, Mammalia) from the Lower Pleistocene hominid-bearing level of Trinchera Dolina 6 (TD6, Atapuerca, Spain). Journal of Human Evolution 3-4, 353-73.

Cuenca-Bescós, G., Melero-Rubio, M., Rofes, J., Martínez, I., Arsuaga, J.L., Blain, H. -A., López-García, J. M., Carbonell, E., Bermúdez de Castro, J.M., 2011. The Early–Middle Pleistocene environmental and climatic change and the human expansion in Western Europe: A case study with small vertebrates (Gran Dolina, Atapuerca, Spain). Journal of Human Evolution 60, 481-491.

Cuenca-Bescós, G., Rofes, J., Garcia-Pimienta, J., 2005. Environmental change across the Early-Middle Pleistocene transition: small mammalian evidence from the Trinchera Dolina cave, Atapuerca, Spain. Geological Society, London, Special Publications 247, 277-286.

Damuth, J., 1993. Cope’s rule, the island rule and the scaling of mammalian population density. Nature 365, 748-750.

Darwin, C., 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life (1ª ed.), London: John Murray Dayan, T., Simberloff, D., 1998. Size patterns among competitors: Ecological character displacement and character release in mammals, with special reference to island populations. Mammal Review 28, 99-124.

Falguères, C., Bahain, J.J., Yokoyama, Y., Arsuaga, J. L., Bermúdez de Castro, J.M., Carbonell, E., Bischoff, J.L., Dolo, J.M., 1999. Earliest humans in Europe: the age of TD6 Gran Dolina, Atapuerca, Spain. Journal of Human Evolution 37, 343-352.

Fejfar, O., Heinrich, W. -D., Lindsay, E.H., 1998. Updating the Neogene Rodent biochronology in Europe. in T. Van Kolfschoten and P. L. Gibbard (eds.), The Dawn of the Quaternary. Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen, 60, 533–554.

Foster, J. B., 1964. The evolution of mammals on islands. Nature 202,234-235.

Heaney, L. R., 1978. Island area and body size of insular mammals: Evidence from the tri-colored squirrel (*Callosciurus prevosti*) of southeast Asia. Evolution 32, 29-44.

Heinrich, W-D., 1978. Zur biometrischen Erfassung eines Evolutionstrends bei *Arvicola* (Rodentia, Mammalia) aus dem Pleistozän Thüringens. Säugetierkundliche Informationen 2, 3-21.

Koenigswald, W. Von., 1973. Veränderungen in der Kleinsäugerfauna von Mitteleuropa zwischen Cromer und Eem (Pleistozän). Eiszeitalter und Gegenwart 23/24, 159-167.

Koenigswald, W. Von., 1982. Zum Verständnis der Morphologie der Wühlmausmolaren (Arvicolidae, Rodentia, Mammalia). Zeitschrift für Geologische Wissenschaften 10, 951-962.

Koenigswald, W. Von., Kolfschoten, T. Van., 1996. The *Mimomys–Arvicola* boundary and the enamel thickness quotient (SDQ) of *Arvicola* as stratigraphic markers in the Middle Pleistocene. In: C. Turner (ed.), Proceedings of the SEQS Cromer Symposium. Norwich/United Kingdom, The Early–Middle Pleistocene in Europe, Norwich, 211-226.

Lister, A. M., 1996. Dwarfing in island elephants and deer: Processes in relation to time of isolation. Symposia of the Zoological Society of London 69, 277-292.

López-García, J. M., 2008. Evolución de la diversidad taxonómica de los micromamíferos en la Península Ibérica y cambios Paleoambientales durante el Pleistoceno Superior [Ph.D. thesis]: Tarragona, Universitat Rovira i Virgili, 407 p.

López-García, J. M., Blain, H.-A., Cuenca-Bescós, G., Alonso, C., Alonso, S., Vaquero, M., 2011. Small vertebrates (Amphibia, Squamata, Mammalia) from the late Pleistocene-Holocene of the Valdavara-1 cave (Galicia, northwestern Spain). Geobios 44, 253-269.

Lozano-Fernández, I., Agustí, J., Cuenca-Bescós, G., Blain, H.- A., López-García, J.M., Vallverdú, J., 2013. Pleistocene evolutionary trends in dental morphology of *Mimomys savini* (Rodentia, Mammalia) from Iberian Peninsula and discussion about the origin of the genus *Arvicola*. Quaternaire 24, 179-190.

Martínez-Navarro, B., Turq, A., Agustí, J., Oms, O., 1997. Fuente Nueva 3 (Orce, Granada, Spain) and the first human occupation of Europe. Journal of Human Evolution 33, 611-620.

Maul, L., 1990. Biharische Kleinsäugerfunde von Untermaßfeld, Voigtstedt und Süßenborn und ihre chronologische Stellung im Rahmen der biharischen Micromammalia-Faunen Europas. [Ph.D. thesis], Humboldt-University. Berlin, 138+20pp

Maul, L., Masini, F., Abbazzi, L., Turner, A., 1998a. The use of different morphometric data for absolute age calibration of some South and Middle European arvicolid populations. Palaeontographia Italica 85, 111-151.

Maul, L., Masini, F., Abbazzi, L., Turner, A., 1998b. Geochronometric application of evolutionary trends in the dentition of fossil Arvicolidae. In: van Kolfschoten, T. and Gibbard, P.L. (Eds.), 1998. The Dawn of the Quaternary. Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO 60, 565-572.

Maul, L., Rekovets, L., Heinrich, W.-D., Keller, T., Storch, G., 2000. *Arvicola mosbachensis* (SCHMIDTGEN 1911) of Mosbach 2: a basic sample for the early evolution of the genus and a reference for further biostratigraphical studies. Senckenbergiana lethaea 80, 129-147.

Millien, V., 2006. Morphological evolution is accelerated among island mammals. Plos Biology 4, 1863-1868.

Millien, V., 2011. Mammals evolve faster on smaller islands. Evolution 65, 1935-1944.

Millien, V., Damuth, J., 2004. Climate change and size evolution in an island rodent species: New perspectives on the island rule. Evolution 58, 1353-1360.

Moreno García, D., 2011. Datation par ESR de quartz optiquement blanchis (ESR-OB) de la région de Atapuerca (Burgos, Espagne). Application au site préhistorique de Gran Dolina (contexte karstique) et aux systèmes fluviatiles quater- naires de l'Arlanzón et l'Arlanza [Ph.D. thesis]: Tarragona, Universitat Rovira i Virgili and Paris, Muséum National d'Histoire Naturelle, 304 p.

Oms, O., Parés, J.M., Martínez-Navarro, B., Agustí, J., Toro, I., Martínez Fernández, G., Turq, A., 2000. Early human occupation of Western Europe: Paleomagnetic dates of two paleolithic sites in Spain. Proceeding of the National Academy of Science 9719, 10666-10670.

Parés, J.M., Pérez-González, A., 1995. Paleomagnetic age for hominid fossils at Atapuerca archaeological site, Spain. Science 269, 830-832.

Piras, P., Marcolini, F., Raia, P., Curcios, M.T., Kotsakis, T., 2008. Testing evolutionary stasis and trends in first lower molar shape of extinct Italian populations of *Terricola savii* (Arvicolidae, Rodentia) by means of geometric morphometircs. Journal of Evolutionary Biology 22, 179-191.

Rodríguez, J., Burjachs, F., Cuenca-Bescós, G., García, N., van der Made, J., Pérez González, A., Blain, H.-A., Expósito, I., López-García, J.M., García Antón, M., Allué, E., Cáceres, I., Huguet, R., Mosquera, M., Ollé, A., Rosell, J., Parés, J.M., Rodríguez, X.P., Díez, C., Rofes, J., Sala, R., Saladié, P., Vallverdú, J., Bennasar, M.L., Blasco, R., Bermúdez de Castro, J.M., Carbonell, E., 2011. One million years of cultural evolution in a stable environment at Atapuerca (Burgos, Spain). Quaternary Science Reviews 30, 1396-1412.

Sesé, C., Villa, P., 2008. Micromammals (rodents and insectivores) from early Late Pleistocene cave site of Bois Roche (Charente, France): Systematics and paleoclimatology. Geobios 41, 399-414.

Simpson, G. G., 1944. Tempo and Mode in Evolution: New York, Columbia University Press.

Sondaar, P. Y., 1991. Island mammals of the past. Science Progress 75, 249-264.

Toro, I., Martínez-Navarro, B., Agustí, J., (ed.). 2010. Ocupaciones Humanas en el Pleistoceno inferior y medio de la Cuenca de Guadix-Baza: Memoria Científica. Junta de Andalucía. Consejería de Cultura. E.P.G. Arqueología Monográfico. 582 p.

Viriot, L., Chaline, J., Schaaf, A., 1990. Quantification du gradualisme phylétique de *Mimomys occitanus* à *Mimomys ostramosensis* (Arvicolinae, Rodentia) à l’aide de l’analyse d’image. Comptes Rendus de l’Academie des Sciences 310, 1755-1760.

CAPÍTULO 3

DATOS BIOCRONOLÓGICOS Y PALEOAMBIENTALES INFERIDOS DE LOS MICROMAMÍFEROS DEL PLEISTOCENO INFERIOR DEL YACIMIENTO DEL BARRANC DE LA BOELLA (TARRAGONA, NORESTE DE ESPAÑA)

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BIOCHRONOLOGICAL AND PALAEOENVIRONMENTAL DATA INFERRED FROM THE EARLY PLEISTOCENE SMALL MAMMALS OF BARRANC DE LA BOELLA SITE (TARRAGONA, NORTHEASTERN SPAIN)

Iván Lozano-Fernández,*,[1] Sandra Bañuls-Cardona,[1] Hugues-Alexandre Blain,[1] Juan Manuel López-García,[2] Josep Vallverdú,[1] Jordi Agustí,[3] and Gloria Cuenca-Bescós,[4]

[1]IPHES, Institut Català de Paleoecologia Humana i Evolució Social, C/ Escorxador s/n, E- 43003 Tarragona, Spain, and Area de Prehistoria, Universitat Rovira i Virgili (URV), Avinguda de Catalunya 35, E-43002 Tarragona, Spain

[2] Sezione di Scienze Preistoriche e Antropologiche , Dipartimento di Studi Umanistici, Università degli Studi di Ferrara, C.so Ercole I d'Este 32, I-44121 Ferrara, Italy

[3]ICREA. IPHES, Institut Català de Paleoecologia Humana i Evolució Social, C/ Escorxador s/n, E-43003 Tarragona, Spain

[4]Área de Paleontología, Dpto. Ciencias de la Tierra, Facultad de Ciencias, Universidad de Zaragoza, E-50009 Zaragoza, Spain.

*Corresponding author: Iván Lozano-Fernández, E-mail: ilozano@iphes.cat

ABSTRACT

In 2007, remains of *Mammuthus meridionalis* and 334 lithic artefacts associated with these remains were recovered in level 2 of Barranc de la Boella. The presence of *Mammuthus meridionalis* dates level 2 as one of the few sites more than 700 ka in age with remains of lithic industry associated with fauna and, as such, it enables us to shed light on questions pertaining to the chronology, the palaeoecology and the biogeography of the earliest European settlements.

In this paper, the small mammals from the Barranc de la Boella site are described for the first time, with special emphasis placed on the arvicolines.

The presence of *Victoriamys chalinei* and *Mimomys savini* allows us to estimate the age of level 2. Level 2 of Barranc de la Boella site ranges between the Jaramillo subchron (1.07-0.99 Ma) and shortly after the Brunhes-Matuyama transition at 0.78 Ma, thus covering a time span of great importance for our knowledge of the earliest human occupations in western Europe.

The presence of the small-mammal species *V. chalinei*, *M. savini*, *Talpa* sp. and *Crocidura* sp. makes it possible to ascertain that the palaeoenvironment at Barranc de la Boella was dominated principally by an open humid habitat.

Keywords: *Mimomys savini*, evolutionary trends, Biochronology, Early Pleistocene, Iberian Peninsula

1 - INTRODUCTION

The existence of faunal remains at Barranc de la Boella was established in the early 20th century with the discovery of a *Mammuthus meridionalis* (Bataller, 1935; Vilaseca, 1920; Vallverdú *et al*., 2008), but it was not until 2007 that preliminary work was undertaken that led to the discovery of remains of *Mammuthus meridionalis* with lithic tools associated. Archaeological work was systematically carried out from 2007 to 2013, leading to the recovery of a large quantity of both palaeontological and archaeological remains.

In 2007, archaeological and palaeontological remains were found in levels 2 and 3 of Unit II. Level 2 has proved to be the richest, yielding 550 remains belonging to large mammals and lithic industry. These remains included two tusks, four molars, a scapula, ribs and vertebrae in anatomical semi-connection belonging to *Mammuthus meridionalis*. Various long, flat bones associated with pieces of lithic industry, which also included hammerstones, were also recovered from this level. In addition to the remains from *Mammuthus meridionalis*, in 2007 remains of cervids were also recovered, as were some bones from smaller animals (although the taxon to which they belonged has not been identified). Associated with the faunal remains from level 2, a total of 138 pieces of lithic industry were recovered, comprising cores, natural bases, flakes and flake fragments. It is noteworthy that some of the faunal remains display cut marks (Saladié *et al.*, 2008; Vallverdú *et al*., 2008).

In level 3, two tusks belonging to *Mammuthus meridionalis* and a small account of lithic industry were found in 2007 (Saladié *et al.*, 2008; Vallverdú *et al.,* 2008).

The total number of archaeological remains recovered from Unit II in 2007 was 334. These remains seem to indicate the presence of the Acheulian in Europe during the Early Pleistocene (Saladié *et al*., 2008; Vallverdú *et al*., 2008).

Rodents are one of the most stratigraphically significant groups of mammals in the European Pleistocene, because they have diversified more than other taxa over this relatively short geological time span. Arvicolines are particularly useful for biochronological correlation, because of the abundance of their remains and their rapid evolutionary rates. In addition, some voles undertook long-range and rapid migrations and may have had extensive geographical distributions, which allow interregional correlations to be made. For these reasons, arvicolines have been used to establish the biostratigraphic subdivisions of the Quaternary (Chaline, 1972; van der Meulen, 1973; Agustí, 1986; Sala and Masini, 2007; Cuenca-Bescós *et al*., 2010b; among many others).

Due to the specific habitat requirements characteristic of each species, the presence of small mammals in the fossil record allows us to infer the environment in which a particular site was formed on the basis of which of these types of fossils it contains.

This paper describes for the first time the small mammals from Unit II of the site of Barranc de la Boella, enabling us to provide a palaeoenvironmental interpretation and a more precise chronology of archaeo-palaeontological level 2 (within Unit II).

2 - GEOGRAPHICAL AND GEOLOGICAL SETTING

The site of Barranc de la Boella (Barranc de La Boella, La Boella Ravine) is situated in the north-east of the Iberian Peninsula in the province of Tarragona, near the municipality of La Canonja (Fig. 1). Two sites are currently being excavated within the ravine of Barranc de la Boella, El Forn (EF) and La Mina (LM). The stratigraphy of the ravine is divided into 6 units (Fig. 2).

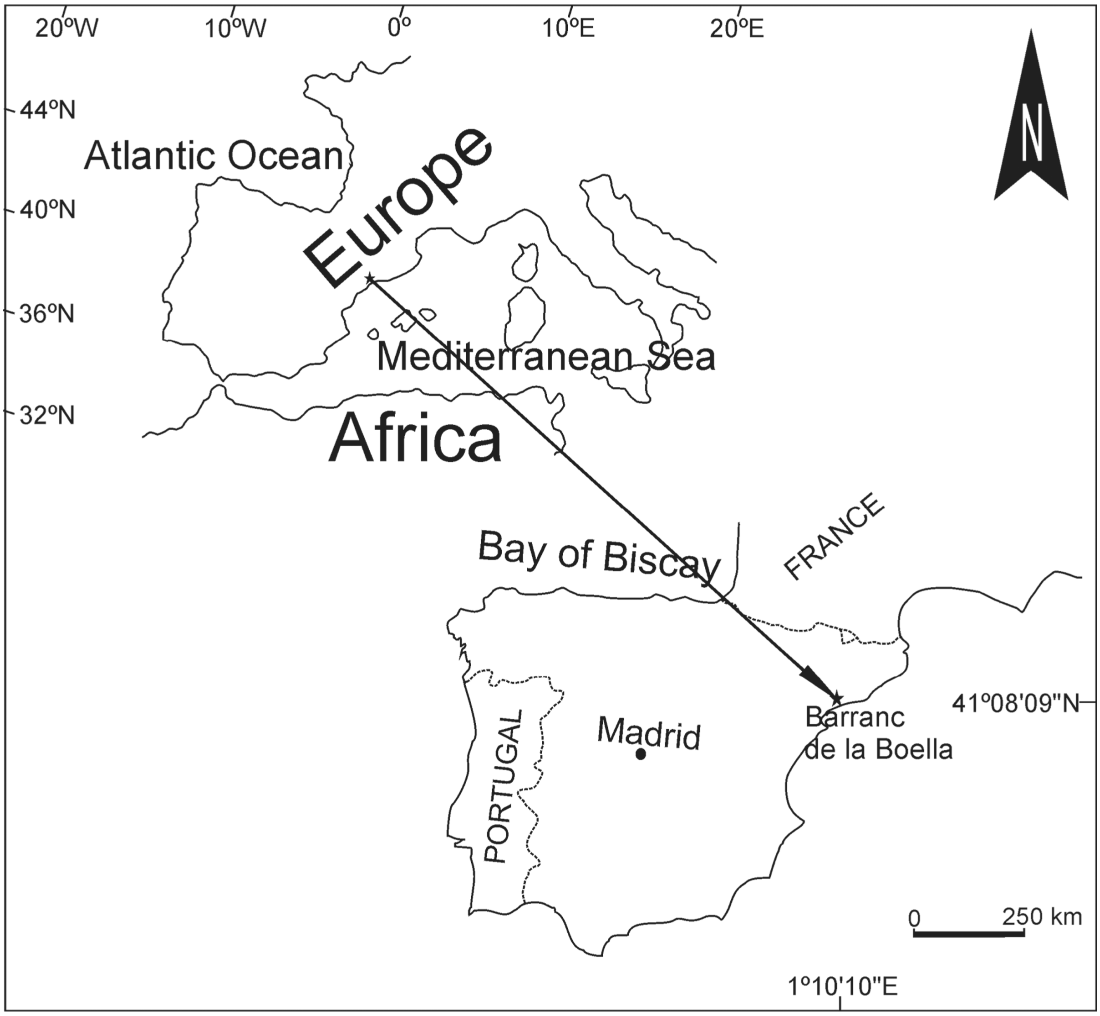

Figure 1. Geographical situation of the site of Barranc de la Boella.

The palaeo-archaeological remains are found in four levels situated within Units II and III. Level 1 is situated in Unit III, and levels 2, 3 and 4 in Unit II. Unit II is basically composed of gravels and sands, whereas Unit III is much more clayey, with sandy areas but without gravels. Of the three palaeo-archaeological levels in Unit II, level 2 displays lithological characteristics that are significantly different from the rest of the unit. This is a level of gravels with deposits consisting of sands and massive clays with low-angle cross-bedding, and in some areas clast orientation can be observed (Fig. 2).

The sedimentary facies of Unit II show a significant abundance of mass-flow deposits (sediment gravity-flow) of sand and gravel. The massive deposits show a large variety of sedimentary facies: clast and sand-matrix-supported gravels, normal and inverse grading, clast-supported and clay-matrix-supported coarse gravels, and massive sand. Among subaerial sedimentary environments, such deposits are very common in alluvial fans, and especially fan deltas (Saladié *et al*., 2008; Vallverdú *et al.,* 2008). Sediment gravity-flow deposits have been classified according to various criteria, but in fact are a final member of a continuum with fluid flows. We have thus also observed normal graded and occasional cross-bedding or imbrication in the sedimentary facies of Unit II, characteristic of fluid flow processes in the Barranc de La Boella sedimentary record. However, the record of this variety of mass and fluid flows in the stratification suggests that the sedimentary processes in fact form a type of unstable stream (Saladié *et al*., 2008; Vallverdú *et al*., 2008).

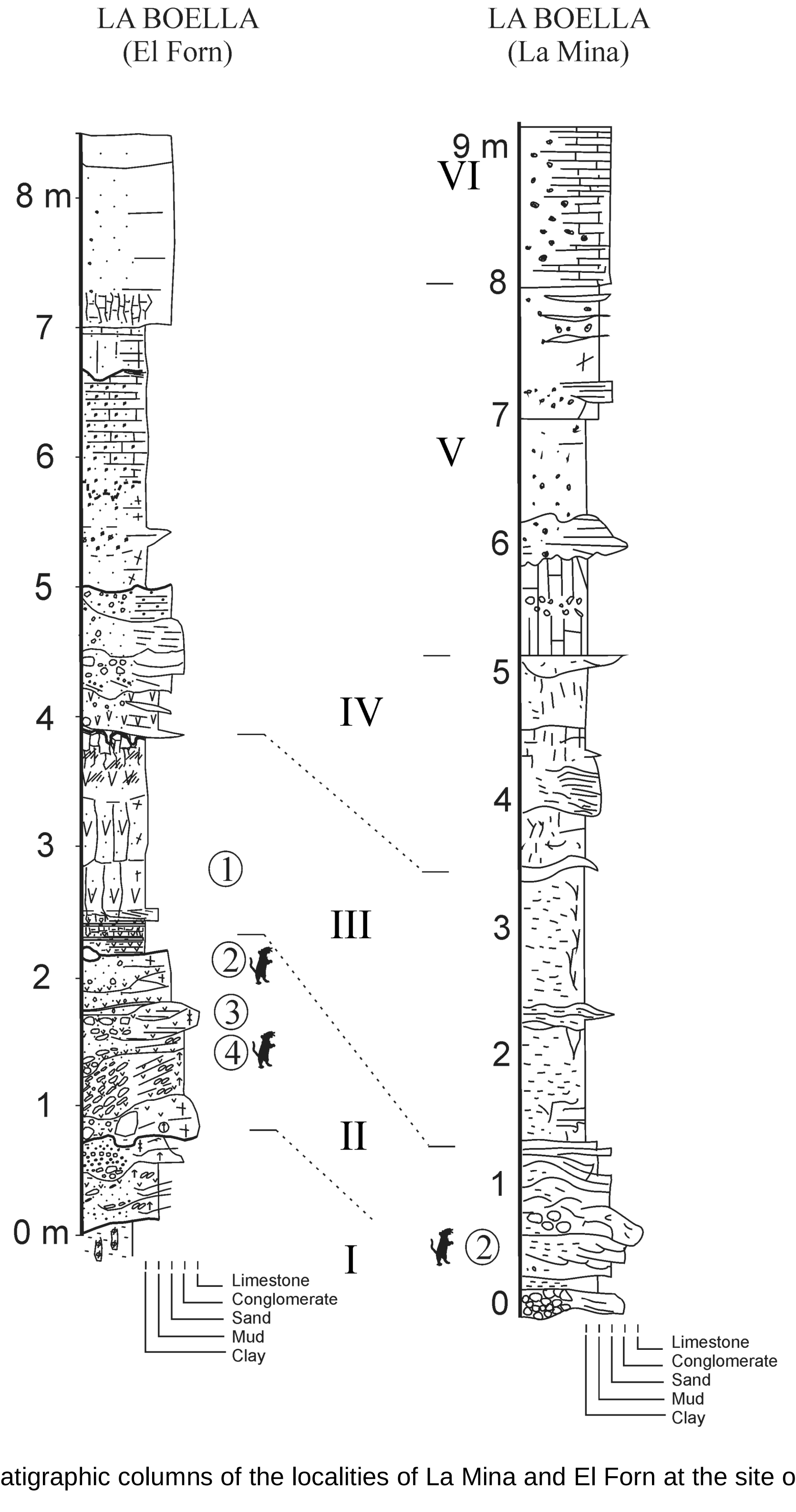

Figure 2. Stratigraphic columns of the localities of La Mina and El Forn at the site of Barranc de la Boella. The geological units are marked in Roman numerals and the palaeo-archaeological levels with a circle and a number. The rodent symbol indicates the origin of the remains within the stratigraphic columns (stratigraphic column by Josep Vallverdú).

3 - MATERIALS AND METHODS

During the excavations of Barranc de la Boella site, sediments from each differentiated level were screen-washed in order to obtain the small-vertebrate remains. The remains were recovered by water-screening the sediment with Freudenthal tables (Daams and Freudenthal, 1988). For the washing tables, mesh sizes of 5 mm, 2 mm and 0.5 mm were used. Most of the remains were extracted from the 2-mm concentrate.

Small mammals are not very abundant and only appear in level 2 and level 4 from Unit II (Fig. 2). The studied material corresponds to the remains recovered during the excavation campaigns that took place in 2007, 2008, 2011 and 2012. All the described specimens are stored in the Institut de Paleoecologia Humana i Evolució Social (IPHES, Tarragona, Spain).

The total number of fossil remains recovered is 82, 23 of which are identifiable at the species/genus level.

The nomenclature used in the descriptions of the teeth of Arvicolinae (only lower first molars have been considered) is modified from van der Meulen (1973), Heinrich (1978) and Rabeder (1981). Length and parameters a, b, and c (Fig. 3) are those proposed by van der Meulen (1973). For *M. savini*, width is modified from van der Meulen (1973), Heinrich (1978) and Rabeder (1981), as proposed by Lozano-Fernández *et al*. (2013a, 2013b).

Finally, the SDQ [enamel differentiation index (Schmelzband-Differenzierung-Quotient)] has been estimated for the m1 of *Mimomys* and *Victoriamys.* The

SDQ is the quotient of the enamel thickness in the trailing edge of each triangle and the enamel thickness in the leading edge.

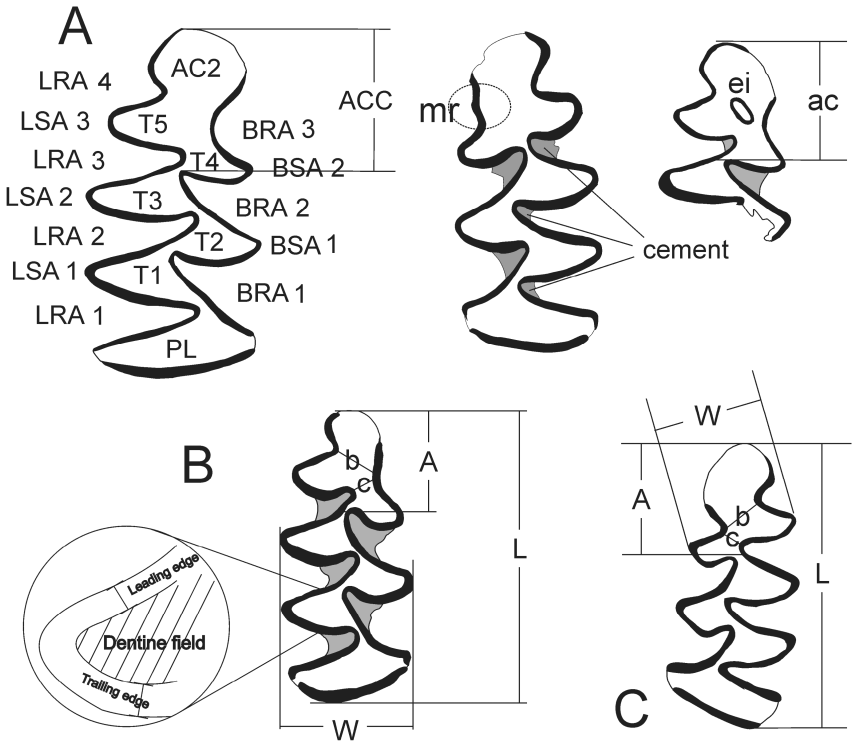

Figure 3. A: nomenclature used in the description of the first molars of the arvicolids: **T1**, **T2**, **T3**, **T4** and **T5** are the various triangles that make up the tooth; **LRA** refers to the various lingual re-entrant angles, and **BRA** to the buccal re-entrant angles; **LSA** refers to the lingual salient angles, and **BSA** to the buccal salient angles; **PL** refers to the posterior lobe; **AC2** refers to the anterior lobe; **ACC** refers to the anteroconid complex (modified from van der Meulen, 1973; Heinrich, 1978; Rabeder, 1981); **mr** refers to the mimomys-ridge; **ei** refers to the enamel islet.

B: measures used for the study and comparison of the remains of *M. savini*. **L** corresponds to the length of the molar; **W** corresponds to the width of the molar; **A** corresponds to the length of the anteroconid complex; **b** and **c** correspond to the necks of the anterior lobe (modified from van der Meulen, 1973; Heinrich, 1978; Rabeder, 1981).

C: measures used for the study and comparison of the remains of *V. chalinei*. **L** corresponds to the length of the molar; **W** corresponds to the width of the molar; **A** corresponds to the length of the anteroconid complex; **b** and **c** correspond to the necks of the anterior lobe (modified from van der Meulen, 1973).

The SDQ was calculated as:

$$SDQ = [\ \Sigma\ (teet \times 100/leet)\ ]\ /\ N$$

where N refers to the number of dentine fields of the studied tooth; teet (trailing edge enamel thickness) refers to the maximum thickness of the posterior enamel band; and leet (leading edge enamel thickness) refers to the maximum thickness of the anterior enamel band of each dentine field (Heinrich, 1978, 1987; von Koenigswald and van Kolfschoten, 1996; modified by Cuenca-Bescós *et al*., 2010).

All the measurements were taken on the occlusal plane of the molars with the image-treatment software Adobe PhotoShop CS5, using photographs from an Infinity X camera coupled to an Olympus SZ-40 binocular microscope.
This software ensures highly reliable measurements made on flat surfaces.

In order to reconstruct the palaeoenvironment, we employed the optimum habitat method (Andrews, 1990; Cuenca-Bescós *et al.,* 2005, 2012; López Antoñanzas and Cuenca-Bescós, 2002). The palaeoecological reconstruction depends on whole assemblages rather than on the presence of only one or two species. The quantitative distribution of small-mammal taxonomic categories in level 2 and level 4 of Barranc de la Boella provides information on the environment during the formation of the site. Each taxon present in level 2 and level 4 of the site of Barranc de la Boella has been assigned to a habitat in accordance with the studies carried out by Chaline (1985) and López Antoñanzas and Cuenca-Bescós (2002) (Table 1).

Level 2				
	n	MNI	Habitat	%
M. savini	10	5	Water edge	56
V. chalinei	2	2	Open humid meadow	22
Talpa sp.	1	1	Open humid meadow	11
Crocidura sp.	1	1	Open dry meadow	11

Table 1. MNI corresponds to the minimum number of individuals of each species; **n** corresponds to the total number of remains identified for each species. The habitat column corresponds to the optimum habitat for each species. The percentage column represents the minimum number of individuals of each species as a percentage of the total minimum number of individuals (i.e. the habitat percentage represented by each species).

Institutional Abbreviations—BB, Barranc de La Boella; **EF**, El Forn; **LM**, La Mina; **IPHES**, Institut de Paleoecologia Humana i Evolució Social.

Anatomical Abbreviations—ACC, anteroconid complex; **AC2**, anterior cap; **BRA**, buccal re-entrant angle; **BSA**, buccal salient angle; **L**, length; **LRA**, lingual re-entrant angle; **LSA**, lingual salient angle; **PL**, posterior lobe; **SDQ**, enamel band differentiation quotient (Schmelzband-Differenzierung-Quotient); **W**, width

4 - SYSTEMATIC PALAEONTOLOGY

Family MURIDAE Illiger, 1811

Subfamily ARVICOLINAE Gray, 1821

Genus *MIMOMYS* Major, 1902

MIMOMYS SAVINI Hinton, 1910

(Fig. 4A-O and Table 2)

Occurrence and Material—La Mina, level 2: two complete m1s [BB11sz11N2, BB1sz11N2(2)] and one partial m1 (BB07CT1N2U2). El Forn, level 2: seven complete m1s (BB12EFN2U2(2), BB12EFN2U2(1), BB12EFN2U2(3), BB12EFN2U2(4), BB11EFN2U2(2), BB11EFN2U2, BB08CT2N2U2) and one partial m1 [BB12EFN4U2(5)]. El Forn, level 4: five partial m1s [BB12EFN4U2(5), BB12EFN4U2(2), BB12EFN4U2(3), BB12EFN4U2(4), BB12EFN4U2(1)].

Measurements—See Table 2.

Description—Only molars from adults were obtained, with both roots closed or in the process of closing. Cement is scarce in all the remains except for two teeth (Fig. 4B and 4H). Most are fractured, and the absence of cement may be a result of poor preservation. The enamel differentiation is negative (the enamel is thicker in the trailing edges than in the leading edges in lower molars); this differentiation is more marked in advanced stages of wear. The *Mimomys*-ridge is practically absent; only one tooth shows an undulation in the BRA3 (Fig. 4A). The posterior lobe, T1, T2 and T3 are faintly confluent. T4 and T5 are broadly confluent with the anteroconid complex. In most specimens, BRA3 and LRA4

are relatively shallow and alternating; in all individuals, the enamel is interrupted in the anterior part of the anteroconid complex and on the lingual and buccal sides of the posterior lobe.

Remarks—*Mimomys savini*, the most abundant arvicoline in levels 2 and 4 of Barranc de la Boella site, is characterized by its large size and rooted molars in adults. In level 4, the remains are fractured and cannot be compared with other populations of *M. savini*. In level 2, the studied molars are longer than those from several primitive populations of *M. savini* such as Beftia 2 and Nogajsk (Maul, 2001) and Barranco León D and Fuente Nueva 3 (Lozano-Fernández et al., 2013a) with an age older than the Jaramillo subchron. The studied material is also somewhat larger than *M. savini* from some localities correlated to the Jaramillo, such as Castagnone (Siori and Sala, 2007) and Untermassfeld (Maul *et al.,* 2007).

The mean length of the measured molars from level 2 of Barranc de la Boella (3.32 mm) is quite similar to the mean value from Monte Peglia (3.30 mm; van der Meulen, 1973), also correlated to the Jaramillo. The mean length from level 2 (3.32 mm) is less than the values of *M. savini* from TD4 (3.43 mm), TD5b (3.46 mm), TD5a (3.49 mm), TD6-3 (3.43 mm), TD6-2 (3.59 mm) and TD6-1 (3.62 mm) in Gran Dolina, Atapuerca (Lozano-Fernández *et al.,* 2013a, 2013b), which preceded the Matuyama-Bruhnes boundary.

It was not possible to calculate the SDQ values for level 4 of Barranc de la Boella due to the fragmentation of the remains. For level 2, the values obtained fall between those from TD6 and TD5 (Lozano-Fernández *et al.,* 2013a).

Finally, the percentage of adult individuals that display *Mimomys*-like characteristics (the enamel islet and/or the mimomys-ridge) in level 2 is 11.1%, a value that falls between TD4 and TD5 (Lozano-Fernández *et al*., 2013a). In level 4, it was not possible to study this character owing to the poor state of preservation of the remains.

Genus *VICTORIAMYS* Martin, 2012

VICTORIAMYS CHALINEI Alcalde, Agustí, and Villalta, 1981

(Fig. 4P-Q and Table 2)

Occurrence and Material— La Mina, level 2: one complete m1 (BB11LMN2U2). El Forn, level 2: one complete m1 [BB12EFN2U2(5)].

Measurements—See Table 2.

Description—These first lower molars consist of a posterior lobe, three closed triangles, and the anteroconid complex (ACC). T4 and T5 are broadly confluent, and also connected with the anterior cap (AC2). The AC2 is very short and broad, and mesiodistally compressed.

The enamel is undifferentiated. The amount of cement in the re-entrant folds is relatively low.

Remarks—The size of the specimens falls within the range of those from the type locality of the species, Cueva Victoria (Alcalde *et al*., 1981). However, the mean size of *V. chalinei* from Barranc de la Boella (level 2) is greater than the mean size from Cueva Victoria (Alcalde *et al.,* 1981). The studied teeth are slightly smaller than those of *V. chalinei* from levels TD4 and TD4B of Atapuerca [Cuenca-Bescós *et al*., 1995 (determined as *Allophaiomys chalinei* in that paper)], level C2 of El Chaparral (López-García *et al*., 2012) and level D5 from Cal Guardiola [Minwer-Barakat *et al*., 2011 (determined as *Allophaiomys chalinei* in that paper)].

Victoriamys chalinei has been identified in several Early Pleistocene sites, such as Cueva Victoria (Alcalde *et al*., 1981), Almenara-Casablanca 3 (Agustí *et al*., 2011), Huétor Tájar 1 and 8 and Tojaire-1 (García-Alix *et al.,* 2009), and TD3–TD6 of Gran Dolina (Cuenca-Bescós *et al*., 1995), with an estimated age of 0.99–0.85 Ma.

Level 2

M.savini

	n	Mean	Max.	Min.	SD
A	9	1.29	1.42	1.13	0.102
b	9	0.663	0.83	0.49	0.096
SDQ	9	151.705	176.122	139.914	10.752
c	10	0.39	0.54	0.25	0.078
L	9	3.32	3.48	3.13	0.102
W	10	1.506	1.63	1.34	0.086
A/L	9	0.388	0.421	0.329	0.029
A/W	9	0.849	0.959	0.693	0.093

V. chalinei

	n	Mean	Max.	Min.	SD
A	2	0.98	1.03	0.93	0.070
b	2	0.315	0.32	0.31	0.007
SDQ	2	99.149	108.775	89.523	13.613
c	2	0.25	0.3	0.2	0.070
L	2	2.655	2.71	2.6	0.077
W	2	0.99	1.03	0.96	0.014
A/L	2	0.368	0.380	0.357	0.015
A/W	2	0.875	0.927	0.823	0.074

Level 4

M.savini

	n	Mean	Max.	Min.	SD
A	1	1.36			
b	1	0.72			
SDQ	0				
c	1	0.4			
L	0				
W	5	1.562	1.65	1.44	0.080
A/L	0				
A/W	1	0.855	0.855		

Table 2. Mean, maximum, minimum and standard deviation (**SD**) of the measurements and indices of the m1 of *Mimomys savini* and *Victoriamys chalinei* from Barranc de la Boella site (levels 2 and 4). Linear data (**L**, **W**, **A**, **b** and **c**; see Fig. 3) are in mm. For abbreviations, see Materials and Methods. The column **n** refers to the number of remains.

Family SORICIDAE Fischer von Waldheim, 1817

Subfamily CROCIDURINAE Milne-Edwards, 1874

Genus *CROCIDURA* Wagler, 1832

CROCIDURA SP.

(Fig. 4R)

Occurrence and Material—El Forn, level 2: one complete incisor [BB12EFN2U2(6)].

Measurements—Length without the root: 2.82 mm; length with the root: 3.93 mm; width: 0.65 mm.

Description—It extends forwards in a straight line in dorsal view. The apex is curved moderately upwards. The dorsal face is cusped. There is no visible cingulum on the posterior margin of the crown. A narrow groove is present on the medial face, running from the tip to the crown/root junction of the tooth. It does not present coloration of any type.

Remarks—The chronological association with *M. savini* and the dimensions of the incisor, which are similar to those of the populations from the Lower Red Unit at Trinchera Elefante, Atapuerca (Rofes and Cuenca-Bescós, 2011), would have allowed us to assign this remnant to *Crocidura kornfeldi*, which was present in Europe between 2 Ma and 1.1 Ma. Nonetheless, in the light of the presence of the narrow groove running from the tip to the crown/root junction of the incisor, which has not been described in *C. kornfeldi*, and the fact that incisors are not diagnostic to species level within the group of shrews, we are only able to determine the material under study to genus level.

Family TALPIDAE Fischer von Waldheim, 1817

Subfamily TALPINAE Fischer von Waldheim, 1817

Genus *TALPA* Linnaeus, 1758

TALPA SP.

(Fig. 4S)

Occurrence and Material—El Forn, level 2: one ulna [BB12EFN2U2(7)].

Measurements—Length: 16.4 mm; width of epiphysis: 1.97 mm; width of diaphysis: 7.46 mm.

Description—The recovered remnant is composed of the proximal epiphysis and part of the diaphysis. It is fractured before the distal epiphysis, which is not preserved. Flaking can be seen on the surface of the bone.

Remarks—The size of the remnant, its geographical situation and its stratigraphic association with *M. savini* and *V. chalinei* (taxa of the Early Pleistocene) might be taken to suggest that it belongs to *Talpa europaea*. As the element in question is not diagnostic to species level, however, it was not considered possible to provide any more than a genus-level determination.

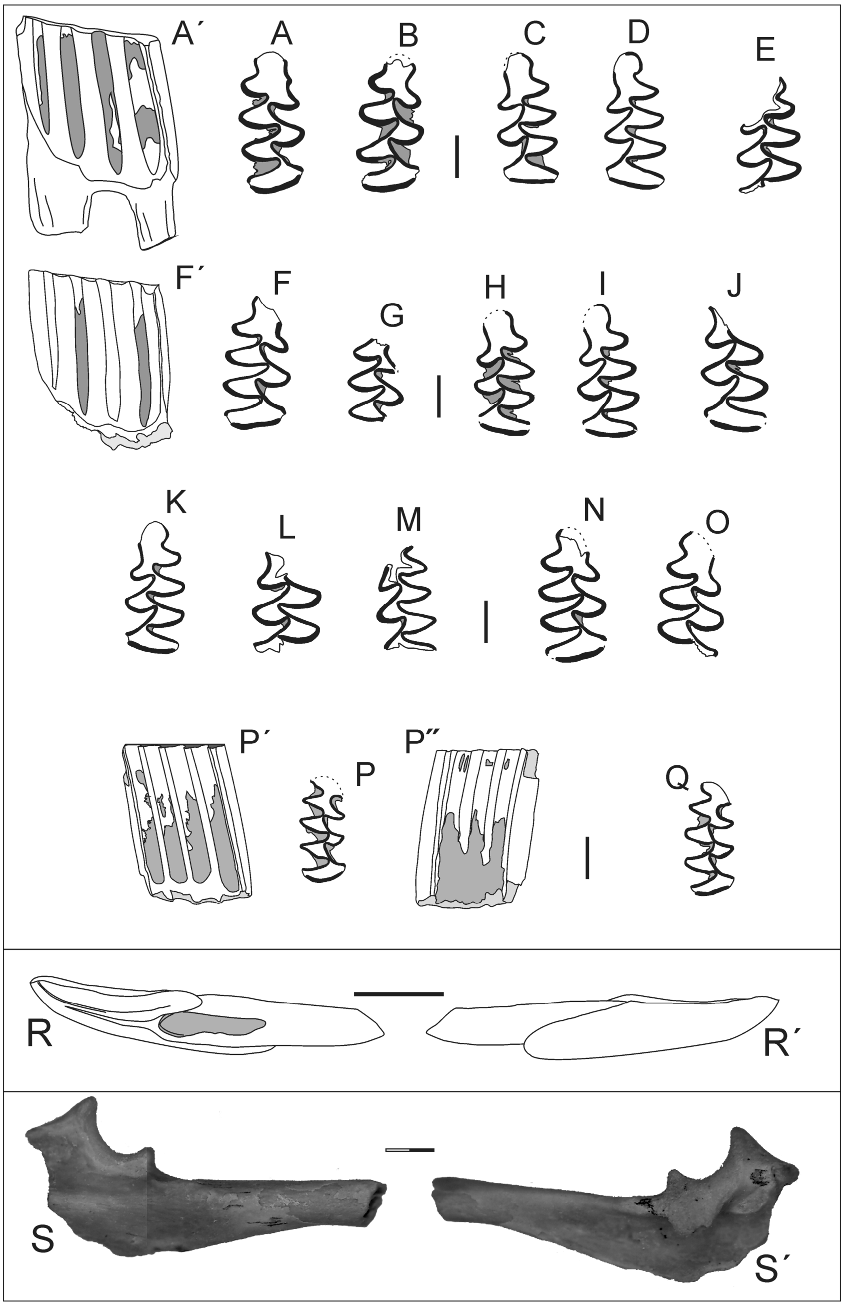

Figure 4. Material recovered from levels 2 and 4 of the site of Barranc de la Boella. The m1s from **A** to **O** correspond to *Mimomys savini*. Beneath these, **P** and **Q** are m1s from *Victoriamys chalinei*, **R** is an incisor from *Crocidura* sp. and **S** is an ulna from *Talpa* sp.

In **A’** and **F’** (lingual views of **A** and **F**) the roots of *M. savini* can be clearly seen (in **A’** in a perfect state of preservation and in **F’** very broken).

The scale bars are equivalent to 1 mm except in the case of **S** and **S’**, which correspond to 2 mm.

5 - BIOCHRONOLOGICAL REMARKS

Small mammals, and particularly arvicolines, evolved rapidly during the Quaternary, so their record provides an important basis for stratigraphical divisions and correlations between distant areas. In particular, the rapid evolutionary radiation of the '*Microtus* group' (including forms ascribed to *Microtus*, *Allophaiomys, Victoriamys*, *Stenocranius*, *Terricola*, *Iberomys* and *Pallasiinus*) and the changes along the *Mimomys-Arvicola* lineage constitute very useful tools for correlating European Pleistocene faunas.

The small-mammal remains present in level 4 of Barranc de la Boella are insufficient for a biochronological study. They consist of a very limited set of remains belonging to a single taxon (*M. savini*) and are rather fractured, making a conclusive biochronological study unfeasible. The stratigraphical situation of level 4 (located beneath level 2) allows us to establish that its age will be equal to or greater than level 2.

As far as level 2 is concerned, the presence of *M. savini* is characteristic of the Biharian (Fejfar *et al.,* 1998), whereas the identification of *V. chalinei* indicates an age corresponding to the final part of the Biharian (Cuenca-Bescós *et al.,* 1999, 2010b; Madurell-Malapeira *et al.,* 2010; López-García *et al*., 2012). The association of *M. savini* and *V. chalinei* indicates that this level corresponds to the *Allophaiomys chalinei* biozone, with a chronology of between 0.78 Ma and 0.9 Ma according to Cuenca-Bescós *et al.* (2010b), although some authors put it at between 0.78 Ma and 0.99 Ma (Minwer-Barakat *et al*., 2011; Agustí and Moyà-Solà, 1992).

The SDQ values of the population of *M. savini* of level 2 of Barranc de la Boella would place it between levels TD5 and TD6 of Gran Dolina, with an age of between 1 Ma and 0.8 Ma (according to Moreno, 2011; Moreno *et al.,* 2012). However, this estimation could be mistaken given that the evolution of the SDQ in *M. savini* displays fluctuating patterns in the Iberian Peninsula (Lozano-Fernández *et al.,* 2013a). As such, it has not been taken into account in producing our chronological estimation of level 2 of Barranc de la Boella.

The percentage of the adult population of *M. savini* that presents *Mimomys*-like characters in level 2 of Barranc de la Boella situates the level between levels TD4 and TD5 of Gran Dolina (in accordance with Lozano-Fernández *et al*., 2013a). As the evolution of this taxon involves a loss of these characters at increasingly juvenile stages (due to wear), this is reflected in a lower percentage of the adult individuals of the fossil population that present them (Cuenca-Bescós *et al.,* 1999; von Koenigswald, 1982; von Koenigswald and van Kolfschoten, 1996; Lozano-Fernández *et al*., 2013a). In other words, the more modern populations show a lower percentage of adult individuals with *Mimomys*-like characters. The values of level 2 of Barranc de la Boella, situated between TD4 and TD5, thus indicate a chronology for the level of between 1 Ma and 0.94 Ma (according to Moreno, 2011; Moreno *et al.,* 2012).

The mean size of the *M. savini* present in level 2 of Barranc de la Boella situates the population between the top of TD4 of Gran Dolina and Fuente Nueva 3 and Barranco León D in Orce (in accordance with Lozano-Fernández *et al.,* 2013a). As the evolution of *M. savini* involves an increase in the size of the individuals (Viriot *et al*., 1990; Chaline *et al*., 1999; Lozano-Fernández *et al*.,

2013a, 2013b), we can estimate an age for level 2 of between 1.19 Ma and 1 Ma (Fuente Nueva 3 corresponds to 1.19 Ma according to Duval *et al*., 2012; the top of TD4 corresponds to 1 Ma according to Moreno, 2011; Moreno *et al*., 2012).

The remains of *V. chalinei* from level 2 of Barranc de la Boella present a size that is slightly greater than the mean for the population of Cueva Victoria (in accordance with Alcalde *et al*., 1981) and less than levels TD4 and TD4B of Gran Dolina (in accordance with Cuenca-Bescós *et al*., 1995), level D5 of Cal Guardiola (in accordance with Minwer-Barakat *et al*., 2011) and level C2 of El Chaparral (in accordance with López-García *et al*., 2012). This indicates that the population of *V. chalinei* from Barranc de la Boella is one of the oldest in the Iberian Peninsula, with an age close to 0.99 Ma. In spite of the low number of *V. chalinei* remains recovered from Barranc de la Boella, the chronological estimation inferred from them is consistent with the estimations made on the basis of *M. savini*.

Level 2 of Barranc de la Boella thus falls a priori within the *Allophaiomys chalinei* biozone, which is defined as between 0.99 Ma and 0.78 Ma in the Iberian Peninsula. Comparison of its population of arvicolids with those from other sites in the Iberian Peninsula would seem to indicate that it lies close to the base of this biozone at 0.99 Ma. Indeed, the data relating to the size of *M. savini* suggest that level 2 is situated at 1 Ma at least or even somewhat lower, with a chronology similar to TD4 of Gran Dolina (Fig. 5). An age of 1 Ma places level 2 of Barranc de la Boella slightly beneath the *Allophaiomys chalinei* biozone. The presence of *Victoriamys chalinei* at around 1 Ma in the Iberian

Peninsula had already been published by Cuenca-Bescós *et al*. (1995), who located the species in TD4 and TD4B of Gran Dolina (determined as *Allophaiomys chalinei* in that paper). Whatever the case, the conjunction of all the biochronological data derived from the small-mammal populations present in level 2 of Barranc de la Boella clearly indicates a minimum age of 0.99 Ma. This chronological estimation concurs with that proposed by Saladié et al. (2008) and Vallverdú *et al*. (2008), who estimated a minimum age of 0.70 Ma, and with the presence of large mammals characteristic of the Villafranchian (between 1.3 and 0.8 Ma according to Martínez-Navarro, 2002; Rook and Martínez-Navarro, 2010).

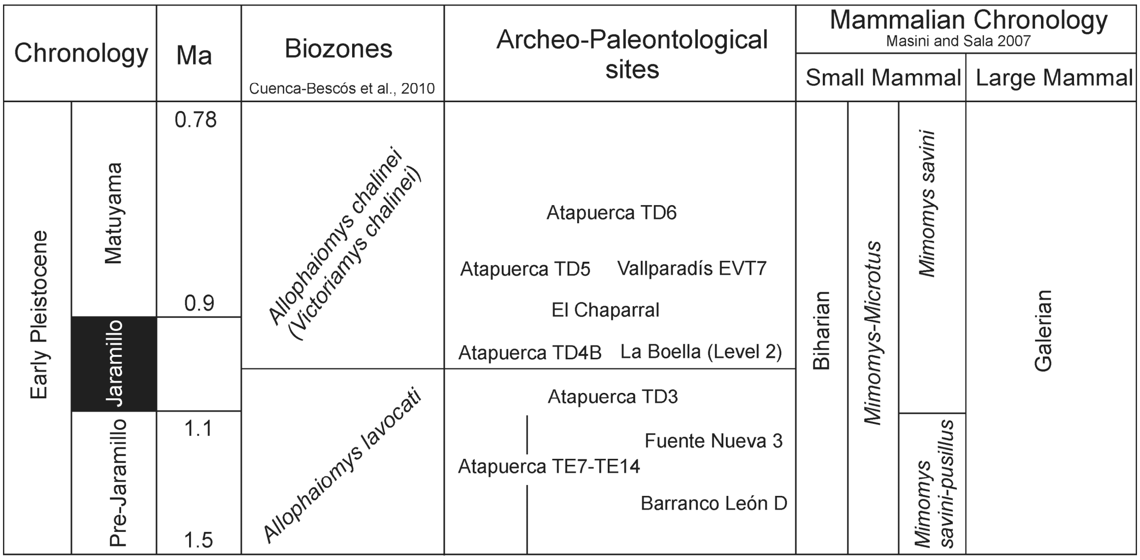

Figure 5. Correlation of the European chronology with the principal Early Pleistocene archaeo-palaeontological sites in the Iberian Peninsula, placing level 2 of Barranc de la Boella site in its context

6 - PALEOENVIRONMENTAL REMARKS

Using the optimum habitat method, the landscape is seen to have been dominated by areas with water (water's edge, 56%) and wetlands (open humid, 33%), with a scarce representation of dry meadowland (open dry, 11%) (Table 1).

The record of *Mimomys savini* reveals the presence of a huge quantity of water within channels and pools, which are also very rich in vegetable resources and where generalist elephants such as *Mammuthus meridionalis* would have been able to survive in good conditions. Although other less water-dependent species such as *Victoriamys chalinei* and *Talpa* sp. are present, they are not abundant. The presence of *Crocidura* sp. and *Talpa* sp. (albeit in low measure) indicates the existence of open areas in the vicinity of the site.

These aquatic palaeoenvironments, with their abundant vegetation, would have been good places for hominins, with vegetable resources in riverbank forests that would have provided protection, as well as animal resources, as shown by the presence of carcasses belonging to megaherbivores and other ungulates.

The scarcity of the remains recovered from level 4 of Barranc de la Boella and the fact that they belong to just one taxon (*M. savini*) allow us to establish only that the level was formed in an environment dominated by water (lacustrine, palustrine or fluvial).

7 - CONCLUSIONS

All the species of small mammals present in levels 2 and 4 of the site of Barranc de la Boella have been described in the present paper.

The small-mammal content of level 2 has made it possible to provide the level with a more precise chronology and ascertain the type of landscape that would have dominated the territory during the first human occupations at Barranc de la Boella. In chronological terms, level 2 of the site of Barranc de la Boella is thus dated to between 0.99 and 0.78 Ma (in the *Allophaiomys* biozone), the interval between the Jaramillo and the Matuyama/Brunhes boundary. A comparison of its population of arvicolids with other sites in the Iberian Peninsula reveals that level 2 is chronologically situated very close to level TD4B of Gran Dolina and beneath Cueva Victoria and level C2 of El Chaparral, with an age close to 0.99 Ma or even slightly older.

Level 2 is therefore one of the oldest sites with a human presence in the west of Europe, together with Barranco León D and Fuente Nueva 3 (Granada, Spain), Sima del Elefante (Burgos, Spain), level TD6 of Gran Dolina (Burgos, Spain) and Layer 10 of Vallparadís (Terrassa, Spain).

The microvertebrate and macrovertebrate faunal community places the site in the context of an ecotone where species characteristic of open areas cohabit with species from woodland areas. This environment would have occurred in the vicinity of a lacustrine area or a fluvial course with a regular and constant flow of water. The landscape at Barranc de la Boella approximately 0.99 Ma was thus dominated by humid areas with a low representation of open areas.

As far as level 4 of the site of Barranc de la Boella is concerned, the small-mammal remains present in the level are insufficient to undertake a biochronological study. Just the stratigraphic situation of level 4 (beneath level 2) allows us to ascertain that its age will be similar to or greater than level 2.

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REFERENCES

Agustí J. 1986. Synthèse biostratigraphique du Plio–Pléstocène de Guadix Baza (Province de Granada, sud-est de l'Espagne). *Geobios* 19: 505-510.

Agustí J, Moyà-Solà S. 1992. Mammalian dispersal events in the Spanish Pleistocene. *Courier Forschungsinstitut Senckenberg* 153: 69-77.

Agustí J, Santos-Cubedo A, Furió M, *et al*. 2011. The late Neogene-early Quaternary small vertebrate succession from the Almenara-Casablanca karst complex (Castellón, Eastern Spain). Chronologic and paleoclimatic context. *Quaternary International* 243: 183-191.

Alcalde G, Agustí J, Villalta FJ. 1981. Un nuevo *Allophaiomys* (Arvicolidae, Rodentia, Mammalia) en el Pleistoceno inferior del sur de España. *Acta Geológica Hispánica* 16: 203-205.

Andrews P. 1990. *Owls, Caves and Fossils. Predation, Preservation and Accumulation of Small Mammal Bones in Caves, with an analysis of the Pleistocene Cave Faunas from Westbury-sub-Mendip, Somerset, UK*. London, The University Chicago Press.

Bataller JR. 1935. Els darrers treballs geològics a les comarques tarragonines en els darrers anys. *Revista del Centre de Lectura* 84-96.

Chaline J. 1972. *Les Rongeurs du Pléistocène Moyen et Supérieur de France (Systématique, Biostratigraphie, Paléoclimatologie*). Cahiers de Paléontologie, C.N.R.S., Paris.

Chaline J. 1985. *Histoire de l’homme et des climats au quaternaire*. Doin, Paris.

Chaline J, Brunet-Lecomte P, Montuire S, *et al.* 1999. Anatomy of the arvicoline radiation (Rodentia): palaeogeographical, palaecoecological history and evolutionary data. *Annales zoologici fennici* 36: 239-267.

Cuenca-Bescós G, Agustí J, Lira J, *et al*. 2010b. A new species of water vole from the Early Pleistocene of Southern Europe. *Acta Palaeontologica Polonica* 55: 565-580.

Cuenca-Bescós G, Canudo Jl, Laplana C. 1995. Los Arvicólidos (Rodentia, Mammalia) de los niveles inferiores de Gran Dolina (Pleistoceno Inferior, Atapuerca, Burgos, Españna). *Revista Española de Paleontología* 10: 202-218.

Cuenca-Bescós G, Laplana C, Canudo JI. 1999. Biochronological implications of the Arvicolidae (Rodentia, Mammalia) from the Lower Pleistocene hominid-bearing level of Trinchera Dolina 6 (TD6, Atapuerca, Spain). *Journal of Human Evolution* 37: 353-373.

Cuenca-Bescós G, Rofes J, García-Pimienta J C. 2005. Early Europeans and environmental change across the Early–Middle Pleistocene transition: small mammalian evidence from Trinchera Dolina cave, Atapuerca, Spain. In: *Early–Middle Pleistocene Transitions: the Land–Ocean Evidence*, Head M J, Gibbard PL (eds). Geological Society, London, 277-286.

Cuenca-Bescós G, Rofes J, López-García JM, *et al*. 2010a. Biochronology of Spanish Quaternary small vertebrate faunas. *Quaternary International* 212: 109-119.

Cuenca-Bescós G, Rofes J, López-García JM, *et al*. 2012. The Small mammals of Sima del Elefante (Atapuerca, Spain) and the first entrance of Homo in Western Europe. *Quaternary International* 272-273: 125-137.

Daams R, Freudenthal M. 1988. Synopsis of the Dutch–Spanish collaboration program in the Neogene of Calatayud–Teruel Basin. 1976–1986. *Scripta Geologica* 1 :3-18.

Fejfar O, Heinrich W-D, Lindsay H. 1998. Updating the Neogene Rodent biochronology in Europe. *Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen Toegepast Natuurwetenschappelijk Onderzoek* 60: 533-554.

Fischer de Waldheim G. 1817. Adversaria zoologica. *Memoires de la Société Impériale des Naturalistes du Moscou* 5: 357-428.

García-Alix A, Minwer-Barakat R, Martín Suárez E, *et al*. 2009. Small mammals from the early Pleistocene of the Granada Basin, southern Spain. *Quaternary Research* 72: 265-274.

Gray JE. 1821. On the natural arrangement of vertebrose animals. *London Medical Repository* 15: 296-310.

Heinrich W-D.1978. Zur biometrischen Erfassung eines Evolutiontrends bei *Arvicola* (Rodentia, Mammalia) aus dem Pleistozän Thüringens. *Säugetierkundliche Informationen* 2: 3-21.

Heinrich W−D. 1987. Neue Ergebnisse zur Evolution und Biostratigraphie von *Arvicola* (Rodentia, Mammalia) im Quartär Europas. *Zeitschrift für geologische Wissenschaften* 15: 389-406.

Hinton MAC. 1910. A preliminary account of the British fossil voles and lemmings; with some remarks on the Pleistocene climate and geography. *Proceedings of the Geologists Association* 21: 489-507.

Illiger C. 1811. *Prodromus systematis mammalium et avium additis terminis zoographicis utriusque classis, eorumque versione germanica*. Sumptibus C. Salfeld, Berlin.

Koenigswald W, Kolfschoten T. 1996. The *Mimomys–Arvicola* boundary and the enamel thickness quotient (SDQ) of *Arvicola* as stratigraphic markers in the Middle PleistoceneIn: *The Early Middle Pleistocene in Europe* Turner Ch (ed.). Balkema, Rotterdam; 211-226.

Linnaeus C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tomus 1. Laurentii Salvii, Stockholm.

López-Antoñanzas R, Cuenca-Bescós G. 2002. The Gran Dolina site (Lower to Middle Pleistocene, Atapuerca, Burgos, Spain): new palaeoenvironmental data based on the distribution of small mammals. *Palaeogeography, Palaeoclimatology, Palaeoecology* 186: 311-334.

López-García JM, Cuenca-Bescós G, Blain H-A, *et al*. 2012. Biochronological data inferred from the Early Pleistocene Arvicolinae (Mammalia, Rodentia) of the El Chaparral site (Sierra del Chaparral, Cádiz, southwestern Spain). *Journal of Vertebrate Paleontology* 32: 1149-1156.

Lozano-Fernández I, Agustí J, Cuenca-Bescós G, *et al*. 2013. Pleistocene evolutionary trends in dental morphology of *Mimomys savini* (Rodentia, Mammalia) from Iberian Peninsula and discussion about the origin of the genus *Arvicola*. *Quaternaire* 24: 165-176.

Lozano-Fernández I, Cuenca-Bescós G, Blain H-A, *et al.* 2013b. *Mimomys savini* size evolution in the Early Pleistocene of south-western Europe and possible biochronological implications. *Quaternary Science Reviews* 76: 96-101.

Madurell-Malapeira J, Minwer-Barakat R, Alba DM, *et al*. 2010. The Vallparadís section (Terrassa, Iberian Peninsula) and the latest Villafranchian faunas of Europe. *Quaternary Science Reviews* 29: 3972-3982.

Major CIF. 1902. Some jaws and teeth of Pliocene voles (*Mimomys* gen. nov.) from the Norwich Crag at Thorpe, and from the Upper Val d'Arno. *Proceedings of the Zoological Society of London* 1: 102-107.

Martin R. 2012. *Victoriamys*, a new generic name for Chaline's vole from the Pleistocene of western Europe. *Geobios* 45: 445-450.

Martínez-Navarro B. 2002. Presence of African large mammals (primates, carnivores and ungulates) in the Lower Pleistocene of the Middle East and Europe. *Annales des Pays Hellèniques* 39: 337-351.

Masini F, Sala B. 2007. Large and small mammal distribution patterns and chronostratigraphic boundaries from the Late Pliocene to the Middle Pleistocene of the Italian Peninsula. *Quaternary International* 160: 43-56.

Maul LC. 2001. Die Kleinsäugerreste (Insectivora, Lagomorpha, Rodentia) aus dem Unterpleistozän von Untermassfeld. In: *Das Pleistozän von Untermassfeld bei Meiningen*, Kahlke R-D (ed). Römisch-Germanisches Zentralmuseum, Monographien Mainz, 40 (3). Rudolf Habelt, Bonn; 783-887.

Maul LC, Heinrich W-D, Parfitt SA, *et al*. 2007. Comment on the correlation between magnetostratigraphy and the evolution of Microtus (Arvicolidae, Rodentia, Mammalia) during the Early and early Middle Pleistocene. *Courier Forschungsinstitut Senckenberg* 259: 243-263.

Meulen AJ Van Der. 1973. Middle Pleistocene smaller mammals from the Monte Peglia (Orvieto, Italy) with special reference to the phylogeny of *Microtus* (Arvicolidae, Rodentia). *Quaternaria* 17: 1-144.

Milne–Edwards H.1874. *Recherches pour servir a l'histoire naturelle des mammifères comprenant des considérations sur la classification de ces animaux*, vol.1–2. Masson,Paris.

Minwer–Barakat R, Madurell-Malapeira J, Alba DM, *et al.* 2011. Pleistocene rodents from the Torrent de Vallparadís section (Terrasa, northeastern Spain) and biochronological implications. *Journal of Vertebrate Paleontology* 31: 849-865.

Moreno D. 2011. *Datation par esr de quartz optiquement blanchis (ESR-OB) de la région de atapuerca (Burgos, Espagne). Application au site préhistorique de gran dolina (contexte karstique) et aux systèmes fluviatiles quaternaires de l'Arlanzón et l'Arlanza*. Ph.D. thesis. Univeristat Rovira i Virgili, Tarragona, Spain and Muséum National d'Histoire Naturelle, Paris.

Moreno D, Falguères C, Pérez–González A, *et al.* 2012. ESR chronology of alluvial deposits in the Arlanzón valley (Atapuerca, Spain): Contemporaneity with Atapuerca Gran Dolina site. *Quaternary Geochronology* 10: 418-423.

Rabeder G. 1981. Die Arvicoliden (Rodentia, Mammalia) aus dem Pliozän und dem älteren Pleistozän von Niederösterreich. *Beiträge zur Paläontologie von Österreich* 8: 1-373.

Rofes J, Cuenca–Bescós G. 2011. Evolutionary history and biogeography of the genus *Crocidura* (Mammalia,Soricidae) in Europe, with emphasis on *Crocidura kornfeldi*. *Mammalian Biology* **76**: 64-78.

Rook L, Martínez–Navarro B. 2010. Villafranchian: The long story of a Plio-Pleistocene European large mammal biochronologic unit. *Quaternary International* 219: 134-144.

Sala B, Masini F. 2007. Late Pliocene and Pleistocene small mammals chronology in the Italian Peninsula. *Quaternary International* 160: 4-16.

Saladié P, Vallverdú J, Bennàsar LL, *et al*. 2008. Resultats preliminars del nivell 2 del sondeig al Centre de Convencions del barranc de la Boella. *Cota Zero* 23: 13-19.

Siori MS, Sala B. 2007. The mammal fauna from the late Early Biharian site of Castagnone (Northern Monferrato, Piedmont, NW Italy). *Geobios* 40: 207-217.

Vallverdú J, Saladié P, Bennàsar LL, *et al.* 2008. El barranc de la Boella de la Canonja (Tarragonès) revisitat en la intervenció arqueològica preventiva de l'any 2007. *Tribuna d'Arqueologia* 2008-2009: 7-28.

Vilaseca S. 1920. *Contribució al estudi dels terrenys triàsics de la província de Tarragona*. Museu Martorell.

Viriot L, Chaline J, Schaaf A. 1990. Quantification du gradualisme phylétique de *Mimomys occitanus* à *Mimomys ostramosensis* (Arvicolinae, Rodentia) à l'aide de l'analyse d'image. *Comptes Rendus de l'Academie des Sciences* 310: 1755-1760.

Wagler JG. 1832. Isis: 275. In: *Mammals Species of the World, a Taxonomical and Geographical Reference*, Wilson DE, Reeder DM. (Eds). The John Hopkins University Press, Baltimore; 220-311.

CAPÍTULO 4

NUEVOS DATOS DE MICROMAMÍFEROS DEL PLEISTOCENO INFERIOR DE LA CAPA EVT7 DE VALLPARADÍS ESTACIÓ (CUENCA VALLÈS-PENEDÈS, NE PENÍNSULA IBÉRICA): IMPLICACIONES BIOCRONOLÓGICAS Y PALEOAMBIENTALES

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NEW DATA ON THE SMALL MAMMALS FROM THE LATE EARLY PLEISTOCENE OF VALLPARADÍS ESTACIÓ LAYER EVT7 (VALLÈS-PENEDÈS BASIN, NE IBERIAN PENINSULA): BIOCHRONOLOGICAL AND PALAEOENVIRONMENTAL IMPLICATIONS

Iván Lozano-Fernández[a,b,*], Juan Manuel López-García[c], Josep Aurell-Garrido[d], David M. Alba[d,e], Joan Madurell-Malapeira[d].

[a] IPHES, Institut Català de Paleoecologia Humana i Evolució Social, c/ Escorxador s/n, E-43003 Tarragona, Spain.

[b] Area de Prehistoria, Universitat Rovira i Virgili (URV), Avinguda de Catalunya 35, E-43002 Tarragona, Spain.

[c] Sezione di Scienze Preistoriche e Antropologiche, Dipartimento di Studi Umanistici, Università degli Studi di Ferrara, C.so Ercole I d'Este 32, I-44121 Ferrara, Italy.

[d] Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, 08193 Cerdanyola del Vallès, Barcelona, Spain.

[e] Dipartimento di Scienze della Terra, Università di Torino, Via Valperga Caluso 35, I-10125 Torino, Italy.

[*]Corresponding author: Iván Lozano-Fernández, ilozano@iphes.cat

ABSTRACT

The chronology of layer EVT7 of the Vallparadís Estació section has been a hotly debated topic during recent years, with some authors supporting an age close to the Early-Middle Pleistocene boundary (0.83 Ma), and others favouring an age older than the Jaramillo magnetostratigraphic subchron (ca. 1.2 Ma). Here we provide new biochronological data based on the study of *Mimomys savini*, which is the most abundant rodent species from this layer. Based on the morphologic and biometric comparison with remains of the same species from other similarly-aged Iberian localities (Gran Dolina TD4-6 from Atapuerca, and Barranco León D and Fuente Nueva 3 from the Guadix-Baza Basin), we propose an estimated age for EVT7 in the chronologic range from 0.99 to 0.94 Ma. We further perform a paleoenviromental study based on the whole small-mammal assemblage from EVT7, which allows us to infer and open and humid environment in the vicinity of a lacustrine area or fluvial course.

Keywords: Early Pleistocene, Vallparadís Estació, *Mimomys savini*, biochronology, palaeoenvironment.

RÉSUMÉ

NOUVELLES DONNEES SUR LES PETITS MAMMIFERES DU PLEISTOCENE INFERIEUR TERMINAL DE VALLPARADIS ESTACIO NIVEAU EVT7 (BASSIN DU VALLES-PENEDES, NE DE LA PENINSULE IBERIQUE): IMPLICATIONS BIOCHRONOLOGIQUES ET PALEOENVIRONNEMENTALES

La chronologie du niveau EVT7 de la section de Vallparadís Estació a été chaudement débattu ces dernières années, avec certains auteurs proposant un âge proche de la limite entre le Pléistocène inférieur et moyen (0,83 Ma), et d’autres en faveur d’un âge antérieur au subchron magnétostratigraphique Jaramillo (approx. 1,2 Ma). Ici nous apportons de nouvelles donnés biochronologiques basées sur l’étude de *Mimomys savini*, qui est l’espèce de rongeur la plus abondante dans ce niveau. En se basant sur la comparaison morphologique et biométrique avec les restes de la même espèce d’autres localités ibériques d’âge similaire (Gran Dolina TD4-6 d’Atapuerca, et Barranco León D et Fuente Nueva 3 du bassin de Guadix-Baza), nous proposons un âge estimé pour EVT7 compris entre 0,99 et 0,94 Ma. Ensuite, nous réalisons une étude paléoenvironnementale en nous basant sur tout l’assemblage de petits mammifères d’EVT7, qui nous permet d’inférer un environnement ouvert et humide aux alentours d’une zone lacustre ou d’un cours d’eau.

Mots-clés: Pléistocène inférieur, Vallparadís Estació, *Mimomys savini*, biochronologie, paléoenvironnement.

1 - INTRODUCTION

The Pleistocene Vallparadís composite section is mainly constituted by alluvial fan and alluvial plain deposits related to the NW and SE active margins of the Vallès-Penedès Basin. This section comprises the excavated sites of Cal Guardiola (CGR) and Vallparadís Estació (EVT; Madurell-Malapeira et al., 2010a; see Fig. 1a). In the site of Vallparadís Estació, there is a 14 m-thick succession mainly composed of conglomerates and mudstones, which are arranged in two units separated by an erosive angular unconformity (Fig. 1b). The depositional environment of the study area during the Early Pleistocene was closely related to the alluvial fan dynamics of the basin and to the Miocene canyon-like paleorelief geometry (Madurell-Malapeira et al., 2010a, 2012). Layer EVT7 corresponds to a 3 m-thick, mud-supported, greenish bed generated by high-density flows (debris-flows and mud-flows) and divided into two major parts (Madurell-Malapeira et al., 2010a, 2011b, 2012). The following small and large mammal species have been identified from this layer (Alba et al., 2008; Madurell-Malapeira et al., 2010a, b, 2011a, b, 2013, in press; Minwer-Barakat et al., 2011): *Macaca sylvanus* cf. *florentina*, *Pachycrocuta brevirostris, Meles meles atavus*, *Ursus deningeri, Lycaon lycaonoides, Canis mosbachensis, Vulpes praeglacialis*, *Panthera gombaszoegensis, Puma pardoides,* Felidae indet. (large form), *Lynx* sp., Elephantidae indet., *Equus altidens, Stephanorhinus hundsheimensis, Hippopotamus antiquus, Sus* sp., *Dama vallonnentensis, Megaloceros savini, Bison* sp., Caprini indet., *Mimomys savini, Iberomys huescarensis, Stenocranius gregaloides, Apodemus* cf. *sylvaticus, Eliomys quercinus, Ungaromys* sp. and *Hystrix refossa.* The herpetofauna identified from EVT7 is composed of *Pelobates* cf. *cultripes*, Anura indet., *Natrix natrix*, cf. *Rhinechis* sp., and Lacertidae indet. (Martínez et al., 2010).

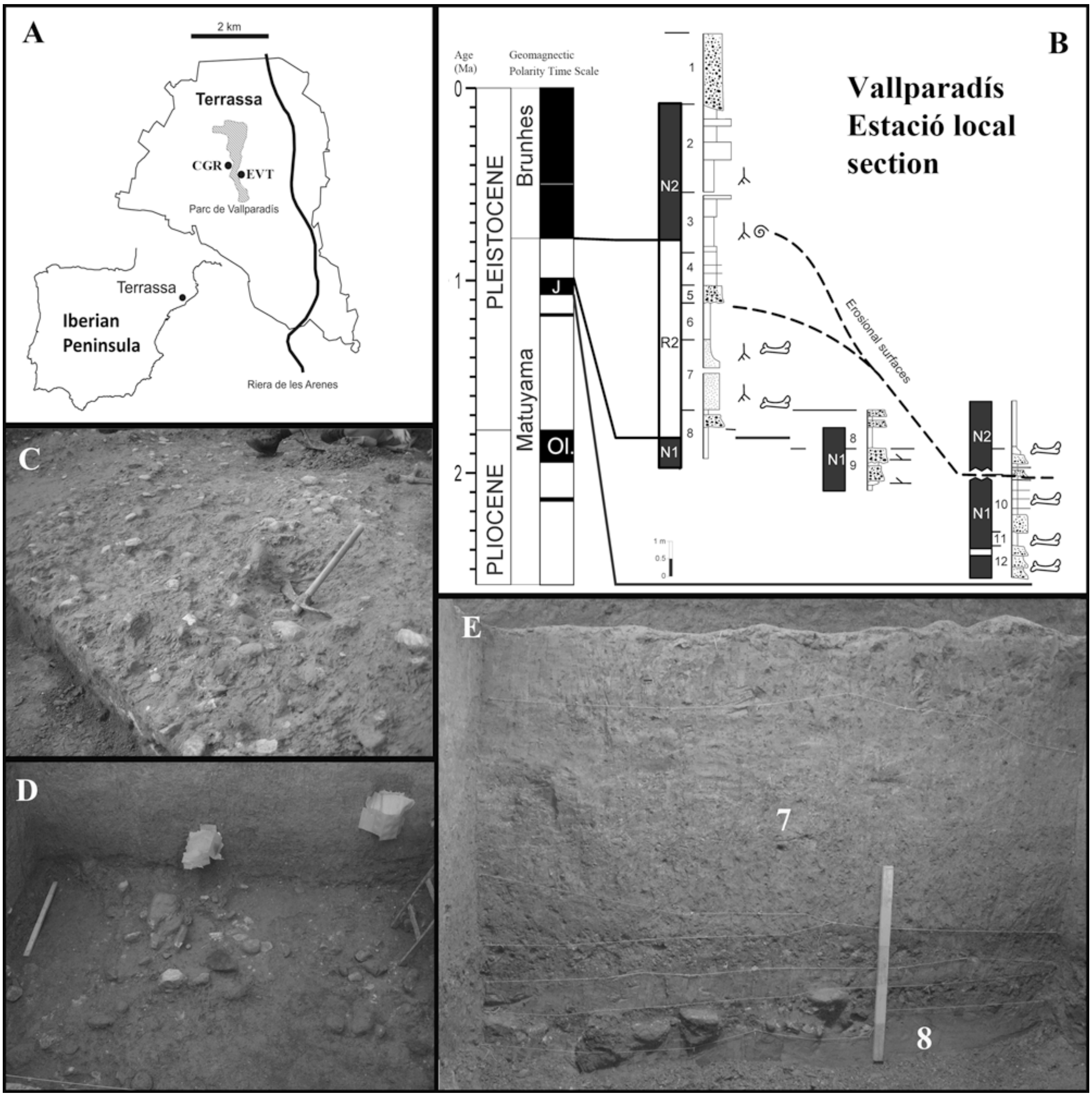

Figure 1. Geographic and geologic context of Vallparadís Estació. **A**, Location map of the localities from the Vallparadís section. **B**, Correlation of the Vallparadís Estació magnetostratigraphy to the geomagnetic polarity time scale. **C–D**, Two views of the lower part of layer EVT7. **E**, Section along layer EVT7.

On the basis of magnetostratigraphic and biostratigraphic data, the reverse polarity EVT7 layer is correlated to the post-Jaramillo interval of the Matuyama chron (ca. 0.99-0.78 Ma; Madurell-Malapeira et al., 2010a; see Fig. 1b). An absolute dating carried out by means of ESR method yielded an estimated age of 0.83 ±0.07 Ma for EVT7 (Duval et al., 2011), being correlated to MIS21 (Madurell-Malapeira et al., 2010a). This notwithstanding, some recent publications asserted that EVT7 is closer in age to Sima del Elefante (Martínez et al., 2010; Garcia et al., 2011), which is dated at 1.2 Ma (Carbonell et al., 2008). These authors supported their age estimate based on the purported resemblance of the lower molars of *Iberomys huescarensis* from EVT7 with those from Sima del Elefante—although, in fact, this taxon has been never reported from the latter locality (see Cuenca-Bescós et al., 2010; Madurell-Malapeira et al., 2012). Such an old dating for EVT7 is further contradicted by the record of the advanced microtine *Stenocranius gregaloides* (see Minwer-Barakat et al., 2011), as well as by the above-mentioned radiometric dating of 0.83 Ma (Duval et al., 2011), which perfectly fit the biocronological and magnetoestratigraphic data (Madurell-Malapeira et al., 2010a, 2012; Minwer-Barakat et al., 2011).

Here we rely on the micromammal assemblage from EVT7 to shed new light on the dating of this layer, as well as to provide a more refined paleoenvironmental reconstruction. Unlike Martínez et al. (2010), who compared the remains of *I. huescarensis* from EVT7 with those from other Iberian sites, we rely on the comparison of the remains of *Mimomys savini* with those from other, similarly-aged localities from the Iberian Peninsula: Fuente Nueva 3 and Barranco León

D, in the Guadix-Baza Basin (Lozano-Fernández et al., 2013a); and Gran Dolina TD4 and TD6, in Atapuerca (Lozano-Fernández et al., 2013a, b). Our reliance on *M. savini* is justified by the well-documented evolutionary trend towards increased size and other morphologic changes in this taxon (Viriot et al., 1990; Chaline et al., 1999; Lozano-Fernández et al., 2012; 2013a; 2013b). In turn, the paleoenvironmental reconstruction of layer EVT7 provided in this paper relies on the application of the “optimum habitat” method (Andrews, 1990; Cuenca-Bescós et al., 2005; 2012; López Antoñanzas and Cuenca-Bescós, 2002) to the small mammal assemblage.

2 - MATERIAL AND METHODS

2.1 - STUDIED SAMPLE

The excavation of 3,940 m^2 at Vallparadís Estació between 2005-2008 led to the recovery of about 26,000 fossil vertebrate remains and plant macroremains. In particular, layer EVT7 yielded 20,286 macromammal fossils and 128 identifiable micromammal remains, which are housed at the Institut Català de Paleontologia M. Crusafont (Sabadell, Spain). The sample studied in this paper includes the 128 available small mammal remains, for which a minimum number of 54 individuals is computed (Table 1). Nine micromammalian taxa have been identified from this sample (Martínez et al. 2010; Minwer-Barakat et al., 2011; this study; see Table 1 and Fig. 2): rodents include the arvicolids *Ungaromys nanus*, *Iberomys huescarensis*, *Mimomys savini*, and *Stenocranius gregaloides*; the glirid *Eliomys quercinus*; the murid *Apodemus* cf. *sylvaticus*; and the hystricid *Hystrix refossa*; insectivores, in turn, include the talpid *Talpa europaea* and the soricid *Crocidura* sp.

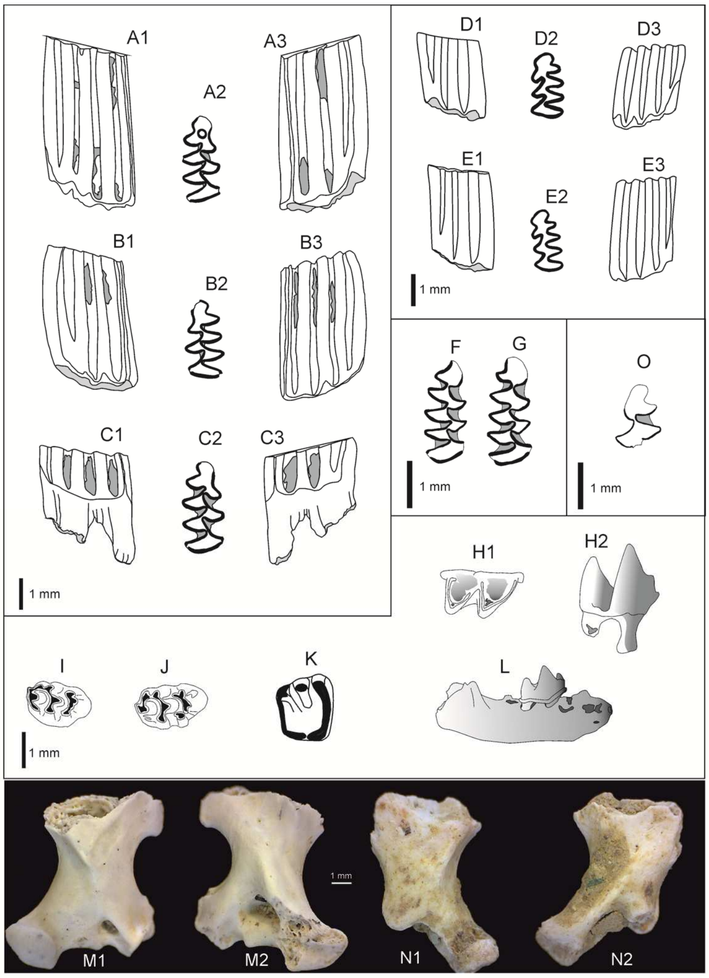

Figure 2. Small mammals recovered from layer EVT7 of Vallparadís Estació. **A–C**, Various morphologies of the m1 of *Mimomys savini* adults: **A**, right m1 IPS73546, adult individual with enamel islet, enamel-free areas, and closing roots, in **A1**, lingual; **A2**, occlusal; **A3**, buccal views; **B**, left m1 IPS73547, adult individual without enamel islet with enamel-free areas and closing roots, in **B1**, buccal; **B2**, occlusal; **B3**, lingual views; **C**, right m1 (IPS73548), adult individual without enamel islet, with enamel-free areas and completely closed/formed roots, in **C1**, lingual; **C2**, occlusal; **C3**, buccal views. **D–E**, Left m1 of *Ungaromys nanus*: IPS73523, in **D1**, buccal; **D2**, occlusal; **D3**, lingual views; IPS73524, in **E1**, buccal; **E2**, occlusal; **E3**, lingual views. **F–G**, right m1 of *Iberomys huescarensis* in occlusal view: **F**, IPS73529; **G**, IPS73530. **H**, Right m2 of *Talpa europaea* IPS73586 in **H1**, occlusal; **H2**, buccal views. **I–J**, Right M1 of *Apodemus* cf. *sylvaticus* in occlusal view: **I**, IPS73587; **J**, IPS73588. **K**, Right m1 of *Eliomys quercinus* IPS73579 in occlusal view. **L**, Right mandible of *Crocidura* sp. IPS73594 in buccal view. **M–N**, Partial humeri of *Talpa europaea*: **M**, left fragment IPS73592 in **M1**, posterior; **M2**, anterior views; **N**, right fragment IPS73593 in **N1**, posterior; **N2,** anterior views. **O**, Right partial m1 of *Stenocranius gregaloides* IPS49472 in occlusal view.

Taxa	MNI	NR	Habitat	%
Ungaromys nanus	4	6	indet	--
Iberomys huescarensis	10	18	Open humid	18.52
Mimomys savini	24	37	Water edge	44.44
Eliomys quercinus	4	9	Woodland and woodland margin	7.41
Apodemus cf. *sylvaticus*	9	45	Woodland and woodland margin	16.67
Stenocranius gregaloides	1	1	Open humid	1.85
Hystrix refossa	1	2	Open dry	1.85
Talpa europaea	2	5	Open humid	3.7
Crocidura sp.	3	6	Open dry	5.56

Table 1. Correspondence between taxa, habitat and the percentage of the landscape represented by this habitat: **MNI**, minimum number of individuals; **NR**, total number of remains.

2.2 - BIOCHRONOLOGY

Several previously-published papers on Vallparadís Estació provide biochronological inferences for layer EVT7 based on the rodent sample, with emphasis on the morphologic similarities of *I. huescarensis* with those from other sites (Martínez et al., 2010; García et al., 2011; Madurell-Malapeira et al., 2010a; Minwer-Barakat et al., 2011). To further reassess previous biochronological inferences, here we rely on the morphologic and biometric comparison of remains of *M. savini* from EVT7 with those from other sites in the Iberian Peninsula (Gran Dolina TD4-TD6, Fuente Nueva 3 and Barranco León D). The evolutionary trends previously documented in *M. savini*—including the loss of *Mimomys*-like characters as well as a size increase (Viriot et al., 1990; Chaline et al., 1999; Lozano-Fernández et al., 2012, 2013a,b)—enables us to ascertain the relative age between EVT7 and other localities, thereby providing a more refined chronology for the former.

Populations with larger individuals will correspond to younger sites (Viriot et al., 1990; Chaline et al., 1999; Lozano-Fernández et al., 2012, 2013a,b). The size

of *M. savini* is calculated based on occlusal mesiodistal length and buccolingual width of the first lower molar (Fig. 3). Similarly, populations with lower percentages of *Mimomys*-like characters (as enamel islet and *Mimomys*-ridge; Fig. 3) will be also younger (Koenigswald, 1982; Koenigswald and Kolfschoten, 1996; Cuenca-Bescós et al., 1999; Lozano-Fernández et al., 2012; 2013a; 2013b).

In this study, measurements were taken to the nearest 0.1 mm using the image-treatment software Adobe PhotoShop CS6 on photographs taken with an Infinity X digital camera coupled to an Olympus SZ-40 stereomicroscope. This software allows one to obtain actual measurements based on photographs of flat surfaces, which in this case correspond to the occlusal plane of the studied teeth.

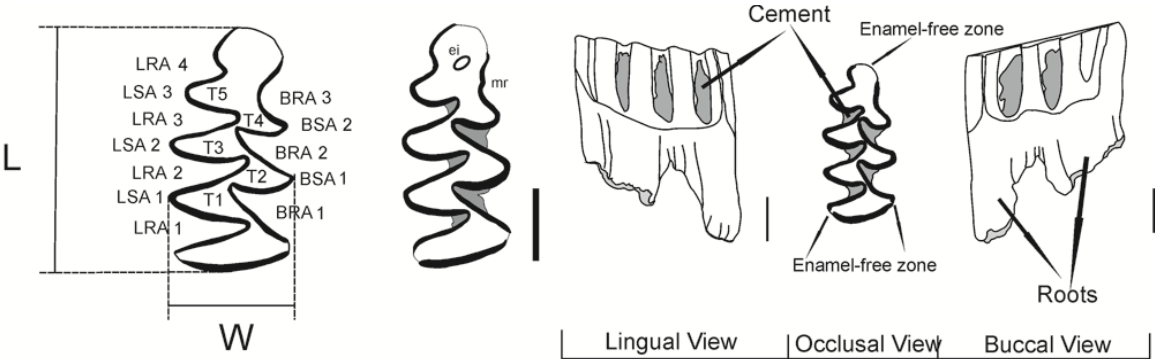

Figure 3. Nomenclature of occlusal morphological details of the m1 of *Mimomys savini* and measurements employed in this study. Abbreviations: **L**, mesiodistal length; **W**, buccolingual width; **T1–T5**, triangles that constitute the tooth; **LRA**, lingual re-entrant angles; **BRA**, buccal re-entrant angles; **LSA**, lingual salient angles; **BSA**, buccal salient angles; **ei**, enamel islet; **mr**, *Mimomys*-ridge. Modified from Meulen (1973), Heinrich (1978) and Rabeder (1981).

2.3 - PALEOENVIRONMENTAL RECONSTRUCTION

In order to infer the palaeoenvironment of layer EVT7, we employed the "optimum habitat" method (Andrews, 1990; Cuenca-Bescós et al., 2005; 2012; López Antoñanzas and Cuenca-Bescós, 2002), which relies on the whole micromammal assemblage, rather than merely on the presence of one or two species. This method assumes that the quantitative distribution of small-mammal taxa in the studied sample provides information on the paleoenvironment during the formation of the site. Each taxon from EVT7 has been assigned to a habitat preference, following previous studies (Chaline, 1985; López Antoñanzas and Cuenca-Bescós, 2002; see Table 1). According to such habitat preferences, the record of *M. savini* would indicate a "water-edge" type of habitat (along streams, lakes and ponds); those of *I. huescarensis*, *Stenocranius gregaloides* and *Talpa europaea* would be indicative of an "open humid" habitat (evergreen meadows with high pasture and suitable topsoil for animal burrowing throughout the year); those of *Crocidura* sp. and *Hystrix refossa* would indicate an "open dry" habitat (meadows under seasonal climate change); and those of *Eliomys quercinus* and *Apodemus* cf. *sylvaticus* would correspond to a "woodland and woodland margin" type of habitat. *Ungaromys nanus*, also present in EVT7, has not been assigned to any preferred habitat by previous authors (Table 1), and hence it has not been employed in our palaeoenvironmental reconstruction for EVT7.

3 - RESULTS AND DISCUSSION

3.1 - BIOCHRONOLOGICAL IMPLICATIONS

The small-mammal assemblage from layer EVT7 is similar to that from Gran Dolina layers TD4-TD6 (Cuenca-Bescós et al., 1995, 1999, 2010; Madurell-Malapeira et al., 2010a; Minwer-Barakat et al., 2011). In contrast, it differs from those of Fuente Nueva 3 and Barranco León D, mainly in the absence of *Allophaiomys lavocati* (Agustí 1986; Agustí and Madurell-Malapeira 2003; Agustí et al., 2010; Minwer-Barakat et al., 2011).

Mimomys savini is characteristic of the Biharian (Fejfar et al., 1998), whereas *I. huescarensis* further indicates an age corresponding to the late Biharian (Cuenca-Bescós et al., 1999, 2010; Madurell-Malapeira et al., 2010a; López-García et al., 2012). The size and occlusal morphology of *M. savini* further enables a refinement of the dating of localities, such as layer EVT7, in which both *M. savini* and *I. huescarensis* are recorded.

The percentage of individuals with an enamel islet and a *Mimomys*-ridge in the EVT7 sample is 12.5%. This figure falls between the percentages in the samples from TD6 (8%) and TD4 (14.2%; Lozano-Fernández et al., 2013a), and far below those in the Fuente Nueva 3 (34.4%) and Barranco León D (24.5%) samples (Lozano-Fernández et al., 2013a). This leads us to conclude that the age of EVT7 probably lies between those of layers TD4 and TD6 of Gran Dolina (Atapuerca). In turn, the mean m1 size of *M. savini* from EVT7 (L = 3.47 mm; W = 1.51 mm) most closely resembles the figures from the TD5a and TD5b samples, being larger than those from Barranco León D, Fuente Nueva 3 and Gran Dolina TD4B, but smaller smaller than those from Gran Dolina TD6-1 and

TD6-2 (Table 2, Fig. 4). Therefore, the size of the m1 in the EVT7 sample is compatible with the intermediate age between TD4 and TD6 suggested by the morphological features, but further suggests an age older than TD6. A chronological range between 0.99 and 0.94 Ma has been previously estimated by Moreno (2011) for TD3-4 and TD5, thereby indicating an age younger than 0.99 Ma but not younger than 0.94 Ma for the EVT7 assemblage.

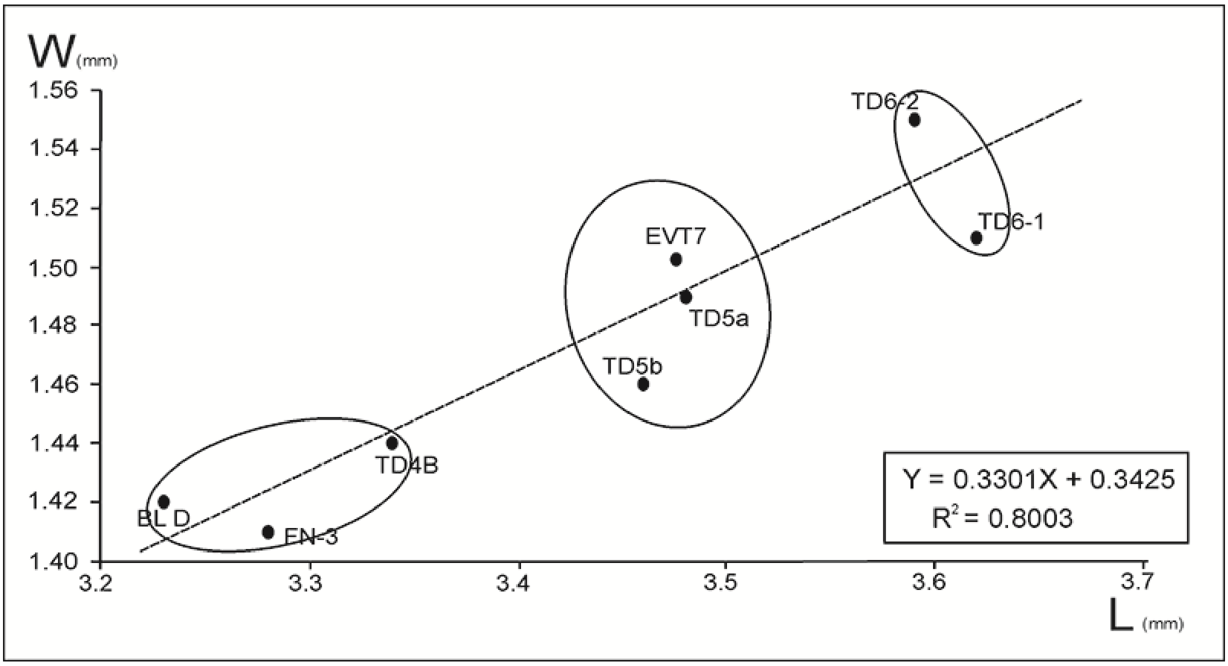

Figure 4. Bivariate plot of average values of m1 buccolingual width (W) vs. mesiodistal length (L) in various Iberian populations of *Mimomys savini*. The line depicts the least-squares regression among all the samples (W = 0.330 L + 0.343, R^2 = 0.800), while hand-drawn ellipses group localities according to their biometric similarities. Abbreviations: BL D, Barranco León D; FN-3, Fuente Nueva 3; TD, Gran Dolina levels; EVT7, Vallparadís Estació layer 7. Note that EVT7 shows similar values to TD5b and TD5a.

	NR	L mean	L max	L min	SD	CI 95%	W mean	W max	W min	SD	CI 95%
TD6-1	9	3.62	3.82	3.26	0.17	0.111	1.51	1.64	1.38	0.08	0.052
TD6-2	10	3.59	3.81	3.36	0.17	0.105	1.55	1.69	1.41	0.11	0.068
TD5a	103	3.48	3.82	3.11	0.14	0.027	1.49	1.67	1.26	0.07	0.013
TD5b	137	3.46	3.78	3.04	0.14	0.023	1.46	1.67	1.27	0.07	0.011
TD4B	12	3.34	3.6	3.25	0.14	0.079	1.44	1.52	1.31	0.02	0.011
FN-3	42	3.28	3.41	3.05	0.09	0.027	1.41	1.59	1.18	0.08	0.024
BL D	34	3.23	3.4	2.92	0.12	0.040	1.42	1.63	1.29	0.07	0.023
EVT7	36	3.47	3.73	3.14	0.15	0.048	1.51	1.69	1.46	0.06	0.019

Table 2. Descriptive statistics of mesiodistal length (L) and buccolingual width (W) of the m1 of *M. savini* studied in this paper. Abbreviations: BL D, Barranco León D; FN-3, Fuente Nueva 3; TD4b, TD5b, TD5a, TD6-2, TD6-1, Gran Dolina; EVT7, Vallparadís Estació layer EVT7. NR refers to the total number of remains studied, SD refers to standard desviation and CI refers to confidence interval.

The results of our morphologic and biometric study of the sample of *M. savini* from EVT7 enables us to provide an estimated chronological range of 0.99–0.94 Ma for this locality. Such a chronology is entirely consistent with previous age estimates for EVT7, based on large-mammal biochronology (Epivillafranchian, between 1.1 and 0.78 Ma; Madurell-Malapeira et al., 2010a), magnetostratigraphic correlation (≤0.99 Ma; Madurell-Malapeira et al., 2010a), and absolute datings (ESR and U-series analysis, 0.83 ±0.07 Ma; Duval et al., 2011). Some previous works noted a discrepancy in the results obtained using rodent biochronology with the above-mentioned previous age estimates for EVT7. Thus, Martínez et al. (2010) and García et al. (2011) proposed an age older than 1.0 Ma, whereas Madurell-Malapeira et al. (2010a, 2012) estimated the age of EVT7 at ca. 0.83 Ma. The age estimate favoured by Martínez et al. (2010) and Garcia et al. (2011) was based on a comparison of the remains of *I. huescarensis* from EVT7 with those from Gran Dolina TD4 and Sima del

Elefante. According to these authors, EVT7 would be older than TD4 (ca. 1.0-0.94; Moreno, 2011; Moreno et al., 2012) and closer in age to Sima del Elefante (ca. 1.2 Ma; Carbonell et al., 2008). However, *I. huescarensis* has been never recorder from Sima del Elefante (Cuenca-Bescós et al., 2010, Madurell-Malapeira et al., 2012). Moreover, Martínez et al. (2010) and Garcia et al. (2011) further supported a similar chronology between EVT7 and Sima del Elefante on the purported absence of the advanced microtine *Stenocranius gregaloides*, which in fact is recorded from EVT7 (Minwer-Barakat et al., 2011). Given the absence of *I. huescarensis* from Sima del Elefante, and the presence of *S. gregaloides* in EVT7, there is no biostratigraphic basis for supporting a similarly old chronology for the latter locality (Madurell-Malapeira et al., 2012).

The older chronology favoured by Martínez et al. (2010) and Garcia et al. (2011) is further contradicted by the above-mentioned age estimates derived by magnetostratigraphic correlation and absolute datings, as well as by the results derived in this paper. The scarcity of remains of *I. huescarensis* from EVT7 might have biased the age estimates provided by the above-mentioned authors. This taxon is recorded at EVT7 by a minimum number of 10 individuals, contrasting with the larger sample (a minimum of 24 individuals; see Table 1) available for *M. savini*, which is the most abundant small mammal from this locality. Therefore, the results derived in this paper based on the morphology and biometry of the latter taxon seem a priori more reliable than those relying exclusively on *I. huescarensis*.

Contrasting with the older chronology favoured by Martínez et al. (2010) and Garcia et al. (2011), Madurell-Malapeira et al. (2010a) and Minwer-Barakat et al. (2011) correlated EVT7 to the *A. chalinei* Zone, mainly on the basis of the

correlation between EVT7 and levels from the neighbouring site of Cal Guardiola (Minwer-Barakat et al., 2011). In the Iberian Peninsula, the *A. chalinei* Zone is defined by the association comprising *I. huescarensis*, *Stenocranius gregaloides*, *Victoriamys chalinei* and *M. savini* (Cuenca-Bescós et al., 2010), spanning from 0.9 to 0.78 Ma—although Minwer-Barakat et al., 2011 finally estimated the chronological range of EVT7 between 0.99 and 0.78 Ma. This chronological range is compatible with the results reported in this paper, which nevertheless further allow us to propose a more refined chronological range between 0.99 and 0.94 Ma.

Minwer-Barakat et al. (2011) established the presence of *S. gregaloides* in EVT7, which together with the record of *M. savini* and *I. huescarensis* led this authors to correlate this locality the *A. chalinei* biozone. However, the simultaneous record of *U. nanus* at EVT7 (see Fig. 2; previously cited as *Ungaromys* sp. by Martínez et al., 2010) has additional biostratigraphic implications, since this species is considered to form part of pre-Jaramillo faunas (Cuenca-Bescós et al., 2010), with a last appearance datum (LAD) of ca. 0.99 Ma. The identification of *U. nanus* and the study of the remains of *M. savini* from EVT7 provided in this paper, together with the identifications previously provided by Minwer-Barakat et al. (2011), led us to estimate a chronological range of 0.99–0.94 Ma for EVT7—probably closer to 0.99 Ma, given the presence of *U. nanus*. Our age estimate for EVT7 is completely consistent with previously-published data provided by large-mammal biochronology, palaeomagnetism and absolute radiometric datings (see references above).

3.2 - PALEOENVIRONMENTAL IMPLICATIONS

We infer the dominant landscape from EVT7 based on the minimum number of individuals for each small mammal taxon (Table 1) and the percentage that they represent within the micromammailan assemblage from this locality (Table 1; Fig. 5). According to our results (Fig. 5 and Table 1), the landscape would have been dominated by areas with water (water edge, 44.44%) and wetlands (open humid, 24.07%), with a scarce representation of woodlands and dry meadowlands (woodland, woodland margin, 24.08%; open dry, 7.41%).

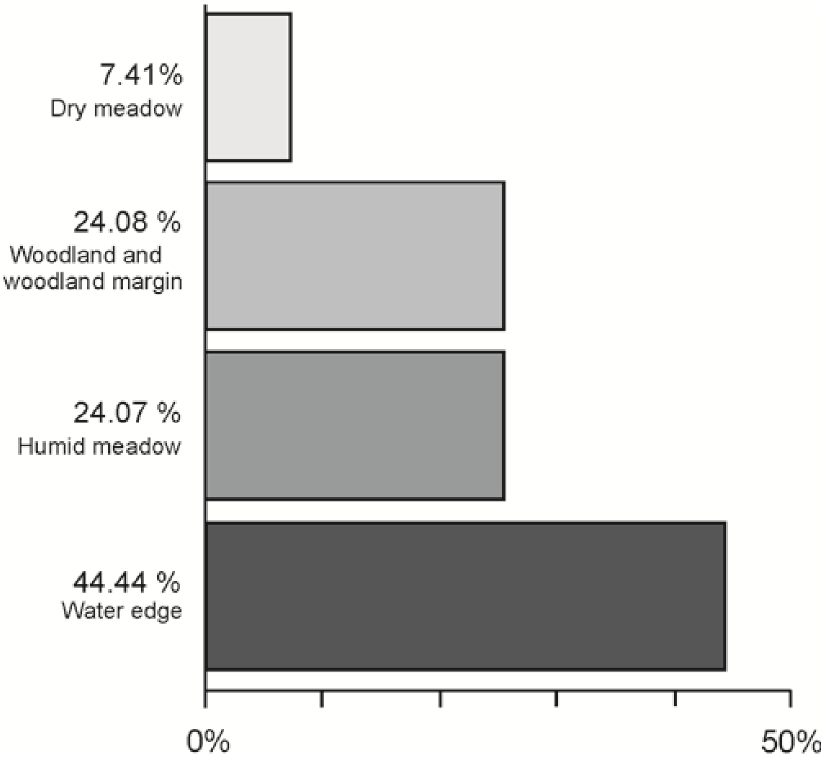

Figure 5. Interpretation of the landscape of layer EVT7 on the basis of its small-mammal content.

In particular, the small-mammal assemblage from layer EVT7 is characterized by the predominance of *M. savini* and *I. huescarensis* (Table 1), whose preferences are considered to correspond to humid habitats characterized by the presence of water (Andrews, 1990; Cuenca-Bescós et al., 2005; 2012;

López Antoñanzas and Cuenca-Bescós, 2002). We therefore conclude that water masses would have been prevalent in the landscape of EVT7. This interpretation is further corroborated by the presence of abundant remains of the semiaquatic hippopotamus *Hippopotamus antiquus* (Kahlke, 2006; Madurell-Malapeira et al., 2010a, 2011b, 2012)—which represents 30.3% of the macromammal identifiable specimens (Madurell-Malapeira et al., 2011b)—as well as by the record of the aquatic snake *Natrix natrix* in this layer (Martínez et al., 2010).

On the other hand, the presence (albeit with a lower prevalence) of *Eliomys quercinus* and *Apodemus* cf. *sylvaticus* at EVT7 would be indicative of some woody areas and woodland margins being present nearby in the landscape. The later conclusion is further reinforced by the abundance of large mammal species with preference for open parklands (e.g., savanna-like environments and sparse woodlands), such as *Dama vallonnetensis*, *Stephanorhinus hundsheimensis* and *Equus altidens*—which respectively represent 17.9%, 14.7% and 13.5% of the identifiable large mammal specimens (Madurell-Malapeira et al., 2011b). Macromammal species with preference for more wooded habitats with abundant water in the vicinity, such as *Panthera gombaszoegensis* and *Macaca sylvanus* cf. *florentina*—respectively, 0.9% and 0.1% of the large mammal identifiable specimens (Madurell-Malapeira et al., 2011b)—are more scarcely represented; however, in this regard it should be taken into account that carnivorans and primates generally display lower population densities than ungulates, thus being frequently less common among fossil thanotocenoces. Among micromammals, the record of *Hystrix refossa* and

Crocidura sp., albeit in a low proportion, indicates the existence of even more open and drier areas in the vicinity of EVT7. This interpretation is further supported by the presence at this locality of the toad *Pelobates* cf. *cultripes* and the ladder snake cf. *Rhinechis* sp. (Martínez et al., 2010), which are characteristic of open dry zones with rocky soils and little or no vegetation (Pleguezuelos and Martínez-Rica, 1997; Pleguezuelos et al., 2002).

The coexistence of *M. savini* and *I. huescarensis* in a large proportion among the micromammal assemblage, and the lower prevalence of *Hystrix refossa* and *Stenocranius gregaloides,* suggest interglacial conditions for EVT7—as is the case in the upper part of layer TD5 of Gran Dolina (López Antoñanzas and Cuenca-Bescós, 2002). In TD5, *Stenocranius gregaloides* is replaced by *Terricola arvalidens* and *Microtus seseae*, and an increase in the relative abundance of *Mimomys savini* and *Pliomys episcopalism* is also observed—indicating interglacial conditions for this locality (López Antoñanzas and Cuenca-Bescós, 2002). The presence of abundant remains of *Hippopotamus antiquus* in EVT7 (Madurell-Malapeira et al., 2010a, 2011b, 2012) further confirms the existence of warm and humid conditions for this locality, since this extinct hippo (closely related to the extant *Hippopotamus amphibius*) is unlikely to have tolerated very cold temperatures leading to the seasonal freezing of the rivers they inhabited (Eltringham, 1999; Kahlke, 2006; Madurell-Malapeira, 2006; Madurell-Malapeira et al., 2010a).

4 - CONCLUSIONS

The chronology of layer EVT7 of the Vallparadís Estació site (Terrassa, Vallès-Penedès Basin, NW Iberian Peninsula) has been previously disputed in previous papers dealing with the micromammal assemblage from that locality. Thus, some scholars supported an age close to the Early-Middle Pleistocene boundary (ca. 0.83 Ma), whereas other researchers favored an older age preceding the Jaramillo magnetostratigraphic subchron (ca. 1.2 Ma). Here we provide additional data from the small mammal assemblage of EVT7, with emphasis on the commonest species (*Mimomys savini*), which allows us to further refine previous age estimates for this locality, as well as to provide a paleoenvironmental reconstruction.

With regard to biochronology, both the percentage of individuals of *M. savini* displaying an enamel islet and/or a *Mimomys*-ridge as well as average length and width values for the m1 of this species enable us to propose a chronological range for EVT7 spanning between 0.99 and 0.94 Ma. Such an age, similar to that inferred for layer TD5 of Gran Dolina, is further reinforced by the record at EVT7 of *Ungaromys nanus*, which is a common species in pre-Jaramillo faunas with LAD at ca. 0.99 Ma. Our results therefore allow us to discount older (ca. 1.2 Ma) ages proposed for EVT7 by some researchers, which unlike the age favoured here, are in disagreement with large-mammal biostratigraphic data as well as absolute radiometric datings for ther site.

Regarding paleoenviromental inferences, the application of the "optimum habitat" method to the small mammal assemblage from EVT7 enables us to infer interglacial climatic conditions, as well as a predominantly humid paleoenvironment with abundant water masses and more or less wooded areas, together with a few more open and drier environments nearby. Overall, we conclude that the faunal community from EVT7 probably corresponds to an ecotone, in which taxa characteristic of open environments coexisted with other species more typical from woodland areas. Such a transitional habitat would have been situated in the vicinity of a lacustrine or fluviatile area with a regular income and/or constant flow of water.

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REFERENCES

Agustí, J., 1986. Synthèse biostratigraphique du Plio-Pleistocène de Guadix Baza (province de Granada, sud est de l'Espagne). Geobios 19, 505–510.

Agustí, J., Madurell, J., 2003. Los arvicólidos (Muroidea, Rodentia, Mammalia) del Pleistoceno inferior de Barranco León y Fuente Nueva 3 (Orce, Granada). Datos preliminares. In: Toro-Moyano, I., Agustí, J., Martínez-Navarro, B. (Eds.), El Pleistoceno inferior de Barranco León y de Fuente Nueva 3, Orce (Granada), Junta de Andalucía. Consejería de Cultura, Sevilla, pp. 137–145.

Agustí, J., Blain, H-A., Furió, M., De Marfá, R., Santos-Cubedo, A., 2010. The early Pleistocene small vertebrate succession from the Orce region (Guadix-Baza Basin, SE Spain) and its bearing on the first human occupation of Europe. Quat. Int. 223–224, 162–169.

Andrews, P. 1990. Owls, Caves and Fossils. Predation. Preservation and Accumulation of Small Mammals Bones in Cave, with an analysis of the Pleistocene Cave Faunas from Westbury-sub-Mendip, Somerset, UK. The University Chicago Press, London.

Alba, D.M., Moyà-Solà, S., Madurell, J., Aurell, J. 2008. Dentognathic remains of *Macaca* (Primates, Cercopithecidae) from the late early Pleistocene of Terrassa (Catalonia, Spain). J. Hum. Evol. 55, 1160–1163.

Chaline, J. 1985. Histoire de l'Homme et des Climats au Quaternaire. Doin, Paris.

Chaline, J., Brunet-Lecomte, P., Montuire, S., Viriot, L., Courant, F. 1999. Anatomy of the arvicoline radiation (Rodentia): palaeogeographical, palaecoecological history and evolutionary data. Ann. Zool. Fenn. 36, 239–267.

Cuenca-Bescós, G., Canudo, J.I., Laplana, C. 1995. Los arvicólidos (Rodentia, Mammalia) de los niveles inferiores de Gran Dolina (Pleistoceno Inferior, Atapuerca, Burgos, España). Rev. Esp. Paleontol. 10, 202–218.

Cuenca-Bescós, G., Laplana, C., Canudo, J.L. 1999. Biochronological implications of the Arvicolidae (Rodentia, Mammalia) from the lower pleistocene hominid-bearing level of Trinchera Dolina 6 (TD6, Atapuerca, Spain). J. Hum. Evol. 37, 353–373.

Cuenca-Bescós, G., Rofes, J., García-Pimienta, J.C. 2005. Early Europeans and environmental change across the Early–Middle Pleistocene transition: small mammalian evidence from Trinchera Dolina cave, Atapuerca, Spain. In: Head, M.J., Gibbard, P.L. (Eds.), Early–Middle Pleistocene Transitions: the Land–Ocean Evidence. Geological Society, London, pp. 277–286.

Cuenca-Bescós, G., Rofes, J., López-García, J.M., Blain, H.-A., de Marfà, J.R., Galindo-Pellicena, M.A., Bennàsar-Serra, M.L., Melero-Rubio, M., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E. 2010. Biochronology of Spain Quaternary small vertebrate faunas. Quat. Int. 212, 109–119.

Cuenca-Bescós, G., Rofes, J., López-García, J.M., Blain, H.-A., Rabal-Garcés, R., Sauqué, V., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell,E. 2013. The small mammals of Sima del Elefante (Atapuerca, Spain) and the first entrance of *Homo* in Western Europe. Quat. Int. 295, 28–38.

Eltringham, S.K., 1999. The Hippos. Academic Press, Cambridge, 184 pp.

Falguères, C., Bahain, J.J., Yokoyama, Y., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., Bischoff, J.L., Dolo, J.M. 1999. Earliest humans in Europe: the age of TD6 Gran Dolina, Atapuerca, Spain. J. Hum. Evol. 37, 343–352.

Fejfar, O., Heinrich, W.-D., Lindsay, E.H. 1998. Updating the Neogene rodent biochronology in Europe. In: van Kolfschoten, T., Gibbard, P.L. (Eds.), The Dawn of the Quaternary. Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen, Harlem, pp. 533–554.

Garcia, J., Martínez, K., Carbonell, E. 2011. Continuity of the first human occupation in the Iberian Peninsula: Closing the archaeological gap. C. R. Palevol 10, 279–284.

Kahlke, R.-D. 2006. Untermassfeld: a late Early Pleistocene (Epivillafranchian) fossil site near Meiningen (Thuringia, Germany) and its position in the development of the European mammal fauna. British Archaeological Reports, International Series 1578, 1–144.

Koenigswald, W. von 1982. Zum Verständnis der Morphologie der Wühlamusmolaren (Arvicolidae, Rodentia, Mammalia). Z. geol. Wiss. 10, 951–962.

Koenigswald, W. von, Kolfschoten T. van 1996. The *Mimomys–Arvicola* boundary and the enamel thickness quotient (SDQ) of *Arvicola* as stratigraphic markers in the Middle Pleistocene. In: Turner, C. (Ed.), Proceedings of the SEQS Cromer Symposium, Norwich/United Kingdom, The Early–Middle Pleistocene in Europe. Norwich, pp. 211–226.

López-Antoñanzas, R., Cuenca-Bescós, G. 2002. The Gran Dolina site (Lower to Middle Pleistocene, Atapuerca, Burgos, Spain): new palaeoenvironmental data based on the distribution of small mammals. Palaeogeogr. Palaeoclimatol. Palaeoecol. 186, 311–334.

López-García, J.M., Cuenca-Bescós, G., Blain, H.-A., Cáceres, I., García, N., Made, J. van der, Gutierrez, J.M., Santiago, A., Giles Pacheco, F. 2012. Biochronological data inferred from the Early Pleistocene Arvicolinae (Mammalia, Rodentia) of the El Chaparral site (Sierra del Chaparral, Cádiz, southwestern Spain). J. Vert. Paleontol. 32, 1149–1156.

Lozano-Fernández, I., Agustí, J., Cuenca-Bescós, G. 2012. Evolución de *Mimomys savini* (Rodentia, Mammalia) en la Península Ibérica durante el Pleistoceno inferior. In: Martínez-Pérez, C., Furió, M., Santos-Cubedo, A., Poza, B. (Eds.), Paleodiversity and Paleoecology of Iberian Ecosystems. Sot de Chera, Valencia, pp. 131–132.

Lozano-Fernández, I., Agustí, J., Cuenca-Bescós, G., Blain, H.-A., López-García, J. M., Vallverdú, J. 2013a. Pleistocene evolutionary trends in dental morphology of *Mimomys savini* (Rodentia, Mammalia) from Iberian Peninsula and discussion about the origin of the genus *Arvicola*. Quaternaire 24, 165–176.

Lozano-Fernández, I., Cuenca-Bescós, G., Blain, H.-A., López-García, J. M., Agustí, J. 2013b. *Mimomys savini* size evolution in the Early Pleistocene of south-western Europe and possible biochronological implications. Quat. Sci. Rev. 76, 96–101.

Madurell-Malapeira, J. 2006. Estudi de les restes d'*Hippopotamus antiquus* (Hippopotamidae, Mammalia) del jaciment del Pleistocè inferior de Cal Guardiola (Terrassa). Master thesis, Universitat Autònoma de Bercelona, Spain.

Madurell-Malapeira, J., Minwer-Barakat, R., Alba, D.M., Garcés, M., Gómez, M., Aurell-Garrido, J., Ros-Montoya, S., Moyà-Solà, S., Berástegui, X. 2010a. The Vallparadís section (Terrassa, Iberian Peninsula) and the latest Villafranchian faunas of Europe. Quat. Sci. Rev. 29, 3972–3982.

Madurell-Malapeira, J., Alba, D.M., Moyà-Solà, S., Aurell-Garrido, J. 2010b. The Iberian record of the puma-like cat *Puma pardoides* (Carnivora, Felidae). C. R. Palevol 9, 55–62.

Madurell-Malapeira, J., Alba, D.M., Marmi, J., Aurell, J., Moyà-Solà, S. 2011a. The taxonomic status of European Plio-Pleistocene badgers. J. Vert. Paleontol. 31, 885–894.

Madurell-Malapeira**, J.**, Alba, D.M., Aurell-Garrido, J., Moyà-Solà, S. 2011b. Taphonomic approach to the last Villafranchian faunas of Europe. The layer 7 of the Vallparadís Estació local Section (Terrassa, NE Iberian Peninsula). In: Pérez-García, A., Gascó, F., Gasulla, J.M., Escaso, F. (Eds.), Viajando a Mundos Pretéritos. Ayuntamiento de Morella, Morella, pp. 203–210.

Madurell-Malapeira, J., Alba, D.M., Minwer-Barakat, R., Aurell-Garrido, J., Moyà-Solà, S. 2012. Early human dispersals into the Iberian Peninsula: A comment on Martínez et al. (2010) and Garcia et al. (2011). J. Hum. Evol. 62, 169–173.

Madurell-Malapeira, J., Ros-Montoya, S., Espigares, M.P., Alba, D.M., Aurell-Garrido, J. 2014. Villafranchian large mammals from the Iberian Peninsula: Paleogeography, paleoecology and dispersal events. J. Iber. Geol. In Press.

Martínez, K., Garcia, J., Carbonell, E., Agustí, J., Bahain, J-J., Blain, H-A., Burjachs, F., Cáceres, I., Duval, M., Falguères, C., Gómez, M., Huguet, R. 2010. A new Lower Pleistocene archeological site in Europe (Vallparadís, Barcelona, Spain). Proc. Natl. Acad. Sci. USA 107, 5762–5767.

Minwer-Barakat, R., Madurell-Malapeira, J., Alba, D.M., Aurell-Garrido, J., De Esteban-Trivigno, S., Moyà-Solà, S. 2011. Pleistocene rodents from the Torrent de Vallparadís section (Terrassa, Northeastern Spain) and biochronological implications. J. Vert. Paleontol. 31, 849–865.

Moreno, D. 2011. Datation par esr de quartz optiquement blanchis (ESR-OB) de la région de atapuerca (Burgos, Espagne). Application au site préhistorique de Gran Dolina (contexte karstique) et aux systèmes fluviatiles quaternaires de l'Arlanzón et l'Arlanza. Ph.D. dissertation, Univeristat Rovira i Virgili, Tarragona and Muséum National d’Histoire Naturelle, Paris.

Moreno, D., Falguères, C., Pérez-González, A., Duval, M., Voinchet, P., Benito-Calvo, A., Ortega, A.I., Bahain, J.-J., Sala, R., Carbonell, E., Bermúdez de Castro, J.M., Arsuaga, J.L. 2012. ESR chronology of alluvial deposits in the Arlanzón valley (Atapuerca, Spain): Contemporaneity with Atapuerca Gran Dolina site. Quat. Geochronol. 10, 418–423.

Viriot, L., Chaline, J., Schaaf, A. 1990. Quantification du gradualisme phylétique de *Mimomys occitanus* à *Mimomys ostramosensis* (Arvicolinae, Rodentia) à l'aide de l'analyse d'image. C. R. Acad. .Sci. Paris 310,1755–1760.

CAPÍTULO 5

BIOCRONOLOGÍA DE LOS PRIMEROS RESTOS HOMÍNIDOS EN EUROPA USANDO LA RATA DE AGUA *MIMOMYS SAVINI*: FUENTE NUEVA 3 Y BARRANCO LEÓN D, CUENCA GUADIX-BAZA, SURESTE DE ESPAÑA

Enviado a la revista Historical Biology

BIOCHRONOLOGY OF THE FIRST HOMINID REMAINS IN EUROPE USING THE VOLE *MIMOMYS SAVINI*: FUENTE NUEVA 3 AND BARRANCO LEÓN D, GUADIX-BAZA BASIN, SOUTHEASTERN SPAIN

Iván Lozano-Fernández [a,b*], Hugues-Alexandre Blain [a,b], Juan Manuel López-García [c], Jordi Agustí [a,b,d],

[a] IPHES, Institut Català de Paleoecologia Humana i Evolució Social, C/ Escorxador s/n, E- 43003 Tarragona, Spain.

[b] Area de Prehistoria, Universitat Rovira i Virgili (URV), Avinguda de Catalunya 35, E-43002 Tarragona, Spain.

[c] Gruppo di Ricerca di Paleobiologia e Preistoria, Dipartimento di Studi Umanistiche, Università degli Studi di Ferrara, C.so Ercole I d'Este 32, I-44121 Ferrara, Italy.

[d] ICREA, Barcelona, Spain.

ABSTRACT

The sites of Barranco León D (BL-D) and Fuente Nueva 3 (FN-3) in the Guadix-Baza Basin (Granada, Spain), together with the site of Sima del Elefante in the Sierra de Atapuerca (Burgos, Spain), constitute the oldest record of the earliest hominid populations in the European continent west of Dmanisi (Georgia, Lesser Caucasus). Whereas in the case of Sima del Elefante there is unanimity among the scientific community regarding the chronology of the unit in which the hominid remains were found (Unit TE9c, 1.22 Ma), there is continuing debate on the chronology of the sites of the Guadix-Baza Basin (FN-3 and BL-D). This applies especially to BL-D, since the numerical datings published for this site have a very high error range (1.4 ± 0.38 Ma). In this paper the chronology of these two sites is determined using as a marker the morphological and morphometric changes undergone by *Mimomys savini* in its first lower molar (m1) over the course of its evolutionary history. It has been possible to confirm that the oldest human presence in the Guadix-Baza Basin and at Sima del Elefante (Atapuerca) share a similar chronology, dated to between 1.1 and 1.4 Ma. Apparently, the oldest site with human remains in Europe is seen to be Barranco León D, dated to 1.26 ± 0.13 Ma, followed by Level TE9c, dated to 1.22 ± 0.16 Ma, and Fuente Nueva 3, dated to 1.20 ± 0.12 Ma.

Keywords: Barranco León D, Fuente Nueva 3, biochronology, *Mimomys savini*, evolutionary trends, Early Pleistocene

1 - INTRODUCTION

Rodents are one of the most chronologically significant groups of mammals in the European Pleistocene, because they have diversified more than other taxa over this relatively short geological time span. Arvicolines (voles) are particularly useful for biochronological correlation, because of the abundance of their remains and their rapid evolutionary rates. In addition, some voles undertook long-range and rapid migrations and may have had extensive geographical distributions, which make interregional correlations possible (Minwer-Barakat et al. 2011). For these reasons, arvicolines have been frequently used to mark the biostratigraphic subdivisions of the Quaternary (Fejfar and Heinrich 1990; Agustí 1986; Sala and Masini 2007; Cuenca-Bescós et al. 2010; among many others).

Some groups of arvicolines present evolutionary trends like that of *Mimomys savini* (an Early/Middle Pleistocene arvicoline), which shows a tendency that brings its molar morphology successively closer to that of the genus *Arvicola* (Viriot et al. 1990; Chaline et al*.* 1999; Lozano-Fernández et al*.* 2013a). This tendency involves a reduction in the percentage of the adult population with an enamel islet and mimomys-ridge and an increase in the size of its first lower molar (m1). This increase was defined by Lozano-Fernández et al. (2013b) and Maul et al. (2013) as a linear tendency, thus establishing the size of the *M. savini* m1 as a biochronological tool.

The new palaeontological and archaeological evidence of recent years has challenged previous understandings of the early human settlements of Europe. Clear examples are the Georgian site of Dmanisi, dated to ~1.8 Ma (Vekua et al.

2002; Lordkipanidze et al. 2007; Ferring et al. 2011) and several sites in the Iberian Peninsula, such as Barranco León D (BL-D), dated to 1.4 Ma (Toro-Moyano et al. 2013), Fuente Nueva 3 (FN-3), dated to 1.19 Ma (Duval et al. 2012), and Sima del Elefante (TE9c), dated to 1.22 Ma (Carbonell et al. 2008).

The human remains of the Guadix-Baza Basin are represented by a human tooth and lithic artefacts attributed to Mode 1 from BL-D and by lithic artefacts attributed to Mode 1 from FN-3 (Martínez-Navarro et al. 1997; Oms et al. 2000; Toro-Moyano et al. 2011, 2013). The archaeo-palaeontological sites of BL-D and FN-3, which are separated by a distance of 4.1 km, are located 124 km north of the city of Granada (SE Spain), in the eastern part of the Guadix-Baza Basin (Fig. 1). These sites have yielded an abundant and diversified assemblage of large-mammal remains (Martínez-Navarro et al. 2003, 2010) as well as Mode 1 lithic tools that, along with the record from Sima del Elefante in Atapuerca, Burgos, Spain (Carbonell et al. 2008), are currently considered some of the oldest in western Europe (Martínez-Navarro et al. 1997; Oms et al. 2000; Toro et al. 2010).

From an archaeological point of view, these localities correspond to areas of early hominid exploitation of large carcasses (mainly hippopotamuses and elephants) on the shore of a large Pleistocene lake. The age of these sites has been established by means of biochronology, indicating their inclusion within the biozone of the rodent *Allophaiomys lavocati* (Agustí and Madurell 2003; Agustí et al. 2010), which, along with the presence of the caprine *Ammotragus europaeus* (Martínez-Navarro et al. 2010), points to an age of approximately 1.2 -1.4 Ma. According to Agustí et al. (2010), BL-D and FN-3 belong to the same biozone, between the site of Venta Micena and the sites of Huéscar 1 and Sima

del Elefante. Palaeomagnetic analysis locates them in the reverse chron below the Jaramillo normal event (Oms et al. 2003), and ESR data yield an age of 1.46 Ma for BL-D and 1.34-1.67 Ma for FN-3 (Duval 2008), both of which are consistent with this biochronological assignment. Recently, FN-3 has been assigned a date of 1.19 (± 0.21) Ma (Duval et al. 2012), and BL-D has been assigned a date of 1.4 (± 0.38) Ma (Toro-Moyano et al. 2013).

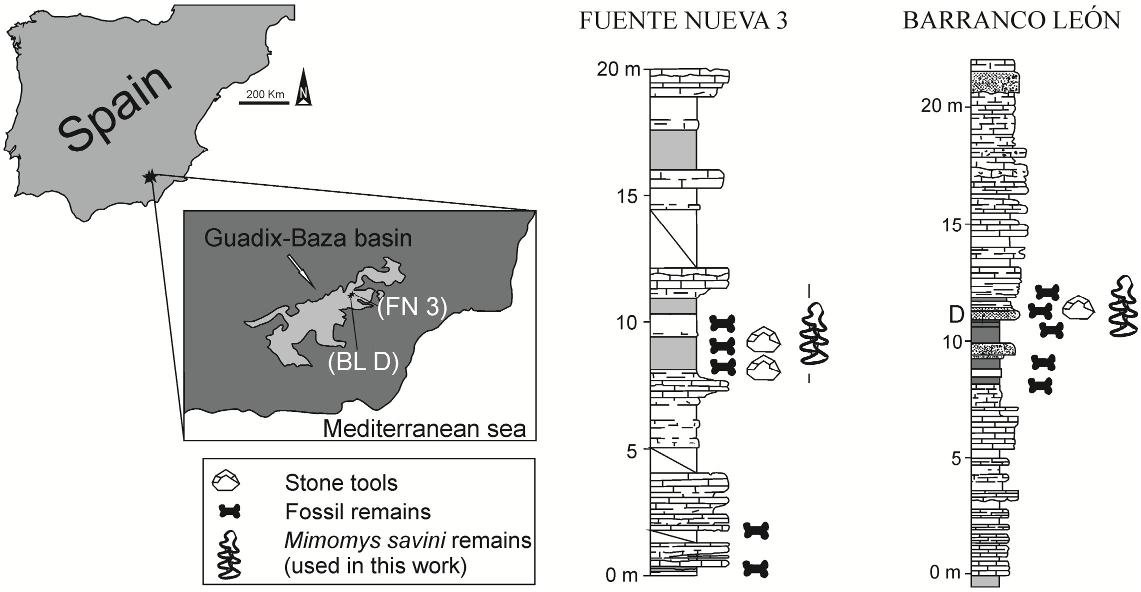

Figure 1. Geographical location of the sites of Fuente Nueva 3 (**FN-3**) and Barranco León D (**BL-D**) and their stratigraphic columns, with the position of the archaeo-palaeontological levels (modified from Toro-Moyano et al., 2010).

This paper aims to test the chronologies of FN-3 and BL-D (in particular BL-D since the numerical chronology published for this site displays a very high error range) and the chronological relationship between these two sites and TE9c at Sima del Elefante, using the evolution of the vole *Mimomys savini* for this purpose.

2 - MATERIAL AND METHODS

The sample from FN-3 consists of 61 m1 (only 42 are complete), and the sample from BL-D consists of 53 m1 (only 34 are complete) (Fig. 2 and Table 1).

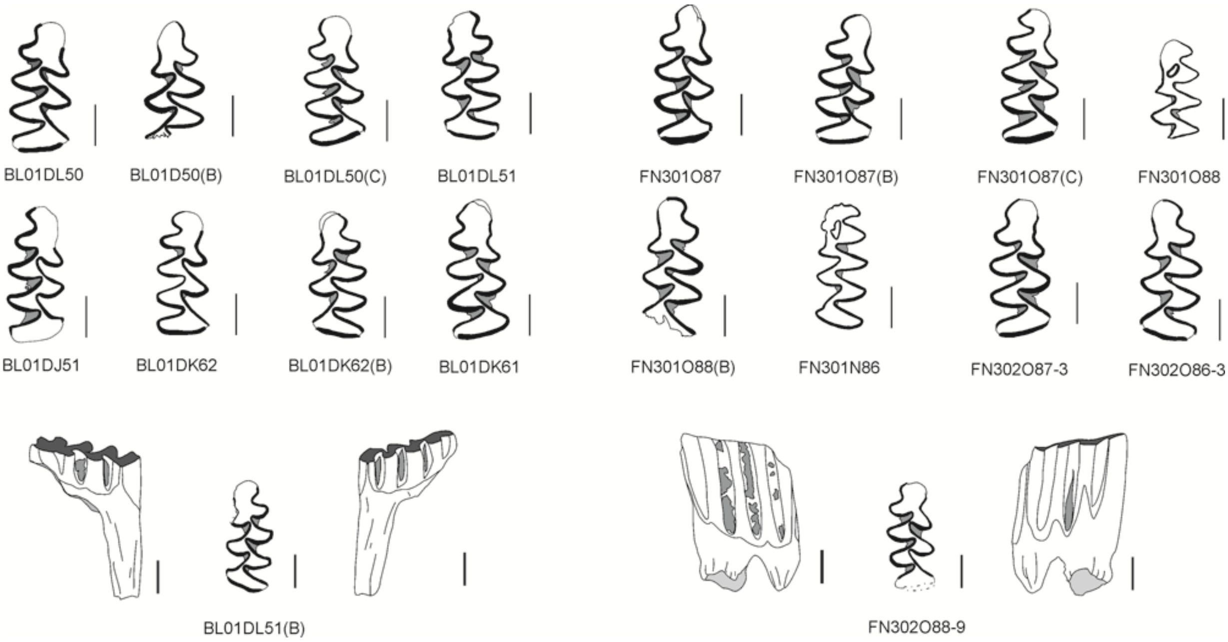

Figure 2. Some of the samples of *M. savini* used in the present paper: the abbreviation **BL01D** refers to Barranco León D, whereas **FN3** refers to Fuente Nueva 3. In samples **BL01DL51**, **BL01DK61** and **FN302O87-3** the mimomys-ridge can be discerned. Samples **FN301O88** and **FN301N86** corresponds to a juvenile individual and present an enamel islet. The lower part of the figure shows the lateral views of two different m1s from *M. savini*.

	n	n (complete)	ei	mr	ei and mr (%)		Length (mm)		Ds	Estimated age (Myr)	Estimated age (Myr)
						min	mean	max		Equation A	Equation B
BLD	53	34	2	11	24.52	2.92	3.23	3.4	0.11	1.13 ± 0.12	1.26 ± 0.13
FN3	61	42	4	17	34.42	3.05	3.28	3.41	0.09	1.09 ± 0.12	1.2 ± 0.12

Table 1. Data used in this paper: **n** corresponds to the total number of remains; **ei** to the number of individuals with an enamel islet; **Mr** to the number of individuals with a mimomys-ridge; **% ei and Mr** corresponds to the percentage of the population that present one or both characters; **Length** refers to the length of the occlusal plane of the m1 of *M. savini* in millimetres; and **Ds** corresponds to the standard deviation of each sample.

The lower first molars (m1) of *Mimomys savini* are characterized by an occlusal surface with a posterior lobe, five alternating triangles and an anteroconid complex; the presence of roots (except in the earliest stages of life); enamel with *Mimomys*-type differentiation (Heinrich 1978, 1987; Koenigswald and Kolfschoten 1996); cement in the re-entrant angles; T4 and T5 scarcely confluent; LRA3 and LRA4 deep, producing a pronounced LSA4; and the neck of the head of the anteroconid complex tends to be wide (Fig. 3).

The remains were recovered by wet-screening the sediment with Freudenthal tables (Daams and Freudenthal 1988). For the washing tables mesh sizes of 5 mm, 2 mm and 0.5 mm were used.

Remains of *Mimomys savini* were extracted from the 2-mm concentrate. Lower first molars only of adult specimens were used for the study in order to prevent the high morphological variability of juvenile forms from biasing the results. We considered the m1 to belong to an adult when enamel-free areas were visible on the occlusal surface and roots were closed or in the process of closing (Fig. 3).

For these teeth, the presence or absence of enamel islets and the mimomys-ridge was registered, and the length (L) of the m1 was measured (Fig. 3).

All the measurements were taken on the occlusal plane of the molars with the image-treatment software Adobe PhotoShop CS5 using photographs from an Infinity X camera coupled to an Olympus SZ-40 binocular microscope. This software ensures that real measurements are made on flat surfaces.

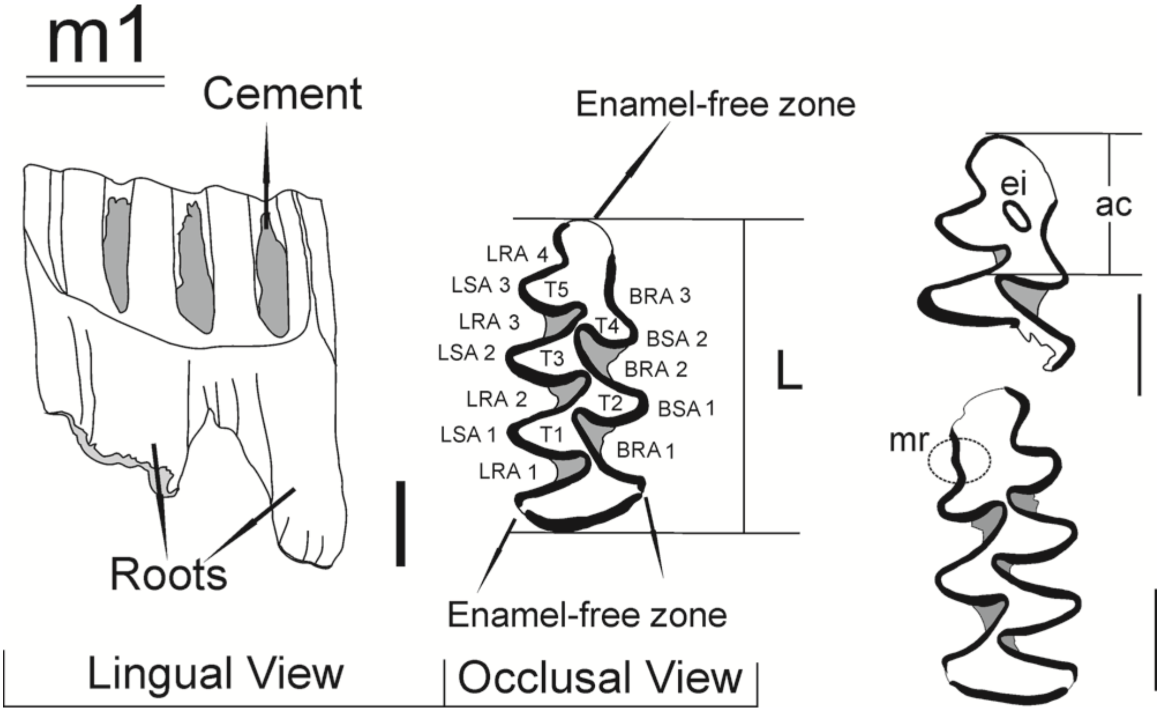

Figure 3. Diagram of the lingual and occlusal views of a right first lower molar of *Mimomys savini* and its various parts: the characteristics that define adult individuals are indicated (enamel-free areas and the presence of roots). Scale: 1 mm.

Nomenclature of the parts that are distinguished in the occlusal plane of an m1, and the measure used in this study: **L** refers to the length; **T1**, **T2**, **T3**, **T4** and **T5** are the various triangles that make up the tooth; **LRA** refers to the various lingual re-entrant angles, and **BRA** to the buccal re-entrant angles; **LSA** refers to the lingual salient angles, and **BSA** to the buccal salient angles; **ei** refers to the enamel islet, and **mr** to the mimomys-ridge (modified from Meulen, 1973; Heinrich, 1978; Rabeder, 1981).

To estimate the age of BL-D and FN-3, different methods were used.

For one side, the length values for the m1 of *M. savini* from these sites were compared with the values obtained at Gran Dolina (Atapuerca) and already published (Lozano-Fernández et al. 2013b). On the basis of the relationship observed between the mean m1 length of the populations of *M. savini* from different levels of Gran Dolina and their chronologies, it was possible to extrapolate the chronology of the sites of BL-D and FN-3 using the equations proposed by Lozano-Fernández et al. (2013b). This extrapolation has been possible because an almost constant trend towards increasing size (i.e., increasing m1 length) in the evoltuion of the water-rat lineage (*M. savini* / *Arvicola*) has been observed (Maul et al. 2013). This trend is a consequence of their semi-aquatic way of life, since an increase in size enable the water-rats to maintain in a more efficient way their body temperature (Maul et al. 2013).

Following this hypothesis of constant increase in size, we compare the date from BL-D and FN-3 with other european sites with *M. savini* in order to infer their relative biochronologic position. Therefore, we have compared BL-D and FN-3 with the following sites: Karaj Dubina (Ukraine; Markova 1990), Huescar-1 (Spain; Maul et al. 2013), Port Katon (Russia; Markova 1990), Gura Dobrogei 4 (Romania; Radulesco and Samson 1993), Beftia 2 (Romania; Maul 2001), Kozi Grzbiet (Poland; Nadachowski 1985), Monte Peglia A (Italy; Meulen 1973), Castagnone (Italy; Siori and Sala 2007), Tarkö layer 16 (Hungary; Jánossy 1976), Voigtstedt (Germany; Maul 2001), Untermassfeld (Germany; Maul 2001), Neuleiningen 5,15 (Germany; Maul et

al. 1998), Neuleiningen 5 (Germany; Maul et al. 1998), West Runton (England; Maul and Parfitt 2010), Přezletice (Czechia; Heinrich 1987) and Koneprusy C718 (Czechia; Heinrich 1987).

Along the same lines, as a further tool for determining the chronology of BL-D and FN-3, a comparison of the percentage of the population that present *Mimomys*-like characters (the mimomys-ridge and the enamel islet) was also made between these two sites and the levels of Gran Dolina from TD4B to TD6, under the hypothesis that the populations with lower percentages of *Mimomys*-like characters would be more modern (Chaline and Sevilla 1990; Koenigswald 1993; Cuenca-Bescós et al. 1999).

3 - RESULTS

Of the total remains at both sites, FN-3 presents more m1s with *Mimomys*-like characters, whether the mimomys-ridge or the enamel islet or both. Compared with the percentage of adult individuals in the Gran Dolina populations (levels from TD4B to TD6) that present these *Mimomys*-like characters, both BL-D and FN-3 yield higher values than Gran Dolina.

As regards the length of m1, FN-3 presents higher values than BL-D in the mean, maximum and minimum (Table 1). The standard deviation of this measurement is 0.09 (FN-3) and 0.11 (BL-D).

For estimate the age applying the ratio of the mean length of m1 and the chronology we used two equations:

$$\textbf{(A)}\ Y=838.86X - 3847.6$$

and

$$\textbf{(B)}\ Y=1178.6X - 5064.3$$

(proposed for the *M. savini* populations of south-western Europe by Lozano-Fernández et al. (2013b), where **X** corresponds to the length of the occlusal plane of m1 in millimetres and **Y** to the chronology in ka).

With the first equation (A), a chronology is obtained of 1.13 Ma for BL-D and of 1.09 Ma for FN-3 (Table 1). And with the second equation (B), a chronology is obtained of 1.26 Ma for BL-D and of 1.20 Ma for FN-3 (Table 1; Fig. 4).

These datings are subject to two error values: on the one hand the error generated by the standard deviation of the samples and on the other hand the base error that was generated in establishing the ratio between the length of the occlusal plane and the chronology of *M. savini*. Since the two errors overlap, the final error will be taken to be the greater of the two (Fig. 4A).

In the case of the first equation (A), the error generated by the deviation of the sample is ±0.09 Ma in the case of BL-D and ±0.07 Ma in FN-3. Given that the base error is ±0.12 Ma, the final datings are established as the following: BL-D 1.13 ±0.12 Ma; FN-3 1.09 ±0.12 Ma (Table 1).

In the case of second equation (B), the error generated by the deviation of the sample is ±0.13 Ma in the case of BL-D and ±0.1 Ma in FN-3. Given that the base error is ±0.12 Ma, the final datings are established as the following: BL-D 1.26 ±0.13 Ma; FN-3 1.2 ±0.12 Ma (Fig. 4A).

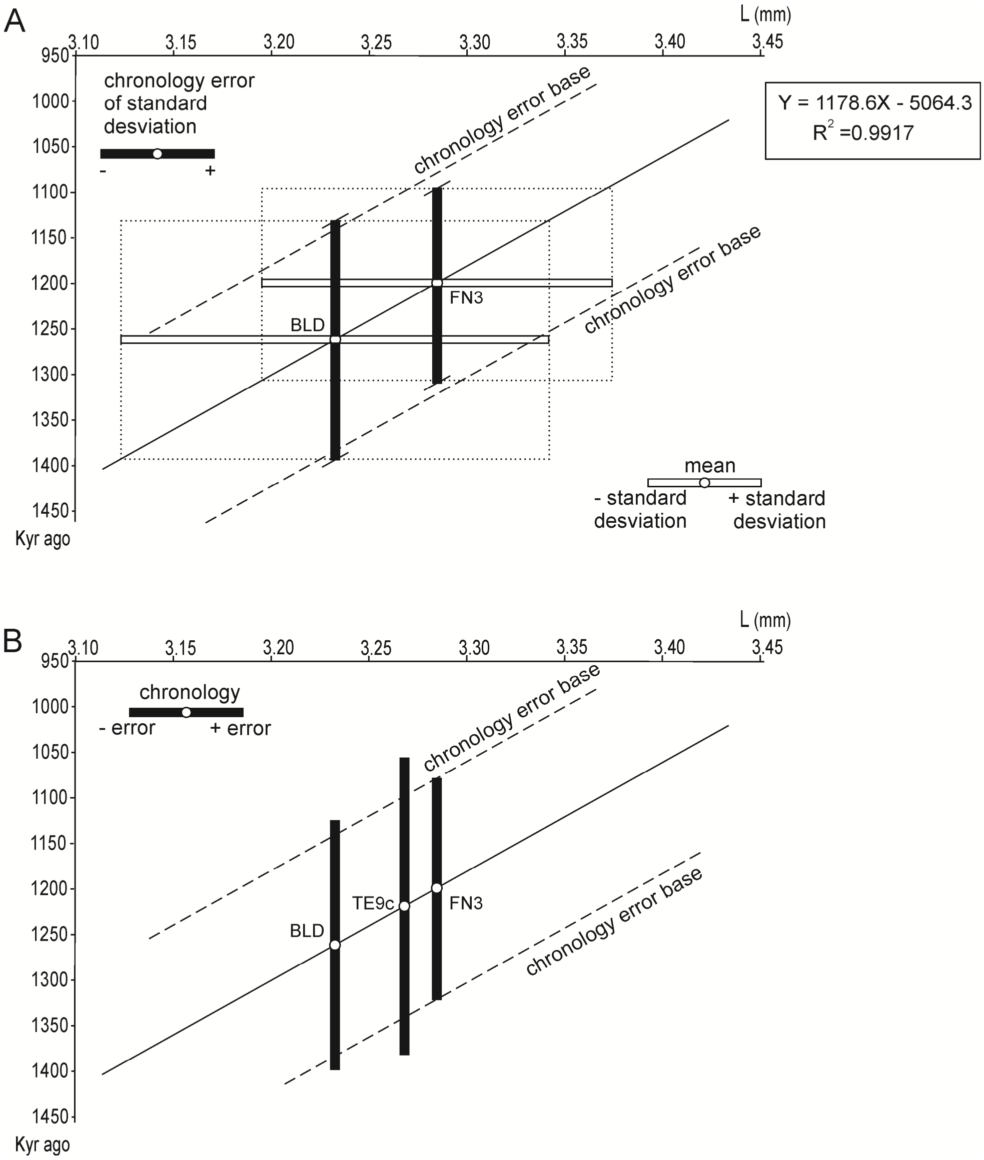

Figure 4. **A**: Graphic representation of the chronology obtained in the present study for **BL-D** and **FN-3**. Two types of error can be seen: the error generated by the standard deviation of the populations and the base error that was generated on establishing the ratio between the length of the occlusal plane and the chronology of *M. savini* by Lozano-Fernández et al. (2013b). As these two errors can be seen to overlapped, the final error for the datings is taken to correspond to the greater of the two in each case. Accordingly, the error in the dating of **BL-D** corresponds to that generated by the standard deviation of this population, whereas that of **FN-3** corresponds to the base error.

B: Chronological position of the sites of Barranco León D, Fuente Nueva 3 and Sima del Elefante (TE9c).

When compared to other European sites, the values of *M. savini* from BL-D and FN-3 are lower than those of Huescar-1 (3.60 mm; Maul et al. 2013), Kozi Grzbiet (3.42 mm; Nadachowski 1985), Voigtstedt (3.38 mm; Maul 2001) y Přezletice (3.35 mm; Heinrich 1987). The are similar to those of the sites of similares a Gura Dobrogei 4 (3.25 mm; Radulesco and Samson 1993), West Runton (3.30 mm; Maul and Parfitt 2010), Monte Peglia A (3.30 mm; Meulen 1973), Castagnone (3.24 mm; Siori and Sala 2007), Untermassfeld (3.28 mm; Maul 2001) and Koneprusy C718 (3.26 mm; Heinrich 1987). Finally, they are higher than those of Karaj Dubina (2.83 mm; Markova 1990), Port Katon (2.93 mm; Markova 1990), Beftia 2 (2.97 mm; Maul 2001), Tarkö layer 16 (3.20 mm; Jánossy 1976), Neuleiningen 5,15 (3.20 mm; Maul et al. 1998) and Neuleiningen 5 (3.16 mm; Maul et al. 1998).

4 - DISCUSSION

In first place, the lower percentage of individuals with Mimomys-like characters in BL-D than in FN-3 would suggest that FN-3 is oldest than BLD (in accordance with Chaline and Sevilla 1990; Koenigswald 1993; Cuenca-Bescós et al. 1999). This does not concur with the evolutionary tendency proposed for this species, since in the course of its evolutionary history *M. savini* increases in size (Viriot et al. 1990; Chaline et al. 1999; Lozano-Fernández et al. 2013a) and in these sites the population with the larger individuals (and thus the more modern population) is FN-3. Since *Mimomys*-like characters are lost as a result of the wear undergone by teeth during the lifetime of the individual, the relative age of the individuals at death could be

the reason for this contradiction. Whatever the case, as the evolutionary history of *M. savini* is known to entail an increasingly premature loss of *Mimomys*-like characters, the high percentage presence of these characters in FN-3 and BL-D would suggest that these sites are older than Levels TD4B, TD5 and TD6 of Gran Dolina (Atapuerca, Spain), where the percentage presence of *Mimomys*-like characters is lower (14.2% in TD4B, 8.1% in TD5 and 8% in TD6 according to Lozano-Fernández et al. 2013a). In other words, the sites in question are of a greater age than Level TD4B of Gran Dolina, dated to 1 Ma by Moreno García (2012).

In second place, in work of Lozano-Fernández et al. (2013b), the ecuation **A** present low coefficients of determination and correlation. This is consequence of one sample (sample from TD6-3, Gran Dolina, Atapuerca) which present lower values in m1 length than should be expected. According to Lozano-Fernández et al. (2013b) this is caused by a mixture of populations from central Europe (smaller) and populations from the Iberian Peninsula (larger).

The equation **B** was calculated ruling out the sample from TD6-3, and the determination and correlation coefficients associated present high values (Lozano-Fernández et al., 2013b).

We know that the results obtained with the equation **A** are unreliable (as indicated their determination and correlation coefficients) and that the results obtained with equation **B** are reliable, but the accuracy of this equation depends on whether really is justified the elimination of the sample from TD6-3.

The increase in size trend in *M. savini* (as in *Arvicola*) is a consequence of their semi-aquatic way of life, since an increase in size enable the water-rats to maintain in a more efficient way their body temperature (Maul et al. 2013). Thus, it seems unlikely that this trend can be reversed.

If we compare population of *M. savini* with similar chronologies and different geographical origin, we can observe that populations from South Europe are lager than populations form Central and North Europe. For example, the population from Huescar-1 (Spain) with a chronology between 700 ka and 800 ka present an average m1s length of 3.60 mm (Maul et al. 2013), while the populations from West Runton (England), Přezletice (Czechia), Koneprusy C718 (Czechia), Voigtstedt (Germany) and Kosi Grzbiet (Poland) with a similar age to Huescar-1, present values of 3.30, 3.35, 3.26, 3.38 and 3.42 respectively (Maul and Parfitt 2010; Heinrich 1987; Maul 2001; Nadachowski 1985). A similar case is observed between Monte Peglia A (Italy) and Port Katon (Russia). Both sites present a similar chronology (1.4–1.2 Ma Port Katon and 1.4–1.0 Ma Monte Peglia A) but the *M. savini* population from Monte Peglia A present high values in m1s length (3.30 mm) than the population from Prot Katon (2.93 mm) (Meulen 1973; Markova 1990).

If we consider these two factors (differences in size according geographical origin and the difficulty that the evolutionary trend is reversed as there is no change in the species habitat) and we add that the transition between TD5 and TD6-3 corresponds to a period in Iberian Peninsula with an input of European faunas (Cuenca-Bescós and García 2007; Cuenca-Bescós et al.

2011), everything seems to indicate that the value from TD6-3 corresponds to a mixture of populations. This justifies the discarding of the sample from TD6-3 and the equation **A**. Therefore, the chronology indicated by *M. savini* populations from BL-D and FN-3 is the age obtained with the equation **B** (1.26 Ma (± 0.13 Ma) for BL-D and 1.2 Ma (± 0.12 Ma) for FN-3).

In third place, the greater length of the m1 from FN-3 (and thus their greater size) than those from BL-D indicates a younger relative age for FN-3 than for BL-D. The numerical datings obtained in this study (using the equation B) of 1.26 Ma (± 0.13 Ma) for BL-D and 1.2 Ma (± 0.12 Ma) for FN-3 present a lower error range and are consistent with the previous datings proposed for these sites on the basis of biochronology, palaeomagnetism and ESR.

Biochronology dates BL-D and FN-3 to between 1.4 and 1.2 Ma in the regional biozone of *Allophaiomys lavocati* (Agustí and Madurell 2003; Agustí et al. 2010). Unit TE9c of the site of Sima del Elefante (Atapuerca), which has hominid remains, is also located within this biozone, even though in the archaeo-palaeontological complex of Atapuerca this biozone was established between 1.5 and 1 Ma (Cuenca-Bescós et al. 2010, 2012).

The palaeomagnetism of the area indicates that these sites (BL-D and FN-3) are of an age prior to the Jaramillo subchron (Oms et al. 1994, 2000, 2003; Agustí et al. 1997, 1999). In other words, they are older than 1.07 Ma, i.e. older than TD4B at Gran Dolina according to the datings made by Moreno García (2012). This result is in accordance with the datings obtained in this study and, as occurs with the biochronology, it locates FN-3 and BL-D in the

same chronological range as TE9c in Sima del Elefante (Carbonell et al. 2008; Cuenca-Bescós et al. 2010, 2012).

Finally, the ESR datings obtained up to 2008 assigned these sites an age of 1.46 Ma for BL-D and between 1.34 and 1.67 Ma for FN-3 (Duval 2008), rather much older than the chronologies of between 1.2 and 1.26 Ma proposed in the present article. In 2012, however, new ESR results were published for FN-3, according to which the age of the site would be 1.19 (± 0.21) Ma (Duval et al. 2012), in agreement with the dating proposed here. It is thus only the ESR results published in 2013 for BL-D (Toro-Moyano et al. 2013) that remain in question. However, the great error range of this ESR dating (± 0.38 Ma) encompasses the dating obtained in our work.

In accordance with the results presented in this paper, the three oldest European sites with remains showing a human presence would be ordered as follows from oldest to most modern. The lithic industry and fossil remains of the genus *Homo* found in BL-D (Toro-Moyano et al. 2011; Martínez-Navarro et al. 2013) would be assigned an age of 1.26 ± 0.13 Ma. Very close to this (according to the datings of Carbonell et al. 2008) are the fossil remains of the genus *Homo* (Bermúdez de Castro et al. 2011) from TE9c in Sima del Elefante, with an age of 1.22 ± 0.16 Ma. Finally, the lithic industry and cut marks found on the large-mammal remains of FN-3 (Toro-Moyano et al. 2011; Martínez-Navarro et al. 2013; Espigares et al. 2012) are the somewhat younger, with an age of 1.20 ± 0.12 Ma (Figure 4B).

In fourth place, the comparison between the *M. savini* populations from BL-D and FN-3 with other European sites reveals similar values with Gura Dobrogei 4 (3.25 mm; Radulesco and Samson 1993), West Runton (3.30 mm; Maul and Parfitt 2010), Monte Peglia A (3.30 mm; Meulen 1973), Castagnone (3.24 mm; Siori and Sala 2007), Untermassfeld (3.28 mm; Maul 2001) and Koneprusy C718 (3.26 mm; Heinrich 1987).

If we rule out the sites situated out of South Europe, the population of *M. savini* from BL-D and FN-3 present values in size similar to Monte Peglia A and Castagnone. This indicate a similar chronology between BL-D, FN-3, Monte Peglia A and Castagnone (between 1.4 Ma and 1 Ma according to Meulen 1973; Siori and Sala 2007 and Maul et al. 2013).

In sum, although apparently BL-D would be the oldest deposits with human presence, the error range in ages published for TE9c, FN-3 and BL-D and the error ranges of ages calculated for FN-3 and BL-D in this study do not permit to determine which of the three sites is older. We can conclude that the three sites are located probably in a period between 1.1 Ma and 1.4 Ma and that BL-D is older than FN-3, but with TE9c can not establish a relative position between them because no elements to compare.

5 - CONCLUSION

The use of evolutionary tendencies for the purpose of numerical dating – in this case the increase in size over the evolutionary history of *M. savini* – has proved to be a method that provides results consistent with other methods such as magnetostratigraphy, biochronology and ESR. As such it is a reliable method for this sort of study. On the basis of it, the age of FN-3 is established as 1.2 ± 0.12 Ma and that of BL-D as 1.26 ± 0.13 Ma.

These results suggest that the site of BL-D is the oldest in Europe with fossil remains of hominids, with an age of 1.26 ± 0.13 Ma, within the same chronological range of the site of Sima del Elefante, also with human remains, dated to 1.22 ± 0.16 Ma (Carbonell et al. 2008) and that of the site of Fuente Nueva 3, with lithic industry attributed to Mode 1, dated to 1.2 ± 0.12 Ma. If we considerer the error range otained in different datations from this three sites, we can conclude that these sites correponds to a similar chronological range between 1.1 Ma and 1.4 Ma.

In base of *M. savini* populations from BL-D and FN-3, we can determine that BL-D is older than FN-3 (although close in age). However, we can not determine which is older, TE9c or BL-D, because TE9c have not *M. savini*.

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REFERENCES

Agustí J. 1986. Synthèse biostratigraphique du Plio-Pleistocène de Guadix Baza (province de Granada, sud est de l'Espagne). Geobios 19 (4):505–510.

Agustí J, Madurell J, 2003. Los arvicólidos (Muroidea, Rodentia, Mammalia) del Pleistoceno inferior de Barranco León y Fuente Nueva 3 (Orce, Granada). Datos preliminares. In: Toro-Moyano, I., Agustí, J., Martínez-Navarro, B. (Eds.), El Pleistoceno inferior de Barranco León y de Fuente Nueva 3, Orce (Granada), Junta de Andalucía. Consejería de Cultura, Sevilla, pp. 137–145.

Agustí J, Blain H-A, Furió M, De Marfá R, Santos-Cubedo A. 2010. The early Pleistocene small vertebrate succession from the Orce region (Guadix-Baza Basin, SE Spain) and its bearing on the first human occupation of Europe. Quaternternary International 223–224:162–169.

Agustí J, Moyà-Solà S, Martín-Suárez E, Marín M. 1987. Faunas de mamíferos en el Pleistoceno inferior de la región de Orce (Granada, España). Paleontologia i Evolució, Mem. Esp. 1:73–86.

Agustí J, Oms O, Garcés M, Parés J.M. 1997. Calibration of the Pliocene-early Pleistocene transition in the continental beds of the Guadix-Baza basin (southeastern Spain). Quaternary International 40:93–100.

Agustí J, Oms O, Parés JM. 1999. Calibration of the Early-Middle Pleistocene transition in the continental beds of the Guadix-Baza Basin (SE Spain). Quaternary Science Review 18:1409–1417.

Alberdi MT. 2010. Estudio de los caballos de los yacimientos de Fuente Nueva-3 y Barranco León-5 (Granada). In: Toro I, Martínez-Navarro B, Agustí J. (Eds.), Ocupaciones humanas en el Pleistoceno inferior y medio de la cuenca de Guadix-Baza. Arqueología Monografías, Sevilla, pp. 291–306.

Bermúdez de Castro JM, Martinón-Torres M, Gómez-Robles A, Prado-Simón L, Martín-Francés L, Lapresa M, Olejniczak A, Carbonell E. 2011. Early Pleistocene human mandible from Sima del Elefante (TE) cave site in Sierra de Atapuerca (Spain): A comparative morphological study. Journal of Human Evolution 61:12–25.

Carbonell E, Bermúdez De Castro JM, Parés JM, Pérez- González A, Cuenca-Bescós G, Ollé A, Mosquera M, Huguet R, Made J. van der, Rosas A, Sala R, Vallverdú J, García N, Granger DE, Martinón-Torres M, Rodríguez XP, Stock GM, Vergès JM, Allué E, Burjachs F, Cáceres I, Canals A, Benito A, Díez C, Lozano M, Mateos A, Navazo M, Rodríguez J, Rosell J, Arsuaga JL. 2008. The first hominin of Europe. Nature 452:465–469.

Chaline J, Brunet-Lecomte P, Montuire S, Viriot L, Courant F. 1999. Anatomy of the arvicoline radiation (Rodentia): palaeogeographical, palaecoecological history and evolutionary data. Annales zoologici fennici, 36;239–267.

Chaline J, Sevilla P. 1990. Phyletic gradualism and developmental heterochronies in a European Plio-Pleistocene *Mimomys* linage (Arvicolidae, Rodentia). In: Fejfar O. and Heinrich W-D. (eds.), International Symposium on the Evolution, Phylogeny and Biostratigraphy of Arvicolids, 85–98.

Cuenca-Bescós G, Canudo JL, Laplana C. 2001. La séquence des rongeurs (Mammalia) des sites du Pléistocène inférieur et moyen d'Atapuerca (Burgos, Espagne). L'Antropologie 105:115–130.

Cuenca-Bescós G, Laplana C, Canudo JI. 1999. Biochronological implications of the Arvicolidae (Rodentia, Mammalia) from the Lower Pleistocene hominid-bearing level of Trinchera Dolina 6 (TD6, Atapuerca, Spain). Journal of Human Evolution 37(3-4):353–373.

Cuenca-Bescós G, Rofes J, López-García JM, Blain H-A, de Marfà R, Galindo-Pellicena MA, Bennàsar-Serra ML, Melero-Rubio M, Arsuaga JL, Bermúdez de Castro JM, CarbonellE. 2010. Biochronology of Spanish Quaternary small vertebrate faunas. Quaternary International 212:109–119.

Cuenca-Bescós G, Rofes J, López-García JM, Blain H-A, Rabal-Garcés R, Sauqué V, Arsuaga JL, Bermúdez de Castro JM, Carbonell E. 2012. The Small mammals of Sima del Elefante (Atapuerca, Spain) and the first entrance of Homo in Western Europe. Quaternary International In Press.

Daams R, Freudenthal M. 1988. Synopsis of the Dutch-Spanish collaboration program in the Neogene of Calatayud - Teruel Basin. 1976-1986. In: M. Freudenthal. Bioestratigraphy and paleoecology of the Neogene micromammalian faunas from the Calatayud-Teruel Basin (Spain), Scripta Geologica 1:3–18.

Duval M. 2008. Évaluation du potentiel de la méthode de datation par Résonance de Spin Electronique (ESR) appliquée aux gisements du Pléistocène inférieur: étude des gisements d'Orce (bassin de Guadix-Baza, Espagne) et contribution à la connaissance des premiers peuplements de l'Europe. Ph.D. thesis. Muséum National d'Histoire Naturelle, Paris, France. 522 p.

Duval M, Falguères C, Bahain J-J, Grün R, Shao Q, Aubert M, Dolo J-M, Agustí J, Martínez-Navarro B, Palmqvist P. 2012 Toro-Moyano, I. On the limits of using combined U-series/ESR method to date fossil teeth from two Early Pleistocene archaeological sites of the Orce area (Guadix-Baza basin, Spain). Quaternary Research 77:482–491.

Espigares M P, Martínez-Navarro B, Palmqvist P, Ros-Montoya S, Toro I, Agustí J, Sala R. 2012. *Homo* vs *Pachycrocuta*: Earliest evidence of competition for an elephant carcass between scavengers at Fuente Nueva-3 (Orce, Spain). Quaternary international. In Press

Fejfar O, Heinrich WD. 1990. Muroid rodent biochronology of the Neogene and Quaternary in Europe. In: Lindsay EH, Fahlbusch V, Mein P. (Eds.), European Neogene Mammal Chronology. NATO ASI Series A: Life Sciences 180, pp. 91–118.

Ferring R, Oms O, Agustí J, Berna F, Nioradze M, Sheila T, Tappen M, Vekua A, Zhvanida D, Lordkipanidze D. 2011. Earliest human occupation at Dmanisi (Georgian Caucasus) dated to 1.85-1.78 Ma. Proc. Natl. Acad. 108:10432–10436.

Heinrich W-D. 1978. Zur biomestrischen Erfassung eines Evolutiontrends bei *Arvicola* (Rodentia, Mammalia) aus dem Pleistozän Thüringens. Säugetierkundliche Informationen 2:3–21.

Heinrich W-D.1987. Neue Ergebnisse zur Evolution und Biostratigraphie von Arvicola (Rodentia, Mammalia) im Quartär Europas. Zeitschrift für geologische Wissenschaften 15:389–406.

Jánossy D. 1976. Die Felsnische Tarkő und die Vertebratenfauna ihrer Ausfüllung. Karszt- és Barlangkutatás. 8:3–106.

Koenigswald W Von. 1993. Heterocronies in morphology and Scmelsmuster of Hysodont molars in the Muroidea (Rodentia). Quaternary International 19:57–61.

Koenigswald W Von, Kolfschoten T Van. 1996. The *Mimomys– Arvicola* boundary and the enamel thickness quotient (SDQ) of Arvicola as stratigraphic markers in the Middle Pleistocene. In: C. Turner (ed.), Proceedings of the SEQS Cromer Symposium. Norwich/United Kingdom, The Early–Middle Pleistocene in Europe, Norwich 211–226.

Lordkipanidze D, Jashashvilli T, Vekua A, Ponce de León MS, Zollikofer CPE, Rightmire GP, Pontzer H, Ferring R, Oms O, Tappen M, Bukhsianidze M, Agustí J, Kahlke R, Kiladze G, Martínez-Navarro B, Moushkelishvili A, Nioradze M, Rook L. 2007. Postcranial evidence from early *Homo* from Dmanisi, Georgia. Nature 449:305–310.

Lozano-Fernández I, Agustí J, Cuenca-Bescós G, Blain H-A, López-García JM, Vallverdú J. 2013a. Pleistocene evolutionary trends in dental morphology of *Mimomys savini* (Rodentia, Mammalia) from Iberian Peninsula and discussion about the origin of the genus *Arvicola*. Quaternaire, 24(2):165–176.

Lozano-Fernández I, Blain H-A, López-García JM, Agustí J. 2013b. Evolutionary trends and biochronological interest in *Mimomys savini* vole from the early pleistocene of southwestern europe. Quaternary science reviews. 76:96–101.

Markova AK. 1990. The Sequence of Early Pleistocene Small-mammal Fauna from the South Russian Plain. Quartärpaläontologie. 8:131–152.

Martínez-Navarro B, Espigares MP, Ros S. 2003. Estudio preliminar de las asociaciones de grandes mamíferos de Fuente Nueva-3 y Barranco León-5 (Orce, Granada, España). In: Toro-Moyano I, Agustí J, Martínez-Navarro B. (Eds.), El Pleistoceno inferior de Barranco León y de Fuente Nueva 3, Orce (Granada), Junta de Andalucía. Consejería de Cultura, Sevilla, pp. 115–136.

Martínez-Navarro B, Palmqvist P, Madurell-Malapeina J, Ros-Montoya S, Espigares MP, Torregorosa V, Pérez-Claros JA. 2010. La fauna de grandes mamíferos de Fuente Nueva-3 y Barranco León-5: Estado de la cuestion. In: Toro I, Martínez-Navarro B, Agustí J. (Eds.), Ocupaciones humanas en el Pleistoceno inferior y medio de la cuenca de Guadix-Baza. Arqueología Monografías, Sevilla, pp. 197–236.

Martínez-Navarro B, Turq A, Agustí J, Oms O. 1997. Fuente Nueva 3 (Orce, Granada, Spain) and the first human occupation of Europe. Journal of Human Evolution 33:611–620.

Maul L. 2001. Die Kleinsäugerreste (Insectivora, Lagomorpha, Rodentia) aus dem Unterpleistozän von Untermassfeld. Römisch-Germanisches Zentralmuseum, Monographien. 40:783–887.

Maul L, Parfitt SA. 2010. Micromammals from the 1995 Mammoth Excavation at West Runton, Norfolk, UK: Morphometric data, biostratigraphy and taxonomic reappraisal. Quaternary International. 228:91–115.

Maul L, Masini F, Abbazzi L, Turner A. 1998. The use of different morphometric data for absolute age calibration of some South and Middle European arvicolid populations. Palaeontographia Italica. 85:111–151.

Maul L, Masini F, Parfit SA, Rekovets L, Savorelli A. 2013. Evolutionary trends in arvicolids and the endemic murid *Mikrotia* - New data and a critical overview. Quaternary Science Reviews. In Press.

Meulen AJ van der. 1973. Middle Pleistocene Smaller Mammals from the Monte Peglia (Orvieto, Italy) with Special Reference to the Phylogeny of *Microtus* (Arvicolidae, Rodentia). Quaternaria. 17:1–144.

Minwer-Barakat R, Madurell-Malapeira J, Alba D, Aurell-Garrido J, Esteban-Trivigno S, Moyà-Solà S. 2011. Pleistocene rodents from the torrent de Vallparadis section (Terrassa, northeastern Spain) and biochronological implications. Journal of Vertebrate Paleontology 31(4):849–865.

Moreno García D. 2011. Datation par ESR de quartz optiquement blanchis (ESR-OB) de la région de Atapuerca (Burgos, Espagne). Application au site préhistorique de Gran Dolina (contexte karstique) et aux systèmes fluviatiles quater- naires de l'Arlanzón et l'Arlanza [Ph.D. thesis]: Tarragona, Universitat Rovira i Virgili and Paris, Muséum National d'Histoire Naturelle, 304 p.

Nadachowski A. 1985. Biharian voles (Arvicolidae, Rodentia, Mammalia) from Kozi Grzbiet (Central Poland). Acta zoologica cracoviensia. 29:13–28.

Oms O, Garcés M, Parés JM, Agustí J, Anadón P, Juliá R. 1994. Magnetostratigraphic characterization of a tick lower Pleistocene lacustrine sequence from the Baza Basin (Betic chain, Southern Spain). Phys. Earth Planet International 85(1–2):173–180.

Oms O, Parés JM, Agustí J. 2003. Datación magnetoestratigráfica de los yacimientos de Fuente Nueva 3 y Barranco León 5 (Orce, Granada). In: Toro-Moyano I, Agustí J, Martínez-Navarro B. (Eds.), El Pleistoceno inferior de Barranco León y de Fuente Nueva 3, Orce (Granada). Junta de Andalucía. Consejería de Cultura, Sevilla, pp. 105–114.

Oms O, Parés JM, Martínez-Navarro B, Agustí J, Toro-Moyano I, Martínez Fernández G, Turq A. 2000. Early human occupation of Western Europe: Paleomagnetic dates of two paleolithic sites in Spain. Proceeding of the National Academy of Science 9719:10666–10670.

Rabeder G. 1981. Die Arvicoliden (Rodentia, Mammalia) aus dem Pliozän und dem älteren Pleistozän von Niederösterreich. Beiträge zur Paläontologie von Österreich 8:1–373.

Radulesco C, Samson P-M. 1993. Dental morphology of the *Mimomys*/*Arvicola* transition forms. Theoretical and Applied Karstology. 6:199–206.

Sala B, Masini F. 2007. Late Pliocene and Pleistocene small mammals chronology in the Italian Peninsula. Quaternary International 160:4–16.

Siori MS, Sala B. 2007 The mammal fauna from the late Early Biharian site of Castagnone (Northern Monferrato, Piedmont, NW Italy). Geobios. 40:207–217.

Toro-Moyano I, Barsky D, Cauche D, Celiberti V, Grégoire S, Lebegue I, Moncel MH, Lumley H de. 2011. The archaic stone tool industry from Barranco León and Fuente Nueva 3 (Orce, Spain): evidence of the earliest hominin presence in southern Europe. Quaternary international 243:80–91.

Toro-Moyano I, Martínez-Navarro B, Agustí J, Sounday C, Bermúdez de Castro JM, Martinón-Torres M, Fajardo B, Duval M, Falguères C, Oms O, Parés JM, Anadón P, Julià R, García-Aguilar JM, Moigne A-M, Espigares MP, Ros-Montoya S, Palmqvist P. 2013. The oldest human fossil in Europe dated to ca. 1.4 Ma at Orce (Spain). Journal of Human Evolution. 65:1–9.

Vekua A, Lordkipanidze D, Rightmire GP, Agustí J, Ferring R, Maisuradze G, Mouskhelishvili A, Nioradze M, Ponce de León M, Tappen M, Tvalchrelidze M, Zollikofer C. 2002. A new skull of early *Homo* from Dmanisi, Georgia. Science 297:85–89.

Vera JA. 1970. Estudio Estratigráfico de la Depresión de Guadix-Baza. Boletín del Instituto Geológico y Minero 84:429–462.

Viriot L, Chaline J, Schaaf A. 1990. Quantification du gradualisme phylétique de *Mimomys occitanus* à *Mimomys ostramosensis* (Arvicolinae, Rodentia) à l’aide de l’analyse d’image. Comptes Rendus de l’Academie des Sciences 310(II):1755–1760.

CONCLUSIONES GENERALES

1 – En la Peninsula Ibérica, *Mimomys savini* presenta dos claras tendencias evolutivas:

- Una sucesiva reducción y perdida de caracteres arcaicos como son el islote de esmalte y el pliegue mimomiano en el primer molar inferior (m1), y el islote de esmalte en el tercer molar superior (M3). Este ultimo sólo presente en poblaciones por encima del millón de años de edad.
- Un aumento del tamaño de sus molares (especialmente patente en la longitud del primer molar inferior) que se interpreta como un aumento en la talla de *Mimomys savini*.

Por otro lado, el índice de diferenciación de esmalte (SDQ) que en otros grupos filogenéticamente próximos a *Mimomys savini* sigue una tendencia evolutiva marcada, en esta especie presenta variaciones oscilatorias.

2 – Debido a su parecido morfológico, la coexistencia temporal de *Arvicola jacobaeus* y *Mimomys savini* permite presuponer la existencia de un ancestro común entre estas dos especies, como ya propuso Cuenca-Bescós et al. (2010a). Sin embargo, existen un conjunto de factores que apuntan en sentido contrario. Si no tenemos en cuenta *Arvicola jacobaeus*, el género *Arvicola* presenta una tendencia a la disminución del índice de diferenciación de esmalte en sus primeros representantes (*Arvicola mosbachensis* y *Arvicola terrestris*). Esta misma tendencia se ha observado en las ultimas poblaciones de *Mimomys savini*. Por otro lado, las poblaciones más antiguas del género *Arvicola* (siempre sin tener en cuenta *Arvicola jacobaeus*) presentan valores similares en el tamaño de los molares y en el índice de diferenciación de esmalte. Además, la perdida progresiva de caracteres mimomianos en

Mimomys savini supone una paulatina aproximación a la morfología dental de los primeros representantes del género *Arvicola* (excluyendo *Arvicola jacobaeus*). La única diferencia significativa entre las últimas poblaciones de *Mimomys savini* y las primeras de *Arvicola mosbachensis* (primer representante del género *Arvicola* si no tenemos en cuenta *Arvicola jacobaeus*) es la ausencia de raíces en *Arvicola mosbachensis*. Finalmente, siguiendo una línea temporal, la aparición de *Arvicola mosbachensis* supone la sustitución de *Mimomys savini* y la ocupación del nicho ecológico que deja este ultimo. Todos estos factores apuntan a que *Mimomys savini* es el ancestro de *Arvicola mosbachensis* (primer representante del género *Arvicola* si no tenemos en cuenta *Arvicola jacobaeus*) como propuso Chaline *et al*. (1999).

A la vista de todos estos argumentos y la existencia de una gran laguna cronológica en la que no se ha encontrado ningún representante del género *Arvicola* entre las poblaciones de *Arvicola jacobaeus* (1.2 Ma aprox.) y las primeras poblaciones de *Arvicola mosbachensis* (0.5 Ma). Todo parece indicar que dos grupos con diferentes orígenes has sido clasificados como *Arvicola*: por un lado *Arvicola jacobaeus*, que compartiría un ancestro común con *Mimomys savini*, y por otro lado *Arvicola mosbachensis* y el resto del linaje *Arvicola*, cuyo ancestro sería *Mimomys savini*.

3 – La secuencia estratigráfica continua de Gran Dolina (Atapuerca, España) entre TD4 y TD6 muestra claramente la tendencia evolutiva al aumento de los molares de *Mimomys savini* (que se interpreta como un aumento del tamaño de los individuos), y que esta tendencia es muy próxima a un modelo lineal con muy buenos coeficientes tanto de correlación como de determinación. Esta

similitud a un modelo lineal se debe a que la tendencia es consecuencia de una mejor adaptación al hábitat que ocupa la especie. Se trata de una especie de vida acuática (igual que el género *Arvicola*) y un mayor tamaño corporal permite mantener mejor la temperatura del organismo.

Esta característica permite en base al tamaño de los primeros molares:

- Por un lado, intrapolar cronologías aproximadas dentro del rango comprendido entre TD4 y TD6.
- Por otro lado, dado que el hábitat de la especie no cambia y por tanto el agente seleccionador de la tendencia al aumento de tamaño se mantendrá mientras exista la especie, extrapolar cronologías aproximadas fuera del rango cronólogico entre TD4 y TD6, dentro del marco cronológico del FAD y el LAD de la especie.

4 – El uso de tendencias evolutivas como método para estimar biocronologías – en este caso el aumento de talla durante la historia evolutiva de *Mimomys savini* – ha resultado ser un método que proporciona resultados consistentes con otros métodos como la magnetoestratigrafía y el ESR.

Este método sin embargo requiere un estudio en profundidad de los factores que pueden modificar estas tendencias (cambios ambientales, mezcla de poblaciones, latitud, ...)

5 – Como se ha podido comprobar en los trabajos de paleoambiente realizados en los yacimientos de el Barranc de la Boella (Tarragona, España), Barranco León (Orce, España) y Vallparadís (Terrassa, España), *Mimomys savini* es un claro indicador de hábitats dominados por la presencia de agua (de forma

permanente) igual que el género *Arvicola* (filogenéticamente muy próximo a *Mimomys savini*).

6 – El contenido en micromamíferos del nivel 2 del yacimiento del Barranc de la Boella ha hecho posible precisar la cronología de este nivel y determinar el tipo de paisaje que dominaba el territorio durante las primeras ocupaciones humanas de este yacimiento.

En términos cronológicos, el nivel 2 del Barranc de la Boella esta situado entre 0.99 y 0.78 Ma (en la biozona de *Allophaiomys*), en el intervalo entre el subcron Jaramillo y el límite Matuyama/Brunhes. La comparación de la población de arvicólidos del nivel 2 del Barranc de la Boella con otros yacimientos de la Península Ibérica ha revelado similitudes entre este nivel y el nivel TD4B de Gran Dolina. Por otro lado, los arvicolinos del nivel 2 del Barranc de la Boella presentan características más antiguas que los de Cueva Victoria y el nivel C2 de El Chaparral. Todo esto indica que el nivel 2 del Barranc de la Boella tendría una edad muy cercana a 0.99 Ma. Por lo tanto, el nivel 2 del Barranc de la Boella constituye uno de los yacimientos más antiguos con presencia humana de Europa, junto con Barranco León D y Fuente Nueva 3 (Granada, España), la Sima del Elefante (Burgos, España), Gran Dolina (Burgos, España) y la capa 10 de Vallparadís (Barcelona, España).

La comunidad faunística presente en el nivel 2 del Barranc de la Boella lo situa en el contexto de un ecotono donde especies características de zonas abiertas conviven con especies de zonas boscosas. Este entorno corresponde a un habitat próximo a una zona lacustre o un curso fluvial con un flujo regular y constante de agua. El paisaje en el Barranc de la Boella hace

aproximadamente 0.99 Ma estaba dominado por zonas húmedas con una baja representación de áreas abiertas.

7 – El contenido en micromamíferos del nivel 4 del yacimiento del Barranc de la Boella es excesivamente escueto para poder llevar a cabo trabajos biocronológico y paleoambientales concluyentes. La presencia de *Mimomys savini* indica la existencia de zonas húmedas con aguas permanentes (zonas lacustres o cursos fluviales regulares y constantes). Pero la mala conservación de los restos, el tipo de contexto sedimetológico y la ausencia de más micromamíferos podría indicar la existencia de un sesgo en la representación taxonómica y por tanto un error en la interpretación paleoambiental.

A nivel cronológico sólo la situación estratigráfica del nivel 4 del Barranc de la Boella nos permite deducir que su edad será similar o mayor al nivel 2 del Barranc de la Boella (0.99 Ma aprox.)

8 – El contenido en micromamíferos de la unidad EVT7 del yacimiento de Vallparadís en Terrassa (España) con especial énfasis en su población de *Mimomys savini* nos ha permitido precisar su cronología, así como ofrecer una reconstrucción paleoambiental de dicha unidad.

Con respecto a la biocronología, las características de la población de *Mimomys savini* de EVT7 permiten proponer una edad comprendida entre hace 0.99 y 0.94 Ma. Este rango cronológico similar a TD5 en Gran Dolina (Atapuerca, España) junto con la presencia de *Ungaromys nanus* en EVT7, indica que este nivel tiene una edad próxima a 0.99 Ma.

En cuanto a las inferencias paleoambientales, la aplicación del método del hábitat óptimo a partir de los restos de micromamíferos recuperados de la unidad EVT7, ha dado como resultado un paleoambiente predominantemente húmedo con abundantes masas de agua y zonas boscosas, que pasaría a ambientes mas abiertos y secos en los alrededores. Se trata de un ecotono en el que taxones característicos de entornos abiertos coexistió con otras especies más típicas de zonas boscosas. Un hábitat de transito próximo a una zona lacustre o fluvial.

9 – Las poblaciones de *Mimomys savini* de Fuente Nueva 3 y Barranco León D corresponden a unas cronologías de 1.2 ± 0.12 Ma y 1.26 ± 0.13 Ma respectivamente. Este marco cronológico corresponde al nivel TE9c de Sima del Elefante (Atapuerca), datado en 1.22 ± 0.16 Ma (Carbonell et al., 2008). La población de *Mimomys savini* de Barranco León D parece ser más arcaica que la de Fuente Nueva 3, por tanto Barranco León D sería más antiguo que Fuente Nueva 3. La ausencia de *Mimomys savini* en TE9c en Sima del Elefante no nos permite utilizar este taxón para determinar una posición cronológica relativa entre Barranco León D y TE9c. Sin embargo, al comparar las poblaciones de *Allophaiomys lavocati* de TE9c y de *Allophaiomys* aff. *lavocati* de Barranco León D, la de este último yacimiento presenta características más arcaicas cosa que indicaría que Barranco León D sería ligeramente más antiguo que TE9c. Por tanto se puede concluir que los tres presentan cronologías similares entre 1.1 y 1.4 Ma siendo Barranco León D aparentemente el más antiguo aunque la cronología de los tres es muy similar.

REFERENCIAS BIBLIOGRÁFICAS

Agustí, J. 1985. Bioestratigrafía de los depósitos Plio-Pleistocenos de la depresión Guadix-Baza (provincia Granada). Paleontologia i Evolució. 18, 13-18.

Agustí, J. 1986. Synthèse biostratigraphique du plio-pleistocène de Guadix-Baza (province de granada, sud-est de l’espagne). Geobios. 19 (4), 505-510.

Agustí, J. 1992. The *Allophaiomys* complex in southern Europe. Geobios. 25, 133-144.

Agustí, J. y Martín Suárez, E. 1986. Un proyecto de análisis ecoestratigráfico en el Plio-Pleistoceno de la depresión Guadix-Baza. Memorias y Jornadas de Paleontología. 21-32.

Agustí, J., Arbiol, S. y Martín Suárez, E. 1987. Roedores y lagomorfos (mammalia) del Pleistoceno Inferior de Venta Micena (depresión de Guadix-Baza, Granada). Paleontologia i Evolució. 1, 95-107.

Agustí, J., Blain, H.-A., Furió, M., de Marfá, R. y Santoscubedo, A. 2010. The Early Pleistocene small vertebrate succession from the Orce region (Guadix-Baza basin, SE Spain) and its bearing on the first human occupation of Europe. Quaternary International. 223-224,162-169.

Alcalde, G. 1988. Els rosegadors en l'arqueología catalana. Cota Zero. 4, 65-69.

Andrews, P. 1990. Olws, caves and fossils. London. 231.

Andrews, P. 1995. Experiments in taphonomy. Journal of Achaeological Science. 22, 147-153.

Badgley, C., Bartels, W. S., Morgan, M. E., Behrensmeyer, A. K. y Raza, S. M. 1995. Taphonomy of vertebrate assamblages from the Paleogene of northwestern Wyoming and Neogene of northern Pakistan. Palaeogeography, Palaeoclimatology, Palaeoecology. 115, 157-180.

Bennàsar Serra, M. Ll. 2010. Tafonomía de micromamíferos del Pleistoceno Inferior de la Sierra de Atapuerca (Burgos): La Sima del Elefante y la Gran Dolina. Universitat Rovira Virgili, Tarragona. 650pp.

Brunet-lecomte, P. y Delibes, M. 1984. Alimentación de la lechuza común *Tyto alba* en la Cuenca del Duero. Doñana Acta Vertebrata. 11, 213-229.

Carbonell, E., Bermúdez de Castro, J. M., Parés, J. M., Pérez-González, A., Cuenca-Bescós, G., Ollé, A., Mosquera, M., Huguet, R., van der Made, J., Rosas, A., Sala, R., Vallverdú, J., García, N., Granger, D. E., Martinón-Torres, M., Rodríguez, X. P., Stock, G. M., Vergès, J. M., Allué, E., Burjachs, F., Cáceres, I., Canals, A., Benito, A., Díez, C., Lozano, M., Mateos, A., Navazo, M., Rodríguez, J., Rosell, J., Arsuaga, J. L., 2008. The first hominin of Europe. Nature. 452 (7186), 465-469.

Chaline, J. 1972. Les rongeurs du Pléistocène moyen et supérieur de France. Systématique, Biostratigraphie, Paléoclimatologie. C.N.R.S.

Chaline, J. 1982. El Cuaternario. La historia humana y su entorno. Akal editorial. Madrid. 549 pp.

Chaline, J. 1987. Arvicoline data (Arvicolinae, Rodentia) and evolutionary concepts. Evolutionary Biology. 21, 137-310.

Chaline, J. 1988. Paleocronòmetres, paleotermòmetres i paleoindicadors dels entorns prehistòrics, els rosegadors irremplaçables. Cota Zero. 4, 61-64.

Chaline, J. y Alcalde, G. 1983. Los roedores y la prehistoria. Revista de Arqueología. 25, 6-11.

Chaline, J. y Michaux, J. 1969. Evolution et signification stratigraphique des Arvicolidés du genre *Mimomys* dans le Plio-Pléistocène de France. C.R. Ac. Sc., ser D, T. 268, 3029-3032.

Chaline, J. y Michaux, J. 1971. Les Rongeurs du Pléistocène inférieur de France. Colloque sur le Néogène Lyon.

Chaline, J. y Sevilla, P. 1990. Phyletic gradualism and developmental heterochronies in a european Plio-Pleistocene *Mimomys* linage (Arvicolidae, Rodentia). in Fejfar, O. y Heinrich, W.-D. (eds.), International symposium on the evolution, phylogeny and biostratigraphy of arvicolids. Prague. 85-98.

Chaline, J., Brunet-Lecomte, P., Montuire, S., Viriot, L. y Courant, F. 1999. Anatomy of the arvicoline radiation (Rodentia): palaeogeographical, palaecoecological history and evolutionary data. Annales Zoologici Fennici, 36, 239-267.

Cuenca-Bescós, G. 2003. The micromammal record as proxy of palaeoenvironmental changes in the Pleistocene of the Sierra de Atapuerca (Burgos, Spain). In Ruiz-Aapata, M. B., Dorado-Valiño, M., Valdeolmillos-Rodríguez, A., Gil-García, M. J., Bardají-Azcarate, T., de Bustamante-Gutierrez, I., Martínez-Mendizabal, I. (eds.), Quaternary climatic changes and environmental crises in the mediterranean region. Universidad de Alcala de Henares. 1330-1380.

Cuenca-Bescós, G. y García, N. 2007. Biostratigraphic succession on the Early and Middle Pleistocene mammal faunas of the Atapuerca cave sites (Burgos, Spain). Courier Forschungsinstitut Senckenberg. 259, 99-110.

Cuenca-Bescós, G., Agustí, J., Lira, J., Melero, M. y Rofes, J. 2010a. A new species of water vole from the Early Pleistocene of southern Europe. Acta Palaeontologica Polonica. 55 (4), 565-580.

Cuenca-Bescós, G., Laplana, C. y Canudo, J. I. 1995. Los arvicólidos (Rodentia, Mammalia) de los niveles inferiores de Gran Dolina (Pleistoceno inferior, Atapuerca, Burgos, España). Revista española de paleontología. 10 (2), 202-218.

Cuenca-Bescós, G., Laplana, D. y Canudo, J. I. 1999. Biochronological implications of the arvicolidae (Rodentia, Mammalia) from the Lower Pleistocene hominid-bearing level of Trinchera Dolina 6 (TD6, Atapuerca, Spain). Journal of Human Evolution. 37 (3-4), 353-373.

Cuenca-Bescós, G., Rofes, J. y García-Pimienta, J.C. 2005. Early europeans and environmental change across the Early-Middle Pleistocene transition: small mammalian evidence from Trinchera Dolina cave, Atapuerca, Spain. in: Head, M. J. y Gibbard, P. L. (eds). Early-Middle Pleistocene transitions: the land-ocean evidence. Journal of the Geological Society. Special publications, 247, 277-286.

Cuenca-Bescós, G., Rofes, J., López-García, J. M., Blain, H.-A., de Marfá, R. J., Galindo-Pellicena, M. A., Bennásar-Serra, M. Ll., Melero-Rubio, M., Arsuaga, J. L., Bermúdez de Castro, J. M. y Carbonell, E., 2010b. Biochronology of Spanish Quaternary small vertebrate faunas. Quaternary International. 212 (2), 109-119.

Cuenca-Bescós, G., Strauss, L. G., González Morales, M. R. y García Pimienta, J. C. 2008. Paleoclima y paisaje del final del Cuaternario en Cantabria: Los pequeños mamíferos de la cueva del Mirón (Ramales de la Victoria). Revista española de paleontología. 23 (1), 91-126.

Daams, R. y Freudenthal, M. 1988. Synopsis of the dutch-spanish collaboration program in the Neogene of Calatayud-Teruel basin. 1976-1986. Scripta Geologica. Special issue, 1, 3-18.

Delany, M. J. 1981. Ecología de los micromamíferos. Ediciones Omega. Barcelona. 72pp.

Fejfar, O., Heinrich, W.-D. y Lindsay, E. H. 1998. Updating the neogene rodent biochronology in Europe. Mededelingen nederlands instituut voor toegepaste geowetenschappen toegepast natuurwetenschappelijk onderzoek. 60, 533-554.

Fernandez-Jalvo, Y. 1988. Tafonomía de microvertebrados en Gran Dolina, Atapuerca (Burgos). Facultad de Ciencias Geológicas. Madrid, Universidad Complutense. 186 pp.

Fernández-Jalvo, Y., Denys, C., Andrews, P., Williams, T., Dauphin, Y. y Humphrey, I. 1998. Taphonomy and palaecology of Olduvai Bed-I (Pleistocene, Tanzania). Journal of Human Evolution. 34, 137-172.

Freudenthal, M., Meijer, T. y Meulen, A. J. van der. 1976. Preliminary report on a field campaign in the continental Pleistocene of Teglen (the Netherlans). Scripta Geologica. 34,1-27.

Gosàlbez, J. 1987. Insectivors i rosegadors de Catalunya. Metodología d'estudi i catàleg faunístic. Ketres editorial. Barcelona. 241pp.

Gray, J. E. 1821. On the natural arrangement of vertebrose animals. Medical repository. London. 15, 296-310.

Heinrich, W.-D. 1978. Zur biometrischen erfassung eines evolutionstrends bei *Arvicola* (Rodentia, Mammalia) aus dem pleistozän thüringens. Säugetierkundliche Informationen. 1 (2), 3-21.

Heinrich, W.-D. 1982. Zur evolution und biostratigraphie von *Arvicola* (Rodentia, Mammalia) im Pleistozän Europas. Zeitschrift für Geologische Wissenschaften. 10, 683-735.

Heinrich, W.-D. 1987. Neue ergebnisse zur evolution und biostratigraphie von Arvicola (Rodentia, Mammalia) im Quartär Europas. Zeitschrift für Geologische Wissenschaften. 15, 389-406.

Hernández Fernández, M. 2001. Bioclimatic discriminant capacity of terrestrial mammal faunas. Global Ecology and Biogeography. 10, 189-204.

Hinton, M. A. C. 1910. A preliminary account of the British fossil voles and lemmings; with some remarks on the Pleistocene climate and geography. Proceedings of the Geologists' Association. 21, 489-507.

Hinton, M. A. C. 1926. Monograph of the voles and lemmings (Microtinae) living and extinct. British Museum (Natural History), London. 487 pp.

Illiger. C. 1811. Prodromus systematis mammalium et avium additis terminis zoographicis utriusque classis, eorumque versione germanica. Sumptibus c. Salfeld. Berlin. 326pp.

Jánossy, D. 1976. Die felsnische tarkő und die vertebratenfauna ihrer ausfüllung. Karszt- és Barlangkutatás. 8, 3-106.

Jánossy, D. 1986. Pleistocene vertebrate faunas of Hungary. Akadémiai Kiadó. Budapest. 208 pp

Koenigswald, W. von. y Kolfschoten, T. van. 1996. The *Mimomys–Arvicola* boundary and the enamel thickness quotient (SDQ) of *Arvicola* as stratigraphic markers in the Middle Pleistocene. in Turner, C. (ed.) Proceedings of the Seqscromer symposium. Norwich/Unitedkingdom, the Early–Middle Pleistocene in Europe. Norwich. 211–226.

Kretzoi, M. 1965. Skizze einer Arvicoliden-Phylogenie. Vertebrata Hungarica. 1, 155-193.

Lippi, P., Masini, F., Maul, L. y Abbazzi, L. 1998. Evolutionary changes of enamel differentiation in Pleistocene Mediterranean and Middle European populations of *Microtus* (Rodentia, Arvicolidae). Paludicola. 2, 50-61.

Major, C. I. F. 1902. Some jaws and teeth of Pliocene voles (*Mimomys* gen. nov.) from the Norwich crag at Thorpe, and from the upper Bal d' Arno. Proceedings of the Zoological Society of London. 1, 102-107.

Markova, A. K. 1982. Pleistotsenovye gryzuny Russkoi ravniny [Pleistocene rodents of the Russian plain]. Nauka editorial. Moscow. 184 pp.

Markova, A. K. 1990. The sequence of Early Peistocene small-mammal fauna from the south Russian plain. Quartärpaläontologie. 8, 131-152.

Markova, A. K. 2004. Pleistocene mammal faunas of eastern Europe. in Konishchev, N. v. y Safyanov, G. A. (eds.). Structure, dynamics and evolution of natural geosystems. Moscow. 583-597.

Maul, L. 2001. Die kleinsäugerreste (Insectivora, Lagomorpha, Rodentia) aus dem unterpleistozän von Untermassfeld. Römisch-Germanisches Zentralmuseum. Monographien. 40, 783–887.

Maul, L. 2002. The Quaternary small mammal faunas of Thuringia (central Germany). in Meyrick, R. A. y Schreve, D. C. (eds.). The Quaternary of central Germany (Thuringia and surroundings). Quaternary Research Association. London. 79-96.

Maul, L. y Parfitt, S. A. 2010. Micromammals from the 1995 mammoth excavation at West Runton, Norfolk, UK: morphometric data, biostratigraphy and taxonomic reappraisal. Quaternary International. 228, 91-115.

Maul, L., Heinrich, W-D., Parfitt, S. A. y Paunescu, A.- C. 2007. Comment on the correlation between magnetostratigraphy and the evolution of microtus (arvicolidae, rodentia, mammalia) during the Early and early Middle Pleistocene. Courier Forschungsinstitut Senckenberg. 259, 243-263.

Maul, L., Masini, F., Abbazzi, L. y Turner, A. 1998. The use of different morphometric data for absolute age calibration of some south and Middle European arvicolid populations. Palaeontographia Italica. 85, 111-151.

Maul, L., Masini, F., Parfit., S. A., Rekovets, L. y Savorelli, A. 2013. Evolutionary trends in arvicolids and the endemic murid Mikrotia - new data and a critical overview. Quaternary Science Reviews. In press.

Meléndez, B. 1986. Vertebrados. Generalidades. in Meléndez, B. Paleontología. Vertebrados. Peces, anfibios, reptiles y aves. Paraninfo. Madrid. 39-63.

Mellet, J. S. 1974. Scatological origin of microvertebrate fossil accumulations. Science. 185, 349-350.

Meulen, A. J. van der. 1973. Middle Pleistocene smaller mammals from the Monte Peglia (Orvieto, Italy), with special reference to the phylogeny of *Microtus* (Arvicolidae, Rodentia). Quaternaria. 17, 1-144.

Meulen, A. J. van der. y Zagwijn, W. H. 1974. *Microtus* (*Allophaiomys pliocaenicus*) from the Lower Pleistocene near Brielle, the Netherlands. Scripta Geologica. 21, 1-12.

Minwer-Barakat, R. 2005. Roedores e insectívoros del Turoliense superior y el Plioceno del sector central de la Cuenca de Guadix. Univ. Granada. 589pp.

Minwer-Barakat, R., Madurell-Malapeira, J., Alba, d., Aurell-Garrido, J., Esteban-Trivigno. S. y Moyà-Solà, S. 2011. Pleistocene rodents from the Torrent de Vallparadis section (Terrassa, Northeastern Spain) and biochronological implications. Journal of Vertebrate Paleontology. 31 (4), 849-865.

Montuire, S., Michaux, J., Legendre, S. y Aguilar, J. P. 1997. Rodents and climate. A model for estimating past temperatures using arvicolids (Mammalia, Rodentia). Palaeogeogr. Palaeoclim. Palaeoecol. 128, 187-206.

Nadachowski, A. 1985. Biharian voles (Arvicolidae, Rodentia, Mammalia) from Kozi Grzbiet (central Poland). Acta Zoologica Cracoviensia. 29, 13–28.

Néraudau, D., Viriot, L., Chaline, J., Laurin, B. y Kolfschoten, T. van. 1995. Discontinuity in the Plio-Pleistocene Eurasian water vole linage. Plaeontology. 38, 77-85.

Pokines, J. 1998. The paleoecology of lower Magdalenian Cantabrian Spain. BAR International Series. Oxford. 713pp.

Rabeder, G. 1981. Die arvicoliden (Rodentia, Mammalia) aus dem Pliozän und dem älteren Pleistozän von Niederösterreich. Beitrage zur Palaontologie von Osterreich. 8, 1-373.

Radulesco, C. y Samson, P.-M. 1993. Dental morphology of the *Mimomys/Arvicola* transition forms. Theoretical and Applied karstology. 6, 199-206.

Rekovets, L. 1994. Melkie mlekopitayushchie antropogena yuzhnoy chaste vostochnoi Evropy [small mammals from the anthropogene of the southern part of east Europe]. Naukova Dumka. Kiev. 371 pp.

Repenning, C. A. 2001. Beringian climate during intercontinental dispersal: a mouse eye view. Quaternary Science Reviews. 20, 25-40.

Sala, B. y Masini, F. 2007. Late Pliocene and Pleistocene small mammal chronology in the Italian Peninsula. Quaternary International. 160, 4-16.

Siori, m. S. y Sala, B. 2007. The mammal fauna from the late Early Biharian site of Castagnone (northern Monferrato, Piedmont, NW Italy). Geobios. 40, 207-217.

Stuart, A. J. 1981. A comparison of the Middle Pleistocene mammal faunas of Voigstedt (Thuringia, GDR) and West Runton (Norfolk, England). Quartarpalaontologie. 4, 155-163.

Topachevskij, V. A. y Skorik, A. F. 1977. Gryzuny rannetamanskoj fauny Tiligul'skogo razreza [Rodents of Early Tamanian faunas of the Tiligul section]. Naukovo Dumka. Kiev. 250 pp.

Viriot, L., Chaline, J. y Schaaf, A. 1990. Quantification du gradualisme phylétique de *Mimomys occitanus* à *Mimomys ostramosensis* (Arvicolinae, Rodentia) à l'aide de l'analyse d'images. C. R. Acad. Sci. 3108, 1755-1760.

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ANEXO


Bla bla bla bla BLA BLA
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Bla bla bla BLA BLA
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Reconstruction du contexte chronologique et environnemental des premières occupations humaines dans le bassin de Guadix-Baza (Grenade, Espagne) : le cas des petits vertébrés*

par Jordi AGUSTÍ[1,2,3], Hugues-Alexandre BLAIN[2,3], Juan Manuel LÓPEZ-GARCÍA[2,3] & Iván LOZANO[2,3]

[1]Institution Catalane de Recherche et d'Études Avancées (ICREA), BARCELONE, Espagne
[2]Institut Catalan de Paléoécologie Humaine et Évolution Sociale (IPHES), TARRAGONE, Espagne
[3]Département de Préhistoire de l'Université Rovira i Virgili (URV), TARRAGONE, Espagne
E-mail : jordi.agusti@icrea.es, hablain@iphes.cat, jlopez@iphes.cat, ilozano@iphes.cat

Résumé. En plus du site de Dmanisi en Géorgie et du complexe karstique d'Atapuerca dans le centre de l'Espagne, le bassin de Guadix-Baza (Grenade, sud-est de l'Espagne) joue un rôle important dans la compréhension du comment et quand des premières occupations humaines de l'Europe. Ce bassin rapporte la plus ancienne présence d'hominidés du Pléistocène inférieur (1,3 Ma) en Europe occidentale, comme le démontrent les milliers d'industries lithiques de Mode 1 trouvés dans les gisements de Barranco León D et Fuente Nueva 3. La très complète succession de petits vertébrés (amphibien, squamate, insectivore, rongeur et lagomorphe) du bassin de Guadix-Baza permet de reconstruire l'évolution paléoenvironnementale et paléoclimatique dans ce bassin, en relation avec ces premières dispersions humaines vers l'Europe occidentale. Ici sont expliquées les méthodes utilisées pour la reconstruction du cadre chronologique, environnemental et climatique des derniers six millions d'années.

Mots clés : petits vertébrés, Miocène à Pléistocène, bassin de Guadix-Baza, Espagne

Abstract. Reconstruction of the chronological and environmental context of the early hominin occupations in the Guadix-Baza basin (Granada Province, Spain) : the case of the small vertebrates. In addition to Dmanisi (Georgia) and the Atapuerca karstic complex (central Spain), the Guadix-Baza Basin (Granada Province, Spain) provides important information on early human settlements in Europe. This basin records the oldest presence of early Pleistocene hominids in Western Europe (1.3 Ma), as indicated by the thousands of Mode 1 lithic tools from the sites of Barranco León D and Fuente Nueva 3. The very complete small vertebrate succession (amphibian, squamate, insectivore, rodent and lagomorph) from the Guadix-Baza Basin enables tracing of the paleoenvironmental and paleoclimatic evolution of this basin, in relation with the first human dispersal into Western Europe. Here are explained the methods used in the reconstruction of the chronological, environmental and climatic context over the last six million years.

Keywords : small vertebrates, Miocene to Pleistocene, Guadix-Baza basin, Spain

Les gisements de Fuente Nueva 3 et Barranco León D, où l'on a détecté les plus anciennes traces de présence humaine en Europe occidentale, constituent en réalité la partie émergée de l'iceberg d'une enclave exceptionnelle pour l'étude de l'évolution biologique et climatique des sept millions d'années derniers : le bassin de Guadix-Baza *(fig. 1).* Avec une surface d'environ 3 000 km^2, ce bassin s'est révélé être une zone d'un grand intérêt pour l'étude du Pléistocène, de par la continuité de son registre géologique, paléontologique et archéologique. Ainsi, le bassin de Guadix-Baza contient une séquence géologique et

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[*] Article traduit de l'espagnol par Hélène BASLÉ, Chargée de communication et partenariats, Office de Tourisme et d'Animation de Villers-sur-Mer (Calvados).

paléontologique pratiquement complète qui va de la fin du Miocène (il y a environ 6 Ma) à la fin du Pléistocène moyen (il y a moins de 200 000 ans). Dans le reste de l'Europe, le registre du Pléistocène est normalement beaucoup plus discontinu et fragmentaire, formé par des remplissages karstiques (dolines ou grottes) ou par des terrasses fluviales. Bien que ces gisements puissent être d'un intérêt extraordinaire par l'énorme quantité de restes fossiles qu'ils arrivent à accumuler, ils souffrent d'une limite importante, s'agissant de dépôts isolés, sans contexte géologique général, qui couvrent un laps de temps très réduit et dont l'information représente une phase très ponctuelle de l'histoire de la Terre. En revanche, avec son registre continu sur 6 Ma, le bassin de Guadix-Baza est comparable aux grandes séquences géologiques que l'on trouve sur le Rift africain, comme c'est le cas de Turkana au Kenya, Olduvai en Tanzanie ou Hadar en Éthiopie.

Contexte environnemental et climatique

La séquence paléontologique de Guadix-Baza se trouve jalonnée par une série d'importants gisements avec de grands et petits vertébrés, comme c'est le cas de Gorafe et Baza (des débuts du Pliocène), Huélago (correspondant au Pliocène moyen), Fuente Nueva 1 et Fonelas (de la fin du Pliocène), Venta Micena (des débuts du Pléistocène), Fuenta Nueva 3, Barranco León 5 et Huéscar (de la fin du Pléistocène inférieur), Cúllar (des débuts du Pléistocène moyen) et Solana de Zamborino (de la fin du Pléistocène moyen). Et surtout, en plus de ces importants gisements comportant des restes de grands vertébrés, on compte par dizaines les niveaux intermédiaires qui ont fourni des ossements de petits vertébrés, couvrant tout le spectre d'âge du bassin. Rassemblée sous le concept générique de « microvertébrés », on rencontre une grande variété de groupes qui inclut les poissons, les amphibiens, les reptiles et les mammifères. Ce type de récolte peut être très abondant dans des niveaux déterminés du bassin et, à la différence de ce qui se passe avec les grands mammifères, il permet d'obtenir des échantillons de dizaines, de centaines voire de milliers de fragments osseux. Les microvertébrés sont souvent d'une grande utilité pour reconstruire le contexte climatique et environnemental du passé puisque, étant donné leur petite taille, ils sont généralement très sensibles aux changements de température et d'humidité. Par exemple, de nombreuses études ont mis en évidence l'étroite relation qui lie les amphibiens et les reptiles dits squamates (essentiellement lézards et serpents) à leur milieu environnemental. Comme dans le cas de la végétation, leur répartition et diversité sont très liées à des paramètres climatiques tels que la radiation solaire ou la température annuelle moyenne, plus que dans n'importe quel autre groupe de microvertébrés.

Étant donné que les amphibiens et les reptiles sont des vertébrés ectothermiques (ce qui veut dire que leur température corporelle dépend de la température du milieu où ils vivent) et, par conséquent, qu'ils sont hautement dépendants de leur habitat local, leur répartition est fortement conditionnée par les paramètres de température et de précipitations. Si bien que ces éléments de la microfaune constituent d'excellents indicateurs des températures et précipitations du passé. Ainsi, on peut utiliser les variations observées dans la composition de ce type de faune pour estimer les valeurs des paramètres climatiques à chaque moment. Ce type d'analyse est principalement basé sur les données de répartition géographique des populations actuelles du même type, puisque, dans leur majorité, on observe une stabilité notable spécifique tout au long du Pléistocène, de sorte que la majeure partie des éléments de cette période peuvent se référer à des espèces actuelles.

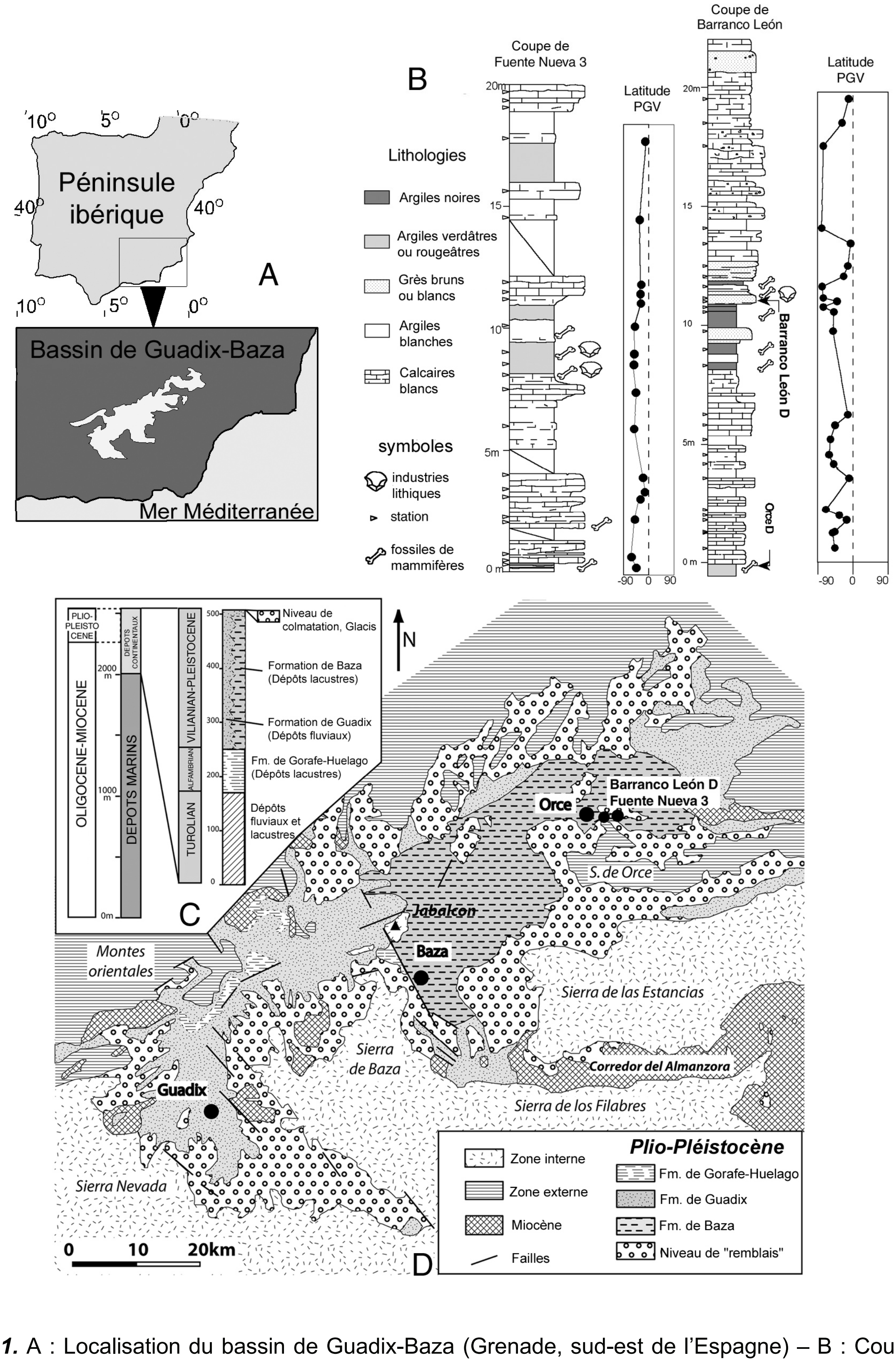

Figure 1. A : Localisation du bassin de Guadix-Baza (Grenade, sud-est de l'Espagne) – B : Coupes géologiques de Barranco León et Fuente Nueva 3, avec indication des niveaux archéologiques et du paléomagnétisme – C : Séquence stratigraphique du remplissage – D : Unités stratigraphiques du bassin de Guadix-Baza. [D'après TORO *et al*., 2010, modifié]

L'analyse de la juxtaposition des zones de répartition des espèces présentes dans un niveau fossilifère nous permet de calculer les conditions climatiques régnant dans cette zone par le passé (ce que l'on connaît comme "mutual climatic range method"). Cette méthode a été utilisée pour déduire températures et précipitations dans d'autres groupes, tels les associations végétales basées sur le pollen ou les coléoptères.

En prenant comme base l'atlas de distribution de la faune d'amphibiens et de reptiles ibériques, nous pouvons identifier pour une zone déterminée (divisée en carrés UTM de 10 x 10 km) quelles sont les conditions climatiques qui correspondent actuellement à une association précise d'espèces du registre fossile. Naturellement, dans ce type d'analyse, il faut se demander – à l'instant où l'on détermine - dans quelle mesure une distribution actuelle correspond à son optimum climatique et si des facteurs comme l'anthropisation du territoire, l'urbanisme, la prédation ou la concurrence avec des nouveaux commensaux ne représentent pas un élément de perturbation trop important.

On évalue les facteurs climatiques en utilisant diverses cartes climatiques d'Espagne, ainsi que des données provenant de l'Institut Espagnol de Météorologie qui couvrent une période de 30 ans. Ainsi, on fait des estimations de température et de précipitation sur chaque carré UTM de 10 x 10 km (ce qui détermine la zone de couverture). À partir de chacune de ces zones à géométrie variable, on peut déterminer les paramètres climatiques pour chaque carré UTM de 10 x 10 km et les comparer avec la station météorologique la plus proche du gisement archéo-paléontologique. Les différences observées entre les valeurs déduites à partir de l'association fossile et les paramètres climatiques actuels pour la même zone correspondent par conséquent à des fluctuations climatiques au fil du temps. Grâce à cette méthodologie, on est parvenu à délimiter les paramètres climatiques de température moyenne annuelle, température du mois le plus froid, température du mois le plus chaud, ou la précipitation moyenne annuelle pour les différents niveaux avec des microvertébrés du bassin de Guadix-Baza.

En plus des amphibiens et des reptiles, quelques groupes de petits mammifères, comme les insectivores (musaraignes, taupes et hérissons) ou les rongeurs (campagnols, souris, hamsters et loirs) se sont aussi révélés remarquables au moment de reconstruire les conditions environnementales du passé.

Contexte chronologique

Différents groupes de rongeurs peuvent être également utiles pour détailler l'âge d'un gisement, étant donné que quelques-uns parmi eux - tels les campagnols - ont modifié très rapidement la forme et la hauteur de la couronne de leurs dents en réponse aux changements qui se sont produits dans la végétation. Par conséquent, en connaissant leur morphologie dentaire et en analysant les changements qui se produisent au fil du temps, on peut parvenir à des niveaux de détermination temporelle très élevés et savoir exactement à quel moment de l'histoire géologique du bassin nous nous trouvons.

Ce type d'analyse, connu comme analyse biostratigraphique, est complété par d'autres techniques comme l'analyse paléomagnétique qui consiste à analyser la polarité du champ magnétique des sédiments parmi lesquels on trouve les microfossiles. La technique du paléomagnétisme est basée sur le fait, aujourd'hui pleinement confirmé, que la polarité du

Figure 2. Vue panoramique du secteur d'Orce, depuis le gisement de Barranco León.
[Photo Jordi MESTRE, IPHES]

Figure 3. Vue du gisement de Barranco León depuis le bas du ravin.
[Photo Jordi MESTRE, IPHES]

champ magnétique terrestre a changé capricieusement tout au long de son histoire. Ainsi, s'il y a un million d'années, l'un des premiers habitants d'Europe avait pu disposer d'une boussole, il aurait constaté que son aiguille s'orientait vers le pôle Sud et non vers le pôle Nord, comme ce qui se passe actuellement.

Cela signifie que, il y a un million d'années, le pôle Nord magnétique était situé au pôle Sud géographique, et vice-versa. Ce type de polarité opposée à celle qui existe à l'heure actuelle reçoit le nom de polarité inversée. La conformation actuelle du champ magnétique, avec le pôle Nord magnétique coïncidant avec ce que nous appelons le pôle Nord géographique, date de 780 000 ans, au moment de l'époque magnétique Brunhes. Avant, toute la Terre se trouvait dans la période de polarité magnétique inversée connue comme Matuyama, qui s'étend depuis le Pliocène supérieur, il y a 2,6 Ma, jusqu'au moment de transition vers l'état Bruhnes.

À notre connaissance, les changements de polarité magnétique, qui normalement s'étendent sur plusieurs milliers d'années, n'entraînent aucun type d'effet catastrophique ni changement estimable sur le fonctionnement de la biosphère : la planète a changé irrégulièrement de polarité sans que ses occupants en soient conscients, ni souffrent d'aucun effet pour un tel changement (à l'exception, peut-être, des oiseaux migrateurs qui s'orientent suivant le champ magnétique pour leurs déplacements). L'ensemble des variations du champ magnétique, parfaitement établi dans le substrat du fond océanique, constitue ainsi une espèce de « code-barres » qui permet de situer chronologiquement n'importe quelle séquence de strates pour laquelle on peut établir sa polarité magnétique. L'avantage de ce code-barres, c'est que chacun des changements de polarité du champ magnétique a pu être daté parfaitement par des méthodes radiométriques : le fond océanique est constitué de basalte, un type de roche volcanique qui s'avère particulièrement appropriée pour réaliser ce type de datation. Or, à l'instar du basalte, n'importe quel sédiment fluide contient une quantité importante de particules sensibles au magnétisme (la magnétite par exemple) qui, au moment de leur dépôt, s'orientent conformément au magnétisme régnant à cette époque. En enregistrant l'orientation dans laquelle sont restées ces particules magnétiques, il est alors possible de déterminer le type de polarité du champ magnétique - normale ou inversée - au moment où ce sédiment s'est déposé.

En combinant la biostratigraphie basée sur les rongeurs avec le paléomagnétisme, on peut parvenir à préciser d'une manière plus exacte l'âge d'un niveau déterminé du bassin. En même temps, cette recherche de l'échelle biostratigraphique régionale a permis d'établir un lien précis avec les autres gisements qui, comme Fuente Nueva 3 et Barranco León D, enregistrent les premières occupations humaines hors de l'Afrique *(fig. 2 et 3)*. C'est le cas de Sima del Elefante, dans le complexe karstique d'Atapuerca, daté par des éléments cosmogéniques à 1,2 Ma, et du gisement de la base du Pléistocène de Dmanisi, en Géorgie. Finalement, les petits vertébrés sont aussi très utiles à l'heure de déterminer le sens des migrations et les zones d'origine des différents groupes. De tels phénomènes d'expansion et de rétraction biogéographiques sont évidemment le reflet des conditions changeantes du milieu dans les zones impliquées ; c'est pourquoi ils ont un sens écogéographique évident. C'est le cas des petits vertébrés : l'expansion d'une espèce depuis sa zone d'origine implique très certainement une expansion des conditions environnementales régnant dans cette zone. Dans le contexte des cycles glaciaire-interglaciaire du Pléistocène, des dispersions avec une forte composante latitudinale présentaient une composante climatique évidente, associée à l'extension vers le sud des faunes les plus froides du nord. Au contraire, des dispersions avec une composante orientale peuvent avoir une interprétation très complexe, associée à l'extension des zones arides. En ce sens, il s'avère particulièrement intéressant de déterminer les possibles connexions nord-africaines ou asiatiques des associations de microvertébrés avec l'aire d'origine des premières populations humaines dans le bassin de Guadix-Baza.

Bibliographie recommandée

AGUSTÍ J. (1986) - Synthèse biostratigraphique du Plio-Pléistocène de Guadix-Baza (province de Granada, sud-est de l'Espagne). *Geobios,* 19 : 505-510.

AGUSTÍ J., BLAIN H.-A., FURIÓ M., DE MARFÁ R. & SANTOS-CUBEDO A. (2010) - The early Pleistocene small vertebrate succession from the Orce region (Guadix-Baza Basin, SE Spain) and its bearing on the first human occupation of Europe. *Quaternary International,* 223-224 (1) : 162-169.

AGUSTÍ J., BLAIN H.-A., CUENCA-BESCÓS G. & BAILON S. (2009) - Climate forcing of first hominid dispersal in Western Europe. *Journal of Human Evolution,* 57 (6) : 815-821.

BAILON S. & BLAIN H.-A. (2007) - Faunes de reptiles et changements climatiques en Europe occidentale autour de la limite Plio-Pléistocène. *Quaternaire*, 18 (1) : 55-63.

BLAIN, H.-A. (2005) - Contribution de la paléoherpétofaune (Amphibia & Squamata) à la connaissance de l'évolution du climat et du paysage du Pliocène supérieur au Pléistocène moyen d'Espagne. Doctorat du Muséum national d'Histoire naturelle de Paris. Département de Préhistoire. Institut de Paléontologie humaine, 402 p., 67 pls.

BLAIN H.-A., BAILON S., AGUSTÍ J., MARTÍNEZ-NAVARRO B. & TORO I. *(sous-presse)* - Paleoenvironmental and paleoclimatic proxies to the Early Pleistocene hominids of Barranco León D and Fuente Nueva 3 (Granada, Spain) by means of their amphibian and reptile assemblages. *Quaternary International.*

FURIÓ BRUNO, M. (2007) - Los Insectívoros (Soricomorpha, Erinaceomorpha, Mammalia) del Neógeno superior del Levante Ibérico. Ph.D. thesis. Univ. Autònoma de Barcelona, 299 p.

GARCÉS M., AGUSTÍ J. & PARÉS J.M. (1996) - Late Pliocene continental magnetochronology in the Guadix-Baza Basin (Betic ranges, Spain). *Earth Planetary Science Letters,* 146 : 677-688.

MARTÍNEZ-NAVARRO B., TURQ A., AGUSTÍ J. & OMS O. (1997) - Fuente Nueva-3 (Orce, Granada, Spain) and the first human occupation of Europe. *Journal of Human Evolution*, 33 : 611-620.

OMS O., PARÉS J.M., MARTÍNEZ-NAVARRO B., AGUSTÍ J., TORO I., MARTÍNEZ-FERNÁNDEZ G., & TURQ A. (2000) - Early human occupation of Western Europe : Paleomagnetic dates for two Paleolithic sites in Spain. *Proceedings of the National Academy of Sciences*, 97 : 10666-10670.

TORO I., MARTÍNEZ-NAVARRO B. & AGUSTÍ J. coords (2010) - Ocupaciones humanas durante el Pleistoceno inferior y medio de la Cuenca de Guadix-Baza. Arqueología Monografías. Junta de Andalucía, Sevilla.

Investigating the Mid-Brunhes Event in the Spanish terrestrial sequence

Hugues-Alexandre Blain[1]*, Gloria Cuenca-Bescós[2]*, Iván Lozano-Fernández[1]*, Juan Manuel López-García[1]*, Andreu Ollé[1]*, Jordi Rosell[1]*, and Jesus Rodríguez[3]*

[1]IPHES (Institut Català de Paleoecologia Humana i Evolució Social), c/ Escorxador s/n, 43003 Tarragona, Spain, and Àrea de Prehistòria, Universitat Rovira i Virgili (URV), Avinguda de Catalunya 35, 43002 Tarragona, Spain
[2]Área de Paleontología, Departamento de Ciencias de la Tierra, Facultad de Ciencias, Universidad of Zaragoza, 50009 Zaragoza, Spain
[3]CENIEH (Centro Nacional de Investigación sobre la Evolución Humana), Avenida de la Paz 28, 09004 Burgos, Spain

ABSTRACT

In the Mediterranean area, which is climatically stressed by limited water resources and extremes of heat, climate variations are known to play a crucial role in the ecosystems and environment. Investigating how climate has changed in the past may help us to understand how it may change in the future and its consequences on temperature and water resources. The Gran Dolina sequence (north-central Spain) provides a unique long paleontological and archaeological record spanning the Mid-Brunhes (ca. 450 ka) climatic transition. A fossil amphibian- and squamate-based reconstruction of temperature and precipitation shows marked peaks that have been related to various interglacial peaks in accordance with numeric dates and paleomagnetic and biochronological data. An analysis of climate and herpetofaunal assemblage changes during the interglacial periods reveals that (1) post-Mid-Brunhes Event (MBE) interglacials were warmer than pre-MBE interglacials, (2) pre-MBE interglacials were warmer than present day, and (3) there were lower levels of rainfall in post-MBE interglacials than in pre-MBE interglacials. The climate trend in the Mediterranean area was found to be congruous with global climate changes as reconstructed from ice and sea-surface temperature records over the past million years.

INTRODUCTION

The Mid-Brunhes Event (MBE) is a climatic transition between marine oxygen isotope stages (MIS) 13 and 11 that separates two climatic modes: (1) early-middle Pleistocene interglacials (780–450 ka), which are characterized by only moderate warmth, and (2) middle and late Pleistocene interglacials (occurring after 450 ka), which are characterized by greater warmth consistent with, or warmer than, the Holocene. This event is observable in a variety of long-term climate records such as the Mapping Spectral Variability in Global Climate Project (SPECMAP) and the European Project for Ice Coring in Antarctica (EPICA) (EPICA community members, 2004; Jouzel et al., 2007), many records of sea-surface temperature (Lisiecki and Raymo, 2005; Becquey and Gersonde, 2002), and some long-term speleothem records (Winograd et al., 1997), but its effect on terrestrial systems is poorly understood due to the absence of detailed long-term records of environmental change (Tzedakis et al., 2006, 2009; Candy et al., 2010). Through their examination of the British terrestrial sequence, Candy et al. (2010) showed that interglacial climates during the early-middle Pleistocene were as warm as those that occurred during the late-middle and late Pleistocene, suggesting that the MBE was not a global climatic transition, but was restricted to specific regions, in particular to higher latitudes of the Southern Hemisphere. Because climate projection models suggest that greater climate changes would be expected under warming conditions at higher latitudes, we would also expect many intracontinental and Mediterranean fringe regions to display considerable temperature increases and precipitation decreases (e.g., Sanderson et al., 2011). In this work we investigate this climatic transition in the long-term terrestrial sequence of Gran Dolina cave (Atapuerca, Burgos, north-central Spain), which spans the MBE transition, by means of the mutual climatic range technique using the amphibian and squamate fossil assemblages.

GEOLOGICAL AND CHRONOLOGICAL SETTING

The Sierra de Atapuerca is ~1080 m above sea level, dominating the now-flat landscape of the Castilian grain-growing plains irrigated by the River Arlanzón near the village of Ibeas de Juarros, located 14 km east of the city of Burgos (Fig. 1).

The ongoing archaeological and paleontological excavations in Gran Dolina, or Trinchera Dolina (TD), cave have been conducted every year since 1976, and have revealed a long, culturally and paleontologically rich sequence dated as between ca. 1 Ma and 250 ka by means of biostratigraphy, electron spin resonance, electron spin resonance on optically bleached quartz dating, U-series, thermoluminescence, infrared-stimulated-luminescence analysis, and paleomagnetic dating (see Appendix DR1 in the GSA Data Repository[1]).

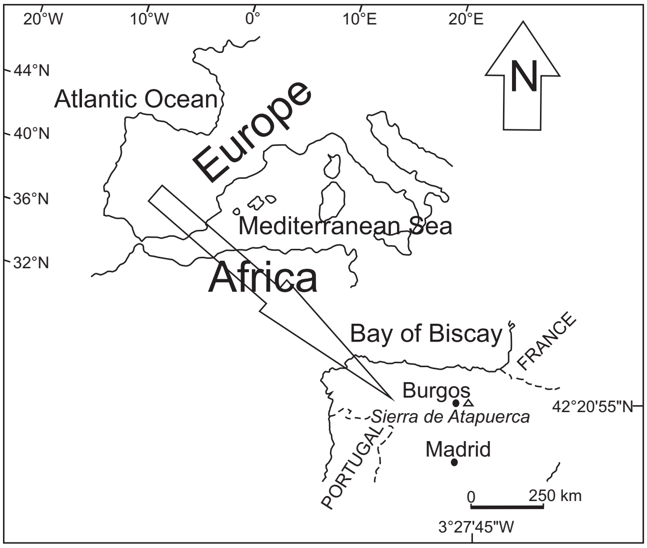

Figure 1. Location of Sierra de Atapuerca (Burgos, Spain).

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*E-mails: hablain@iphes.cat; ilozano@iphes.cat; jmlopez@iphes.cat; aolle@iphes.cat; jordi.rosell@urv.cat; cuencag@unizar.es; jesus.rodriguez@cenieh.es.

[1] GSA Data Repository item 2012296, Appendices DR1 and DR2, Figure DR1, geological and chronological setting of Gran Dolina cave, and Table DR1, is available online at www.geosociety.org/pubs/ft2012.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

GEOLOGY, November 2012; v. 40; no. 11; p. 1051–1054; Data Repository item 2012296 | doi:10.1130/G33427.1

MATERIAL AND METHODS

The small-vertebrate fossil remains used for this study consist of disarticulated bone fragments collected by means of water screening during work on the test excavation (~9 m^2) that comprises level TD5 at the bottom to level TD10 at the top (see Appendix DR1). The excavation was divided into ~10-cm-thick excavation layers (T). The small vertebrates have been processed and studied according to these excavation layers (Cuenca-Bescós et al., 2005, 2010, 2011). A total of 5596 kg of sediment was processed, corresponding to 76 samples. The amphibian and squamate assemblage contains ~40,000 fragments corresponding to a minimum of 6145 specimens, representing at least 20 taxa, including newts, toads and frogs, amphisbaenians, lacertids, anguids, and snakes (Blain, 2005; Blain et al., 2008, 2009).

The taphonomic patterns of the herpetofaunal accumulations were discussed in Blain et al. (2008, 2009). Taphonomic observations on the collections of small vertebrates at Gran Dolina suggest, based on the type of digestion evidence and the fractures in the fossils, that the remains were mostly the prey of nocturnal birds such as the eagle owl (*Bubo bubo*), an opportunist that hunts a wide range of prey (Bennàsar Serra, 2010).

Paleoclimatic Reconstruction

Because most amphibians are water dependent and most reptiles are temperature dependent, the climatic and/or environmental parameters in their immediate environment mark their distribution. Paleoclimatic interpretations are based on the presence of herpetofaunal species from each of the excavation layers. The mutual climatic range (MCR) method is used to quantify paleotemperature and paleoprecipitation (see Blain et al., 2009), specifically, mean annual temperature (MAT), mean temperature of the warmest month (MTW), mean temperature of the coldest month (MTC), mean annual precipitation (MAP), and winter (DJF, December-January-February) and summer (JJA, June-July-August) precipitation. Analysis of the MCR in each T layer is based on the distribution atlas of Iberian herpetofauna (Pleguezuelos et al., 2004), divided into 10 × 10 km UTM (Universal Transverse Mercator) squares. Climatic parameters have been estimated for each 10 × 10 km UTM square, using various climatic maps from the Iberian Peninsula (Font Tullot, 1983, 2000). The chronology of the interglacial peaks was assigned by means of numeric dates, and by paleomagnetic and biochronological data as shown in Appendix DR1.

Environmental Reconstruction

Two paleoenvironmental parameters were used in this study: (1) the representation of amphibian and squamate taxa associated with woodland and woodland-edge areas, and (2) the representation of small mammal taxa inhabitants of open-dry environments (dry meadows, steppes, and rocky areas). These two variables were inferred from the paleoenvironmental data for the amphibian and squamate assemblages obtained by Blain et al. (2008) and small mammal assemblage data obtained by Cuenca-Bescós et al. (2005).

RESULTS AND DISCUSSION

On the basis of the paleoherpetological associations, paleoclimatic parameters were estimated relating to MAT, MTC, and MTW months, winter (DJF) and summer (JJA) precipitation, and MAP (Appendix DR2). According to the ΔMAT curve (representing the deviation from the present values), our results first suggest that only warm periods (i.e., interglacials) are evident in the TD sequence. The general trends of the curve (ΔMAT in Fig. 2), in accordance with the numeric dates and paleomagnetic and biochronological data, show three distinct peaks in the time interval represented by level TD10 (T0 to T22): a first small peak (T1) ca. 244 ± 26 ka (Berger et al., 2008) identified as MIS 7; then two higher peaks between 0.33 and 0.40 Ma (Falguères et al., 2001; Moreno García, 2011), which have been correlated with MIS 9 (T9) and MIS 11 (T17). After these, the numeric estimations obtained for the upper part of TD9 (0.42 Ma; Moreno García, 2011) suggest a probable correlation with MIS 13, due to the high values obtained in the lowermost part of TD10 (T21). Level TD8 (T24–T27) certainly corresponds to MIS 15 or MIS 16 with a numeric estimation of 0.60 Ma (Moreno García, 2011). Unfortunately, the low number of herpetofaunal remains in this level does not permit its climatic conditions to be reconstructed. Nevertheless, the occurrence of the amphisbaenian *Blanus cinereus* in T27, slightly north of its current distribution in Spain (Blain, 2005), suggests that this layer corresponds to climatic conditions that were warmer than or similar to those of today. The Brunhes-Matuyama boundary located between levels TD7 and TD8 yields an age close to 780 ka for the lower part of level TD8 and consequently, the highest temperature correlates to MIS 19 (T28). The following succession of high values

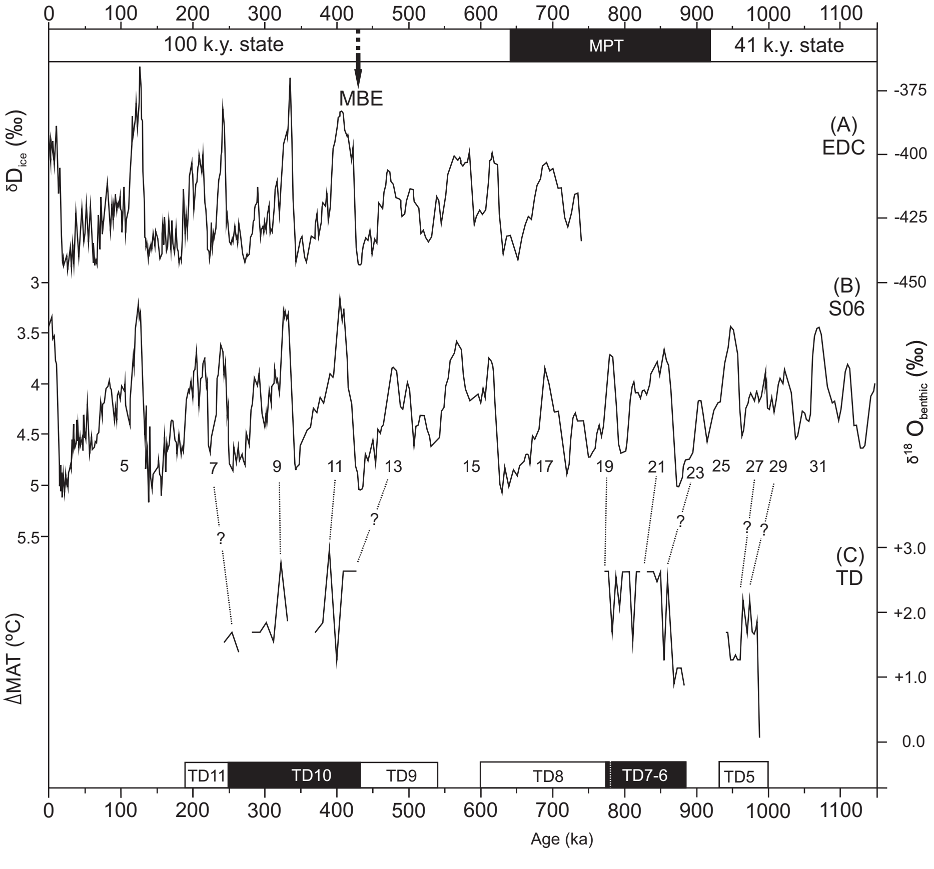

Figure 2. Correlation and comparison between ice, sea-surface, and Gran Dolina temperature records. MBE—Mid-Brunhes Event; MPT—Mid-Pleistocene transition; TD—Trinchera Dolina. A: EPICA (European Project for Ice Coring in Antarctica; EPICA community members, 2004) Dome C (EDC) deuterium (δD) record. B: S06 δ^{18}O$_{benthic}$ composite record from sites in equatorial east Pacific (Tzedakis et al., 2006). C: Trinchera Dolina (TD) herpetofauna-based mean annual temperature (ΔMAT) plotted on numeric date time scale. Position of MBE is indicated, as are interglacial marine isotopic stages (numbers).

within level TD6 (T33, T35–T37, T40, T41, T43–T45, T48, and T50), numerically attributed to the late-early Pleistocene (from 0.80 to 0.88 Ma; Moreno García, 2011), may correspond to MIS 21 and MIS 23. Because the highest MAT reaches the same value for this period, a single layer (T43) is used to characterize MIS 21. T50 is cautiously correlated with MIS 23. Within level TD5 (ranging between 0.94 and 1.00 Ma; Moreno García, 2011), two small peaks appear at T65 and T68, and are tentatively correlated with MIS 27 and MIS 29.

Because the ΔMAT curve (Fig. 2) does not represent absolute values, but rather relative values regarding the deviation from today's values, our results first suggest that all post-MBE and pre-MBE interglacials were warmer than present-day temperatures. Together with the relatively high percentages (30%–40%) in taxa with plant cover requirements ("% wood" in Appendix DR2) and the fact that no typical large glacial mammals have been recovered (Rodríguez et al., 2011), this may suggest that only warm periods (i.e., interglacials) have been documented in the Gran Dolina sequence. Independent of their absolute values, the ΔMAT curve (Fig. 2) shows interesting trends. When compared (Fig. 3), post-MBE interglacials (at least MIS 11 and MIS 9) reach higher temperatures than pre-MBE interglacials (MIS 13, MIS 19, MIS 21, MIS 23, MIS 27, and MIS 29) in accordance with ice (SPECMAP and EPICA) and marine sea-surface temperature records (EPICA community members, 2004; Jouzel et al., 2007, Lisiecki and Raymo, 2005; Becquey and Gersonde, 2002). This may suggest that a MBE climatic transition occurred in the terrestrial environments of northern Spain.

The fact that pre-MBE interglacials are estimated to have been warmer than present day (i.e., Holocene) contradicts the MBE, because all ice and marine records show lower than present values in pre-MBE interglacial temperatures. However, other terrestrial sequences spanning the MBE have also suggested that pre-MBE interglacials were warmer than present day. This phenomenon has been well documented in the terrestrial record of Britain (Candy et al., 2010) and in the long pollen record of Tenaghi Philippon (Greece), where the amplitude of interglacials, as reflected in variations in the Arborean pollen (AP) curve, does not appear to significantly affect the extent of the tree population expansions of the various forest stages. With particular reference to the terrestrial equivalents of MIS 13 and MIS 15, not only the AP maxima, but also their vegetational character (mainly dominated by *Quercus* and *Carpinus*), are similar to post-MBE interglacials (Tzedakis et al., 2006).

According to our estimation, in northern Spain, MIS 11 was the warmest interglacial, followed by MIS 9 and MIS 7. MIS 5 is unfortunately not represented in the Gran Dolina sequence; moreover, to date no clear MIS 5.5 paleontological site has been studied on the Iberian Peninsula. Global simulations by Yin and Berger (2010) suggest that MIS 9.3 is probably the warmest post-MBE interglacial, followed by MIS 5.5, MIS 11.3, MIS 1, and MIS 7.5 is the coolest. In addition, paleontological evidence from Britain strongly suggests that the MIS 9 temperate stage was warmer than the temperate stages of MIS 11 and MIS 7 or the Holocene, and approached the temperatures typical of the Eemian-Ipswichian (MIS 5.5) in terms of warmth (Green et al., 2006). However, based on evidence derived from the EPICA ice record, Masson-Delmotte et al. (2010) suggested that MIS 5.5 and MIS 11 were the warmest interglacial maxima.

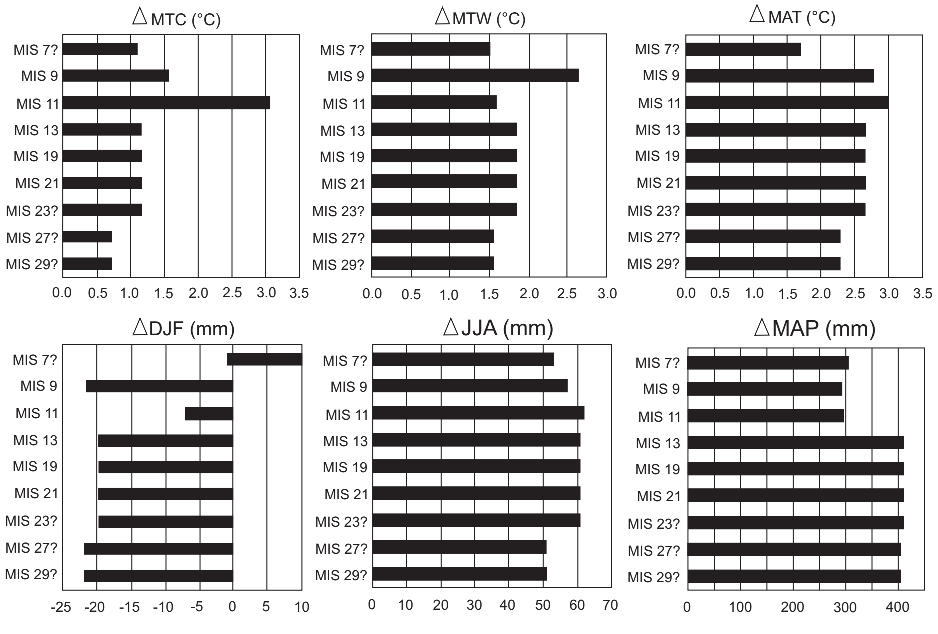

Figure 3. Comparison between interglacials identified in Trinchera Dolina sequence. Abbreviations: ΔMTC—difference between mean temperature of coldest month and present day; ΔMTW—difference between mean temperature of warmest month and present day; ΔMAT—difference between mean annual temperature and present day; ΔDJF—difference between winter precipitation and present day (DJF is December, January, February); ΔJJA—difference between summer precipitation and present day (JJA is June, July, August); ΔMAP—difference between mean annual precipitation and present day; MIS—marine oxygen isotope stage.

The seasonal variation of temperature simulated by Yin and Berger (2010) for post-MBE interglacials shows that the higher MAT is mainly due to warming during boreal winter: over the Northern Hemisphere, the linear response to astronomical forcing leads to a slightly warmer Northern Hemisphere in winter and a cooler Northern Hemisphere in summer. Our results (except for MIS 11) disagree with these simulations, in that MTW increases are higher than MTC for all pre-MBE and post-MBE interglacials. Only for MIS 11 is the MTC increase much higher than the MTW (Fig. 3).

MAP drops by ~100 mm after the MBE transition, but the minima do not coincide with interglacial peaks. Seasonal variations suggest more precipitation in summer (ΔJJA) compared to today's levels and, except for MIS 7, less precipitation during winter (ΔDJF). According to these results, middle Pleistocene interglacials were characterized in this region by a more homogeneous rainfall distribution throughout the year. Because the summer drought period is the main feature that characterizes the Mediterranean climate, increased summer rainfall suggests a reduced Mediterranean character for these interglacial climates. A higher moisture level than within current climatic conditions in northern Spain is in accordance with the development of woodland areas and wet meadows supporting grazer and browser type of large mammals represented in the paleontological record of Gran Dolina. The decrease in MAP after the MBE is in accordance with the increase in the representation of open dry environment–preferring small-mammal taxa in level TD10 (Cuenca-Bescós et al., 2005; "% OD+R" in Appendix DR2) as well as with the changes documented in the large mammal communities toward herbivores better adapted to arid conditions in level TD10, like the large bisons (*Bison priscus*), aurochs (*Bos primigenius*), caballoid horses (*Equus germanicus* and *E. mosbachensis*), and stronger rhinos (*Stephanorhinus hemitoechus*) (Cuenca-Bescós and García, 2007).

CONCLUSIONS

The analysis of the differences between the successive interglacial peaks reveals the following.

1. Post-MBE interglacials were warmer than pre-MBE interglacials in accordance with the MBE climate transition as documented by ice (EPICA and SPECMAP) and sea-surface temperature records.
2. Pre-MBE interglacials were warmer than present day.
3. The reconstructed MIS 11 mean annual temperature is slightly warmer than MIS 9, and much warmer than MIS 7 in northern Spain. MIS 5 is not represented in the Gran Dolina sequence.
4. Post-MBE interglacials had lower rainfalls than pre-MBE interglacials, resulting in the increasing development of open dry environments on the Iberian Peninsula. This is in accordance with the increase in the presence of dry-terrain small mammals in the Gran Dolina sequence after the MBE, as well as with the turnover documented in large mammal communities toward herbivores better adapted to arid conditions.

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REFERENCES CITED

Becquey, S., and Gersonde, R., 2002, Past hydrographic and climatic changes in the Subantarctic Zone of the South Atlantic—The Pleistocene record from ODP Site 1090: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 182, p. 221–239, doi:10.1016/S0031-0182(01)00497-7.

Bennàsar Serra, M.L., 2010, Estudio tafonómico de los micromamíferos de los yacimientos del Pleistoceno Inferior de los yacimientos de Gran Dolina y Sima del Elefante. (Atapuerca, Burgos, Spain) [Ph.D. thesis]: Tarragona, Universitat Rovira i Virgili, 602 p.

Berger, G.W., Pérez-González, A., Carbonell, E., Arsuaga, J.L., Bermúdez de Castro, J.-M., and Ku, T.-L., 2008, Luminescence chronology of cave sediments at the Atapuerca paleoanthropological site, Spain: Journal of Human Evolution, v. 55, p. 300–311, doi:10.1016/j.jhevol.2008.02.012.

Blain, H.-A., 2005, Contribution de la Paléoherpétofaune (Amphibia et Squamata) à la connaissance de l'évolution du climat et du paysage du Pliocène supérieur au Pléistocène moyen d'Espagne [Ph.D. thesis]: Paris, Muséum National d'Histoire Naturelle, 402 p.

Blain, H.-A., Bailon, S., and Cuenca-Bescós, G., 2008, The early-middle Pleistocene palaeoenvironmental change based on the squamate reptile and amphibian proxies at the Gran Dolina site, Atapuerca, Spain: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 261, p. 177–192, doi:10.1016/j.palaeo.2008.01.015.

Blain, H.-A., Bailon, S., Cuenca-Bescos, G., Arsuaga, J.L., Bermúdez de Castro, J.M., and Carbonell, E., 2009, Long-term climate record inferred from early-middle Pleistocene amphibian and squamate reptile assemblages at the Gran Dolina Cave, Atapuerca, Spain: Journal of Human Evolution, v. 56, p. 55–65, doi:10.1016/j.jhevol.2008.08.020.

Candy, I., Coope, G.R., Lee, J.R., Parfitt, S.A., Preece, R.C., Rose, J., and Schreve, D.C., 2010, Pronounced warmth during early middle Pleistocene interglacials: Investigating the Mid-Brunhes Event in the British terrestrial sequence: Earth-Science Reviews, v. 103, p. 183–196, doi:10.1016/j.earscirev.2010.09.007.

Cuenca-Bescós, G., and García, N., 2007, Biostratigraphic succession of the early and middle Pleistocene mammal faunas of the Atapuerca cave sites (Burgos, Spain): Courier Forschunginstitut Senckenberg, v. 259, p. 99–110.

Cuenca-Bescós, G., Rofes, J., and García-Pimienta, J., 2005, Environmental change across the Early-Middle Pleistocene transition: Small mammalian evidence from the Trinchera Dolina cave, Atapuerca, Spain, *in* Head, M.J., and Gibbard, P.L., eds., Early-Middle Pleistocene transitions: The land-ocean evidence: Geological Society of London Special Publication 247, p. 277–286, doi:10.1144/GSL.SP.2005.247.01.16.

Cuenca-Bescós, G., Rofes, J., López-García, J.M., Blain, H.-A., De Marfá, R.J., Galindo-Pellicena, M.A., Bennàsar-Serra, M.L., Melero-Rubio, M., Arsuaga, J.L., Bermúdez de Castro, J.M., and Carbonell, E., 2010, Biochronology of Spanish Quaternary small vertebrate faunas: Quaternary International, v. 212, p. 109–119, doi:10.1016/j.quaint.2009.06.007.

Cuenca-Bescós, G., Melero-Rubio, M., Rofes, J., Arsuaga, J.L., Martínez, I., Blain, H.-A., López-García, J.M., Carbonell, E., and Bermúdez de Castro, J.M., 2011, The Early-Middle Pleistocene environmental and climatic change and the human expansion in Western Europe: A case study with small vertebrates (Gran Dolina, Atapuerca, Spain): Journal of Human Evolution, v. 60, p. 481–491, doi:10.1016/j.jhevol.2010.04.002.

EPICA community members, 2004, Eight glacial cycles from an Antarctic ice core: Nature, v. 429, p. 623–628, doi:10.1038/nature02599.

Falguères, C., Bahain, J.-J., Yokoyama, Y., Bischoff, J.L., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., and Dolo, J.M., 2001, Datations par RPE et U-Th des sites pléistocènes d'Atapuerca: Sima de los Huesos, Trinchera Dolina et Trinchera Galería. Bilan géochronologique: L'Anthropologie, v. 105, p. 71–81, doi:10.1016/S0003-5521(01)80006-6.

Font Tullot, I., 1983, Atlas Climatico de España: Madrid, Spain, Ministerio de Transportes, Turismo y Communicaciones, Instituto Nacional de Meteorologia, 43 plates.

Font Tullot, I., 2000, Climatología de España y Portugal: Salamanca, Spain, Ediciones Universidad de Salamanca, 422 p.

Green, C.P., Branch, N.P., Coope, G.R., Field, M.H., Keen, D.H., Wells, J.M., Schwenninger, J.L., Preece, R.C., Schreve, D.C., Canti, M.G., and Gleed-Owen, C.P., 2006, Marine Isotope Stage 9 environments of fluvial deposits at Hackney, north London, UK: Quaternary Science Reviews, v. 25, p. 89–113, doi:10.1016/j.quascirev.2004.10.011.

Jouzel, J., and 31 others, 2007, Orbital and millennial Antarctic climate variability over the past 800,000 years: Science, v. 317, p. 793–796, doi:10.1126/science.1141038.

Lisiecki, L.E., and Raymo, M.E., 2005, A Pliocene–Pleistocene stack of 57 globally-distributed benthic δ^{18}O records: Paleoceanography, v. 20, PA1003, doi:10.1029/2004PA001071.

Masson-Delmotte, V., and 17 others, 2010, EPICA Dome C record of glacial and interglacial intensities: Quaternary Science Reviews, v. 29, p. 113–128, doi:10.1016/j.quascirev.2009.09.030.

Moreno García, D., 2011, Datation par ESR de quartz optiquement blanchis (ESR-OB) de la région de Atapuerca (Burgos, Espagne). Application au site préhistorique de Gran Dolina (contexte karstique) et aux systèmes fluviatiles quaternaires de l'Arlanzón et l'Arlanza [Ph.D. thesis]: Tarragona, Universitat Rovira i Virgili and Paris, Muséum National d'Histoire Naturelle, 304 p.

Pleguezuelos, J.M., Márquez, M., and Lizana, M., eds., 2004, Atlas y libro rojo de los anfibios y reptiles de España: Madrid, Spain, Asociación Herpetologica Española, Dirección General de Conservación de la Naturaleza, 584 p.

Rodríguez, J., and 26 others, 2011, One million years of cultural evolution in a stable environment at Atapuerca (Burgos, Spain): Quaternary Science Reviews, v. 30, p. 1396–1412, doi:10.1016/j.quascirev.2010.02.021.

Sanderson, M.G., Hemming, D.L., and Betts, R.A., 2011, Regional temperature and precipitation changes under high-end (≥4°C) global warming: Royal Society of London Philosophical Transactions, ser. A, v. 369, p. 85–98, doi:10.1098/rsta.2010.0283.

Tzedakis, P.C., Hooghiemstra, H., and Pälike, H., 2006, The last 1.35 million years at Tenaghi Philippon: Revised chronostratigraphy and long-term vegetation trends: Quaternary Science Reviews, v. 25, p. 3416–3430, doi:10.1016/j.quascirev.2006.09.002.

Tzedakis, P.C., Raynouad, D., McManus, J.F., Berger, A., Brovkin, V., and Kiefer, T., 2009, Interglacial diversity: Nature Geoscience, v. 2, p. 751–755, doi:10.1038/ngeo660.

Winograd, I.J., Landwehr, J.M., Ludwig, K.R., Coplen, T.B., and Riggs, A.C., 1997, Duration and structure of the past four interglaciations: Quaternary Research, v. 48, p. 141–154, doi:10.1006/qres.1997.1918.

Yin, Q.Z., and Berger, A., 2010, Insolation and CO_2 contribution to the interglacial climate before and after the Mid-Brunhes Event: Nature Geoscience, v. 3, p. 243–246, doi:10.1038/ngeo771.

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Early Pleistocene palaeoenvironments at the time of the *Homo antecessor* settlement in the Gran Dolina cave (Atapuerca, Spain)

HUGUES-ALEXANDRE BLAIN,[1,2]* GLORIA CUENCA-BESCÓS,[3] FRANCESC BURJACHS,[1,2,4] JUAN MANUEL LÓPEZ-GARCÍA,[5] IVÁN LOZANO-FERNÁNDEZ[1,2] and JORDI ROSELL[1,2]
[1]IPHES, Institut Català de Paleoecologia Humana i Evolució Social, Tarragona, Spain
[2]Àrea de Prehistòria, Universitat Rovira i Virgili (URV), Tarragona, Spain
[3]Área de Paleontología, Departamento de Ciencias de la Tierra, Facultad de Ciencias, Universidad de Zaragoza, Zaragoza, Spain
[4]ICREA, Institució Catalana de Recerca i Estudis Avançats, Barcelona, Spain
[5]Gruppo di Ricerca di Paleobiologia e Preistoria, Dipartimento di Studi Umanistiche, Università degli Studi di Ferrara, Ferrara, Italy

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ABSTRACT: Hominin remains unearthed from level TD6-2 of Gran Dolina have been dated to slightly more than 0.8 Ma. Owing to the importance of this discovery, every effort is being made to reconstruct the environment where these hominins once lived. In this paper, the mutual climatic range and habitat weighting methods are applied to the herpetofaunal assemblages in order to estimate climatic and environmental parameters. TD6-2 is thus characterized by a warm and humid climate. Mean annual temperature is estimated at 2.1°C higher than at present in Burgos, with a greater increase in temperature during summer (+3.1°C) than during winter (+1.4°C). Rainfall was more abundant than at present (+407.2 mm), occurring as at present principally during spring and autumn. Humid meadows and riparian woody habitats were common. The association between warm climatic conditions and the not fully developed forest suggests that the several episodes of high-intensity occupation in TD6-2 may correspond to a recolonization by *Homo antecessor* of the high inland plateaus of the Iberian Peninsula from the Mediterranean seashore, using the Ebro valley as a savannah-type corridor after a cold glacial period. Copyright © 2013 John Wiley & Sons, Ltd.

KEYWORDS: *Homo antecessor*; herpetofauna; palaeoclimate; palaeoenvironment; Early Pleistocene; Spain.

Introduction

The Sierra de Atapuerca lies about 1080 m above sea level, dominating the now flat landscape of the Castilian grain-growing plains irrigated by the River Arlanzón near the village of Ibeas de Juarros, located 14 km east of the city of Burgos (Fig. 1). Gran Dolina or Trinchera Dolina (TD) has a vertical section of 18 m thickness and divided into 11 lithostratigraphic levels that have been dated to between roughly 1 Ma and 250 ka (Fig. 2). The TD sequence was partially excavated during a preliminary evaluation of its archaeological and palaeontological significance known as 'Trinchera Dolina Sondeo Sur' which lasted from 1993 to 1999. Hominin remains were first unearthed in 1994 and 1995 from level TD6, and dated to slightly more than 780 ka on the basis of palaeomagnetic and microfaunal evidence, making these, at the time, the oldest known hominins in Europe, described as a new species, *Homo antecessor* (Carbonell *et al.*, 1995; Bermúdez de Castro *et al.*, 1997).

Layer TD6, composed of 2–2.5 m of blocks and gravels within a poor clayey matrix, has been divided into three lithostratigraphical units, from the base to the top: TD6-3, TD6-2 and TD6-1 (Rodríguez *et al.*, 2011). Unit TD6-2 (also called Aurora Stratum and corresponding to sublevels T38–T41 from the test excavation) has a thickness of approximately 25–30 cm and is composed of red–yellowish lutites with calcareous gravels (Pérez-González *et al.*, 2001). TD6 has a pre-Matuyama negative polarity (>0.78 Ma) (Parés and Pérez-González, 1995). Biostratigraphy confirms an Early Pleistocene age for level TD6 (Cuenca-Bescós *et al.*, 1999, 2010; Cuenca-Bescós and García, 2007). Radiometric dating by electron spin resonance, electron spin resonance dating of optically bleached quartz and U-series methods has provided an age for TD6 of between 800 and 880 ka (Falguères *et al.*, 1999; Moreno García, 2011) and consequently TD6 has been associated with the Marine Isotope Stage (MIS) 21 (Cuenca-Bescós and García, 2007; Cuenca-Bescós *et al.*, 2011; Blain *et al.*, 2012a).

Testifying to hominin activities in the TD cave, some 830 lithic artefacts pertaining to cultural Mode 1 have also been recovered (Carbonell *et al.*, 1995, 2005; Ollé *et al.*, 2011). High levels of anthropization are evidenced by the diverse large-mammal assemblage (eight ungulate species and six carnivores) and all stages of carcass processing have been documented, from skinning to bone marrow extraction and defleshing and visceral removal (Díez *et al.*, 1999; Rosell, 2001; Huguet, 2007; Saladié, 2009). Primary access to animals (i.e. before carnivores) by hominids has been reported, suggesting hunting activities (Díez *et al.*, 1999). One of the most striking features of the behaviour of *H. antecessor* documented at TD6-2 is probably the practice of cannibalism (Fernández-Jalvo *et al.*, 1996, 1999). More than 150 human fossil remains belonging to a minimum of 10 individuals including children, juveniles and young adults have been recovered (Bermúdez de Castro *et al.*, 2008). Given the importance of these discoveries, every effort has been made to reconstruct the landscapes where these hominins once lived (Cuenca-Bescós *et al.*, 2005, 2011; Blain *et al.*, 2008, 2009; Rodríguez *et al.*, 2011). Amphibians and squamates have been studied and quantified by Blain (2005). Previous publications have dealt with the climatic and environmental reconstructions of the entire TD cave sequence (Blain *et al.*, 2008, 2009), as well as the correlation between the calculated mean annual temperature and oxygen isotope record from ice and marine cores (Blain *et al.*, 2012a). Here we focus on the TD6-2 level and

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*Correspondence to: H.-A. Blain, IPHES, as above
E-mail: hablain@iphes.cat

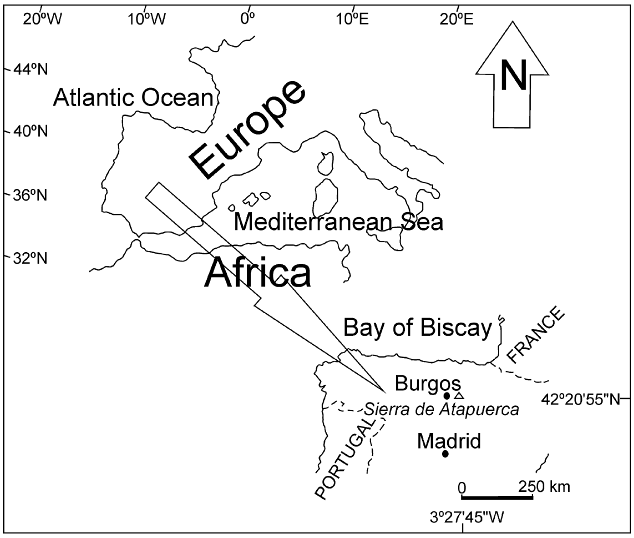

Figure 1. Location of the Sierra de Atapuerca (Burgos, Spain).

calculate some 20 new climatic parameters (and four aridity indexes) in order to better define the climate at this time, thereby placing the hominin settlement into a firm climatic and environmental context.

Geographical and ecological setting of the Sierra de Atapuerca

The Sierra de Atapuerca is located in the northeastern sector of the Cenozoic Duero Basin, north-central Iberian Peninsula, which connects in its eastern sector with the Ebro Basin through the Bureba Corridor. The northeastern sector of the Duero Basin is bounded by the Cantabrian Mountains and the Iberian Chain to the north and south, respectively. However, on account of its location the Sierra de Atapuerca is also situated near to a natural connecting route passing between the Meseta or High Plateaus of the Central Iberian Peninsula and the Cantabrian region, the Basque Country and from there to France. The river Arlanzón runs along the southern flank of the Sierra de Atapuerca, while the river Vena, a tributary of the Arlanzón River, runs along its northern side.

The Burgos region currently features a continental Mediterranean or moderate continental climate, with cold winters including snowfalls and minimum temperatures often below freezing (sometimes reaching −10°C). Summer is temperate, with mean temperatures that do not exceed 20°C in July and August. Precipitation has a typical Mediterranean pattern and, though concentrated in spring and autumn, can be observed throughout the year. Nevertheless, the lesser influence of the sea means that the climate in the Burgos area is drier than typical. In fact, the Burgos climate has temperatures approximately 2–5°C lower than in other areas with a similar type of climate, mainly due to its higher altitude of between 800 and 1000 m above sea level. The climatic data from the weather station INM-2331 of Burgos 'Villafría' give us a good knowledge of the current climate in the area close to the archaeological site. The mean annual temperature (MAT) is 10.2°C, and the mean annual precipitation (MAP) is 555.3 mm (Ninyerola *et al.*, 2005). The average difference between the warmest and coldest month is equal to 16.1°C. The arid period in summer lasts 2 months (July and August).

At present, a corridor of Atlantic influence runs through the north of the province of Burgos. This connects the oceanic

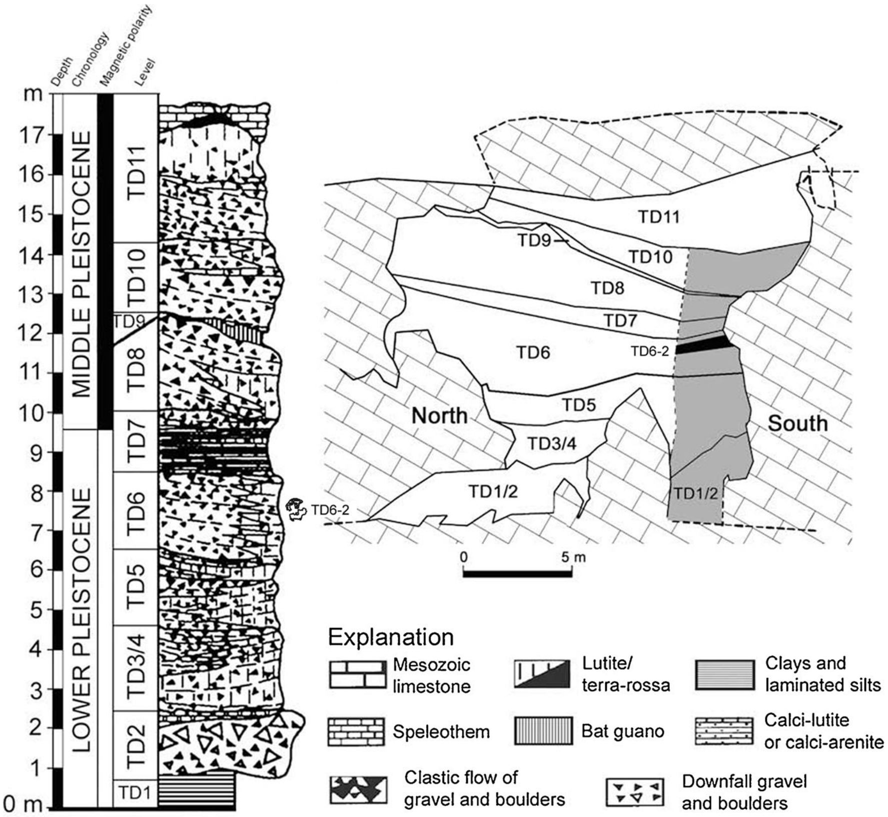

Figure 2. Geological context of the Gran Dolina site (Sierra de Atapuerca, Spain). The synthetic column on the left shows the different lithostratigraphic units (from Parés and Pérez-González, 1999), and on the right is the topography of the infillings (according to R. Pérez Martínez in Huguet, 2007), indicating the test excavation called Trinchera Dolina Sondeo Sur (TDS, in grey) and sublevel TD6-2, also called Aurora Stratum (in black).

climate of the Eurosiberian region with the Mediterranean bioclimatic area, which comprises by far the greater part of the autonomous region of Castilla–León, except for its northernmost regions, which are unquestionably Eurosiberian. The Sierra de Atapuerca is located at the centre of this more humid enclave, which is reflected in the presence of significant Atlantic plant species. Today, sparse continental oak and holm oak woodland grows on the limestones of the sierra. *Quercus rotundifolia* (evergreen oak) and *Quercus faginea* (Portuguese oak) are present on the sunny and more shaded slopes, respectively. The undergrowth is poor in lianas such as honeysuckles (*Lonicera* spp.) or ivy (*Hedera helix*) but is rich, by contrast, in Mediterranean shrubs (*Rhamnus alaternus*, *Crataegus monogyna*, *Prunus spinosa*, *Rosa* spp. and *Rubus* spp.), which grow in response to the level of aggression – grazing and trampling – to which the land is subject. The open spaces are colonized by heliophilous species such as *Genista scorpius*, *Thymus zygis*, *Teucrium polium* and *Asphodelus cerasiferus*.

The species that give a hint of an Atlantic influence, such as *Erica vagans*, *Calluna vulgaris*, *Lonicera periclymenum* and *Helleborus viridis*, are present in small clayey depressions where there is a greater accumulation of moisture. Below the sierra there are stands of Pyrenean oak (*Quercus pyrenaica*) on the siliceous substrata of the terraces of the river Arlanzón, though today these areas are largely under cultivation. What is unique about the vegetation of the area is its mixture of plant associations showing Atlantic, Mediterranean and continental influences, which finds expression in a heightened biodiversity (García-Antón, 1995; García-Antón and Sainz-Ollero, 1991; Bermúdez de Castro *et al.*, 1995).

Similar conditions occur among the living amphibians and squamates of the Sierra de Atapuerca, which also constitute a mixture comprising a majority of taxa with clear Mediterranean requirements such as *Discoglossus jeanneae*, *Pelophylax perezi*, *Timon lepidus*, *Podarcis hispanica*, *Coronella girondica*, *Rhinechis scalaris*, *Natrix maura* and *Vipera latastei* in conjunction with typical Eurosiberian (or at least Atlantic) species such as *Lissotriton helveticus*, *Triturus marmoratus*, *Anguis fragilis* and *Lacerta bilineata* (Diego-Rasilla and Ortiz-Santaliestra, 2009; Ortiz-Santaliestra *et al.*, 2011).

Material and methods

Fieldwork and sorting

The small-vertebrate fossil remains used for this study consist of disarticulated bone fragments collected by water screening during work on the test excavation (around 9 m^2) (Blain, 2005). The excavation was divided into archaeological sublevels around 10 cm thick. The sediment was water screened using superimposed 10, 5 and 0.5 mm mesh screens and bagged by square, layer and excavation sublevels. In subsequent years, the microfossils were processed, sorted and classed into large categories at the Palaeontology Section of the Earth Sciences Department of the University of Zaragoza (Spain).

Climatic reconstruction

Palaeoclimatic interpretations are based on the presence of herpetile species from each level. The mutual climatic range (MCR) method is used to quantify palaeotemperature and palaeoprecipitation, whereby we simply identify the geographic region (divided into 10 × 10 km Universal Transverse Mercator (UTM) squares) where all the species present in a given locality or stratigraphical level currently live. Careful attention is paid to ensure that the current distribution corresponds to the potential ecological/climatic distribution and is not strongly affected by other limiting or perturbing parameters such as urban development, landscape anthropization, predation, competition with other species, etc. Analysis of the MCR in each level is based on the distribution atlases of the Iberian herpetofauna (Pleguezuelos *et al.*, 2004; Godinho *et al.*, 1999), divided into 10 × 10 km squares in the UTM coordinate system. Climatic parameters have been estimated for each 10 × 10 km UTM square, using various climatic maps of the Iberian Peninsula (Ninyerola *et al.*, 2005). A total of 26 climatic parameters have been calculated for this study.

To compare our data with current climatic data, we used the record from weather station INM-2331 of Burgos 'Villafría' (Ninyerola *et al.*, 2005), located 5 km to the east of the city of Burgos (*X*, *Y*: 449281.1, 4689583.3; longitude, latitude: $-3°\ 36'\ 56.9988''$, $42°\ 21'\ 21.9996''$).

To measure aridity we used the Gaussen, Lautensach–Meyer, Dantin–Revenga and De Martonne indexes. The Gaussen index ($P < 2 \times T$) considers a month to be dry if the pluviometric level for that month (P), measured in millimetres, is less than twice the value of the average temperature in degrees Celsius for that month (T). The Lautensach–Meyer index is a classification of climates based on the number of dry months according to the Gaussen index. The Dantin–Revenga index is calculated as (100 × MAT/MAP) and the De Martonne aridity index as MAP/(MAT + 10), where MAT is mean annual temperature and MAP is mean annual precipitation.

Environmental reconstruction

The taphonomic patterns of the TD herpetile accumulations are discussed in Blain *et al.* (2008, 2009). The small vertebrate collections at Gran Dolina suggest that, given the evidence of digestion and the fractures in the fossils, the remains are mostly produced by nocturnal birds of prey such as the eagle owl (*Bubo bubo*), an opportunist that hunts a wide range of prey (Bennàsar, 2010). From a quantitative point of view, bones of the natterjack toad (*Bufo calamita*) are very abundant throughout the TD sequence, often accounting for more than 50% of the total in each sample (Blain, 2005, 2009; Blain *et al.*, 2008). Among the fossil material analysed here, they correspond to 291 specimens (i.e. 84.6%) and to 42 individuals (i.e. 59.1%). The ratio between the number of identified specimens and the minimum number of individuals (NISP/MNI ratio) has a value of about 7, whereas for all the other species this ratio has lower index values (Table 1). These results may indicate a difference in the representation of *B. calamita* in relation to all the other species: *B. calamita* seems to be overrepresented in the fossil assemblage, which may well correspond to greater *in situ* mortality in the cave, a factor that should thus be removed from the quantitative palaeoenvironmental analysis (Blain, 2005, 2009; Blain *et al.*, 2008).

In order to reconstruct the environment, we used the method of habitat weightings, distributing each amphibian (excluding *B. calamita*) and reptile taxon in the habitat(s) where it is possible to find them at present in the Iberian Peninsula. Because bones of amphibians and reptiles recovered from the site do not differ from those of extant species, the current species habitat distribution may be used for the habitat weightings. The habitats are divided into five types: open land in which dry and wet meadows are distinguished, woodland and woodland margin areas, areas surrounding water and rocky areas (Table 1). The distribution data and ecological requirements are from Pleguezuelos and Martínez-

Table 1. Amphibians and squamates from TD6-2 in number of identified specimens (NISP) and minimum number of individuals (MNI) and distribution of each taxon in the habitats where they can be found today in the Iberian Peninsula.

TD6-2	NISP	MNI	NISP/MNI	Open–dry	Open–humid	Woodland	Rocky	Water-edge
Alytes obstetricans	14	6	2.3		0.6	0.2		0.2
Pelobates cultripes	1	1	1.0	0.8				0.2
Pelodytes punctatus	4	4	1.0	0.5		0.2	0.1	0.2
Bufo bufo	1	1	1.0	0.1	0.3	0.4		0.2
Bufo calamita	291	42	6.9	0.65			0.25	0.1
Rana sp.	10	3	3.3		0.4	0.4		0.2
Lacerta s.l.	1	1	1.0					
Lacertidae indet.	15	8	1.9					
Coronella austriaca	5	3	1.7		0.5	0.25	0.25	
Vipera aspis	2	2	1.0		0.25	0.5	0.25	
TOTAL	344	71						

Rica (1997), Salvador (1997), Carrascal and Salvador (2002–2012), García-París *et al.* (2004), Pleguezuelos *et al.* (2004), Velasco *et al.* (2005), Diego-Rasilla and Ortiz-Santaliestra (2009) and Ortiz-Santaliestra *et al.* (2011).

Results

Amphibian and reptile assemblages

The amphibian and squamate bone remains from TD6-2 include 344 elements, which correspond to a minimum of 71 individuals, representing at least 10 taxa, including five toads, one frog, two lizards and two snakes (Table 1). Such an assemblage is less diverse in number of species than the current herpetofaunal assemblage of the Sierra de Atapuerca (Diego-Rasilla and Ortiz-Santaliestra, 2009; Ortiz-Santaliestra *et al.*, 2011; and personal observations during field campaigns), which comprise two newts (*Lissotriton helveticus* and *Triturus marmoratus*), seven toads and frogs (*Alytes obstetricans, Discoglossus jeanneae, Pelodytes punctatus, Bufo bufo, Bufo calamita, Hyla arborea* and *Pelophylax perezi*), four lizards (*Anguis fragilis, Lacerta bilineata, Timon lepidus* and *Podarcis hispanica*) and five snakes (*Coronella girondica, Rhinechis scalaris, Natrix maura, Natrix natrix* and *Vipera latastei*).

Taking into account that taphonomic processes may have modified the composition of the fossil assemblage, TD6-2 is characterized by the presence of more Eurosiberian/Atlantic species such as *Rana* sp., *Coronella austriaca* and *Vipera aspis*, currently absent from the Sierra de Atapuerca, but well represented in the northeastern part of the province of Burgos. At the same time, it is interesting to note the presence in TD6-2 of *Pelobates cultripes*, a mainly Mediterranean species currently absent from the Sierra de Atapuerca (Diego-Rasilla and Ortiz-Santaliestra, 2009; Ortiz-Santaliestra *et al.*, 2011), but at the limit of its current northernmost distribution in the region of Castilla-León (Velasco *et al.*, 2005).

Climate reconstruction

The overlap of amphibians and squamates represented as fossils in TD6-2 gives a total of eight UTM squares occurring in the northeastern Iberian Peninsula (Fig. 3A). The estimated MAT is 12.3°C, and the MAP is 962.5 mm (Table 2). The climate is temperate, with a high atmospheric temperature range. The summer is temperate and the winter is cold, with three months with mean temperatures below 6°C. Rainfall is abundant and its distribution is regular, occurring throughout the year, with the highest levels during spring. The aridity indexes suggest a humid, temperate, continental climate with no dry months in summer (Fig. 3B and Table 3). In comparison with current climatic data from the Burgos 'Villafria' weather station, the TD6-2 MAT is estimated at 2.1°C higher, well out of the range of the standard deviation, with a greater increase in temperature during summer (+3.1°C) than during winter (+1.4°C). The total amount of rainfall is higher (+407.2 mm) than the current level, occurring as today principally during spring. The duration of the dry period during summer (represented by the Gaussen index) is well reduced with no dry months, whereas today there are two dry months (July and August) (Fig. 3B). This is also clearly suggested by the values of the De Martonne aridity index, which is higher than 30 (humid climate) in TD6-2, whereas for the Burgos 'Villafria' weather station the value is lower than 30 (semi-humid climate), suggesting that today conditions are more arid than those occurring during the formation of TD6-2.

The overall climate pattern in TD6-2 is concordant with a continental Mediterranean climate, with temperate summers and cold winters and rainfall maximums corresponding to spring and autumn. Nevertheless, some aspects of the climatic conditions estimated for TD6-2 do not conform well to a typical continental Mediterranean climate, such as the significantly higher MAP and the absence of a dry period during summer: these latter characteristics are normally more concordant with oceanic or mountain climates in the Iberian Peninsula.

Environmental reconstruction

Reconstruction from the amphibian and reptile assemblages suggests that during the formation of TD6-2 level there was a patchy landscape with humid meadows and woody habitats (Fig. 3C). Some taxa, such as *Alytes obstetricans, Bufo bufo, Rana* sp., *Coronella austriaca* and *Vipera aspis*, preferentially live in open woodlands and/or humid meadows. *Pelobates cultripes* and to a lesser extent *Bufo calamita* and *Pelodytes punctatus* are inhabitants of drier, open environments with poor and short plant cover and with loose or stony soils, which must have been well represented in the Sierra de Atapuerca calcareous substrate in the vicinity of the cave. Woodlands are reasonably well represented, totalling 29% of the landscape.

Discussion

The results obtained here agree with previous studies using amphibian and squamate remains from the TD site that estimated MAT levels ranging between 10 and 13°C, higher rainfall throughout the TD sequence (Blain, 2005, 2009; Blain *et al.*, 2009), the presence of open–dry habitats, together with a representation of woodland areas around 30% of the landscape in the lower part of the TD sequence (TD5-TD8)

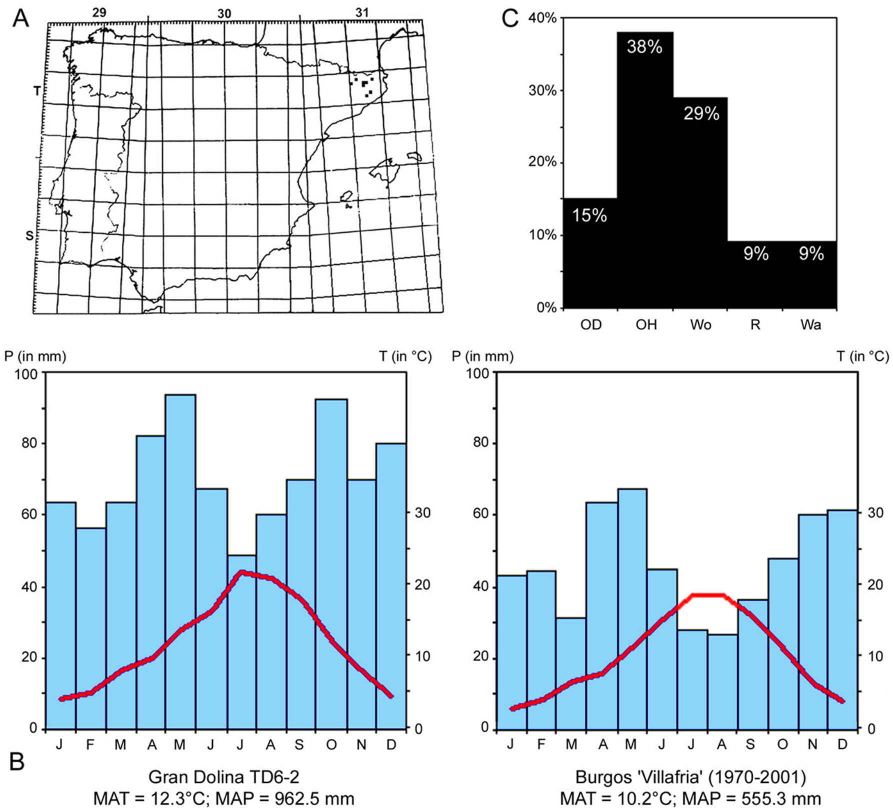

Figure 3. (A) Overlap of the current distribution of all the amphibians and squamates represented as fossils in sublevel TD6-2. Principal grid comprises 100 × 100 km UTM squares. (B) Climatograms showing on the left the reconstructed climate for TD6-2 according to the mutual climatic range method and on the right the current climatic conditions in Burgos (weather station INM-2331 of Burgos 'Villafría' according to Ninyerola *et al.*, 2005). (C) Reconstruction of the landscape in TD6-2 according to the habitat weighting method. MAT, mean annual temperature; MAP, mean annual precipitation; OD, open–dry: OH, open–humid; Wo, woodland and woodland edges; R, rocky or stony; Wa, water-edge. This figure is available in colour online at wileyonlinelibrary.com.

(Blain, 2005, 2009; Blain *et al.*, 2008). Implications for hominin palaeoecology are clear: *H. antecessor* (TD6-2) was present in the Iberian Peninsula during a warm and rather humid period (Blain *et al.*, 2009). However, the new results detailed here enable an improved understanding of the climatic background to the TD6-2 hominin settlement. The TD sequence was previously thought to be more or less continuous and, because all proxies suggested warm and humid conditions, the environment was interpreted as being stable (Rodriguez *et al.*, 2011). However, correlations of TD sequence with global ice and/or marine climate records (Blain *et al.*, 2012a) suggest that only warm periods (i.e. interglacials) are registered by faunal and pollen proxies and that full glacial periods are not necessarily represented. Such a new complexity in the climatic interpretation of the TD sequence is important because it suggests that Atapuerca was not necessarily always a suitable place for the activities of *H. antecessor*.

Palynological studies at Gran Dolina have documented varyingly rich pollen spectra (García-Antón, 1989, 1995; García-Antón and Sainz-Ollero, 1991; Burjachs, 2001). The TD6 pollen spectra are rather poor but document more or less open forest cover (around 45–60% arboreal pollen), in which Mediterranean taxa such as *Quercus* type *ilex–coccifera*, *Olea*, *Celtis*, *Pistacia* and *Coriaria* are dominant. Mesophilous taxa such as deciduous *Quercus*, *Acer*, *Tilia*, *Prunus*, *Carpinus* and *Corylus* are also well represented, suggesting a temperate period, with no intensely cold conditions and rainfall sufficient to maintain deciduous trees (Burjachs, 2001). The high abundance of *Celtis* seeds at TD6-2 is also a notable proof of Mediterranean conditions (Rodríguez *et al.*, 2011).

In the Mediterranean basin of today, the olive tree constitutes a complex of wild type, cultivated varieties and secondary feral forms. *Olea europaea* L. var. *sylvestris*, the oleaster, tends to take a shrubby form, whereas *O. europaea* L. var. *europaea* is tree-like. The oleaster occupies the warmest areas of the Mediterranean, coinciding approximately with the thermo-Mediterranean bioclimatic level or with the lower meso-Mediterranean (Ozenda, 1975; Rivas-Martínez, 1987). In the western Mediterranean, it extends over low warm areas with a MAT of between 17 and 19°C. However, some wild populations are present on the coast of Asturias and Cantabria with a MAT of around 12°C (Eurosiberian bioclimatic realm; Rubio *et al.*, 2002). The limiting factor for its development seems to be the mean temperature of the coldest month (MTC), which should not be below 6°C (Rubio *et al.*, 2002; Carrión *et al.*, 2010). Accordingly, the MTC calculated for TD6-2 (4.3 ± 1.7°C; Table 2), although higher than the current MTC (2.9°C), seems not to be warm enough for the presence of *Olea* in TD6. Nevertheless, the cultivated variety, *O. europaea* L. var. *europaea*, has become more adaptable to a wider range of climatic and environmental conditions and extends beyond the previously described area. It penetrates toward higher, colder and more continental lands, growing mainly on calcareous soils, terra rossa and sandy marls (Carrión *et al.*, 2010). In the lower meso-Mediterranean, the presence of *Olea* seems to be strongly linked to favourable orographic conditions, having been reported primarily in areas such as sunny slopes and valley bottoms that are warm and protected from continentality (Rodríguez-Ariza and Montes, 2005; Carrión *et al.*, 2010). Its occurrence in TD6 is probably to be explained as inland

Table 2. Climatic values (1970–2001) from the weather station INM-2331 of Burgos 'Villafría' (Ninyerola *et al.*, 2005) and climatic parameters calculated for TD6-2 (°C, temperature; mm, precipitation) by the mutual climatic range method.

	TD6-2*	1970–2001	Δ
Temperature (°C)			
J	4.3 ± 1.7	2.9	1.4
F	5.0 ± 2.1	4.2	0.8
M	8.3 ± 1.7	6.7	1.6
A	10.0 ± 1.5	7.9	2.1
M	14.1 ± 0.8	11.4	2.7
J	16.5 ± 1.3	15.5	1.0
J	22.0 ± 0.0	18.9	3.1
A	21.1 ± 2.0	19.0	2.1
S	18.3 ± 1.7	15.9	2.4
O	12.5 ± 2.0	11.3	1.2
N	8.3 ± 1.7	6.4	1.9
D	4.6 ± 2.1	4.0	0.6
MAT	12.3 ± 1.7	10.2	2.1
Precipitation (mm)			
J	63.8 ± 5.2	43.4	20.4
F	56.3 ± 7.4	44.6	11.7
M	63.8 ± 7.4	31.3	32.5
A	82.5 ± 7.1	63.5	19.0
M	93.8 ± 11.6	67.4	26.4
J	67.5 ± 4.6	45.0	22.5
J	48.8 ± 3.5	28.2	20.6
A	60.0 ± 0.0	26.5	33.5
S	70.0 ± 0.0	36.5	33.5
O	92.5 ± 12.8	48.2	44.3
N	70.0 ± 9.3	60.3	9.7
D	80.0 ± 0.0	61.5	18.5
MAP	962.5 ± 51.8	555.3	407.2

MAT, mean annual temperature; MAP, mean annual precipitation; Δ; difference between TD6-2 and current values.
*Mean ± SD.

penetration of warm conditions and thermophilous vegetation along river courses, probably the Ebro River.

Large mammals, represented in TD6 by *Canis mosbachensis*, *Mustela palerminea* and *Lynx* sp., also document a warm and relatively wooded landscape (Cuenca-Bescós and García, 2007). Nevertheless, the presence of *Mammuthus* sp. shows that open country was also significant at this time. The presence of Mediterranean taxa towards the top of TD6 suggests a temperate climate for TD6-2, coinciding with the Mediterranean character of the large porcupine *Hystrix refossa* present at the bottom of TD6-2 (Laplana and Cuenca-Bescós, 1996; Cuenca-Bescós *et al.*, 2005). In addition, the presence of *Castor fiber*, the giant shrew *Dolinasorex glyphodon* and *Mimomys savini* in TD6-2 is notable (Cuenca-Bescós *et al.*, 2005; Rofes and Cuenca-Bescós, 2009; Lozano-Fernández *et al.*, 2013), indicating the existence of a permanent water stream in the surroundings. Similarly, the birds at TD6 are predominantly species of open-country and bushland habitats, while the presence of waterfowl (*Anas* sp.) and waders (*Limosa limosa*, *Scolopax rusticola*) constitutes additional evidence supporting the existence of a large body of water (Sánchez-Marco, 1999).

Reconstruction of the palaeoenvironments at TD6-2 using small-mammal assemblages yields a rather open landscape, less than 10% of the species being characteristic of woodland areas (Cuenca-Bescós *et al.*, 2005, 2011). The predominant category is open–humid small mammals, which constitute fully 60% of the assemblage, followed by open–dry and rocky small mammals, which together make up around 25% of the total. In contrast, water-edge small mammals make up less than 8% of the assemblage.

Despite some differences in the results among the various proxies used to quantify the extension of woodland areas in TD6-2, they all coincide in characterizing the environment of TD6-2 as not fully developed forest, since they do not reach the values usually obtained by analyses of fully interglacial climatic conditions: more than 80% arboreal pollen (for terrestrial records; Roucoux *et al.*, 2006; e.g. Tzedakis *et al.*, 2006), 40% of amphibian and reptile taxa (e.g. Blain *et al.*, 2012b) and 70% of small mammals (Cuenca-Bescós *et al.*, 2008, 2009) with woodland affinities.

A clear association has been established for the whole of the Plio-Pleistocene between *Homo* and ecologically rich, semi-open savannah-type ecotonal and mosaic landscapes in which wetlands, coastal and rocky habitats are a regular and prominent feature (Finlayson *et al.*, 2011). As already stressed by Blain *et al.* (2010), the reconstructed landscape for TD6-2 (Aurora Stratum) is very similar to those reconstructed for other Iberian Early Pleistocene sites that have yielded strong evidence of a hominin presence, such as Trinchera Elefante (Atapuerca, Burgos; Blain *et al.*, 2010), Barranco León D and Fuente Nueva 3 (Orce, Granada; Blain *et al.*, 2011), having a good representation of woodland and water-edge areas in common. Early *Homo* may therefore have lived under a

Table 3. Climatic interpretation of the climatograms.

	TD6-2	Burgos 'Villafría' (1970–2001)
Temperature		
Mean annual temperature	12.3°C (Temperate)	10.2°C (Cold)
Atmospheric temperature range	17.8°C (High)	16.1°C (High)
Summer temperature	No month > 22°C (Temperate)	No month > 22°C (Temperate)
Winter temperature	MTC = 4.3°C (Cold)	MTC = 2.9°C (Cold)
Rainfall		
Mean annual precipitation	962.5 mm (Abundant)	555.3 mm (Low)
Distribution of rainfall	All months > 30mm (Regular)	2 months < 30 mm (Fairly regular)
Type of precipitation	Rain	Rain
Aridity		
Gaussen index	0 (Oceanic)	2 (Oceanic)
Lautensach–Meyer index	0 (Humid)	2 (Semi-humid)
Dantin–Revenga index	1.3 (Humid)	1.8 (Humid)
De Martonne index	43.3 (Humid)	27.5 (Semi-humid)

MTC, mean temperature of the coldest month.

warm-humid climate in a patchy landscape mainly composed of humid meadows and riparian woodlands. Such a landscape may have provided favourable conditions for a high diversity of large mammals, as well as for hiding and escaping from large carnivores. The occurrence of such habitats and landscapes along coastal areas has been used to explain the regular use of coastal corridors of dispersal by *Homo* (Bailey *et al.*, 2008; Carrión *et al.*, 2008; Bailey and King, 2011). Routes inland are likely to have followed river networks and savannah-type corridors (Finlayson *et al.*, 2011). Moreover, according to Leroy *et al.* (2011), the presence of ancient hominins in Europe is only possible at the transition from glacial to interglacial periods, the full glacial being too cold for them and the transition from interglacial to glacial too forested. It is the lag of the vegetation optimum behind the climatic optimum in each interglacial that provided a window of opportunity for the dispersal of large herbivore herds and hominins. Such a situation seems to have been the case for TD6-2, given on the one hand that the landscape is not fully forested and on the other hand that the underlying level TD6-3 and the upper part of TD5 seem in fact to have been colder than TD6-2 (Blain, 2005, 2009; Blain *et al.*, 2008, 2009).

Consequently, if the age of TD6-2 is accepted as being post-MIS 22 (Cuenca-Bescós *et al.*, 2011; Blain *et al.*, 2012a), and taking into account that MIS 22 is the first really cold glacial period of the Pleistocene (Head and Gibbard, 2005; Muttoni *et al.*, 2010; Tzedakis *et al.*, 2006), we can imagine that the hominins of the time, whose presence in Europe was strongly constrained by climatic and environmental conditions (Agustí *et al.*, 2009; Leroy *et al.*, 2011), would have newly colonized the inland Iberian Peninsula from the Mediterranean seashore using the Ebro valley as a consequence of its better climatic conditions, probably in the same way as thermophilous arboreal taxa such as *Olea* and *Celtis* or the western spadefoot toad (*P. cultripes*) and later the thermophilous ladder snake (*Rhinechis scalaris*), which reappears in the overlying level TD6-1 (Blain, 2005, 2009; Blain *et al.*, 2008, 2009). Such recolonization is well attested by several episodes of high-intensity occupation in TD6-2, which as yet represents the earliest base camp known at Atapuerca, despite some previous incursions as registered by a few lithic tools in TD3-4 or the human remains from Trinchera Elefante (Carbonell *et al.*, 2008; Rodríguez *et al.*, 2011).

Conclusion

Among the archaeological and palaeontological discoveries made in the Sierra de Atapuerca since 1976, the excavations at level TD6-2, formerly known as Aurora Stratum, and the description of a new European early hominin, *Homo antecessor*, have been of great relevance in throwing light on the controversy of the first colonization of western Europe, the anatomy of these first Europeans and their way of life. As the bones of amphibians and reptiles recovered from level TD6-2 do not differ from those of extant herpetofauna of the Iberian Peninsula, they can contribute to a reconstruction of the landscape and climate where these hominins once lived.

Our conclusions are as follows:

1. TD6-2 is characterized by warm and humid climatic conditions. Mean annual temperature is estimated at 2.1°C higher than at present in Burgos, with a greater increase in temperature during summer (+3.1°C) than during winter (+1.4°C). The rainfall was more abundant than currently (+407.2 mm), occurring as at present principally during spring and autumn.
2. The overall pattern of the TD6-2 climate is concordant with a continental Mediterranean climate, with the exceptions of the high mean annual precipitation and the absence of dry months in summer.
3. The landscape reconstruction at TD6-2 based on the amphibian and reptile assemblages suggests a patchy landscape with a large representation of humid meadows and riparian woody habitats. This may be correlated with a transitional phase of forest development during a cold-to-warm climatic transition (possibly correlated with the MIS 22/21 transition; see Cuenca-Bescós *et al.*, 2011; Blain *et al.*, 2012a).
4. According to the hypothesis put forward by Leroy *et al.* (2011), the association between warm climatic conditions and the not fully developed forest suggests that the several episodes of high-intensity occupation at TD6-2 correspond to a recolonization of the high inland plateaus of the Iberian Peninsula from the Mediterranean seashore using the Ebro valley as a savannah-type corridor.

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Abbreviations. MAP, mean annual precipitation; MAT, mean annual temperature; MCR, mutual climatic range; MIS, Marine Isotope Stage; MNI, minimum number of individuals; MTC, mean temperature of the coldest month; NISP, number of identified specimens; TD, Trinchera Dolina; UTM, Universal Transverse Mercator.

References

Agustí J, Blain H-A, Cuenca-Bescós G, *et al.* 2009. Climate forcing of first hominid dispersal in Western Europe. *Journal of Human Evolution* **57**: 815–821.

Bailey G, King GCP. 2011. Dynamic landscapes and human dispersal patterns: tectonics, coastlines, and the reconstruction of human habitats. *Quaternary Science Reviews* **30**: 1533–1553.

Bailey G, Carrión JS, Fa DA, *et al.* 2008. The coastal shelf of the Mediterranean and beyond: corridor and refugium for human populations in the Pleistocene. *Quaternary Science Reviews* **27**: 2095–2099.

Bennàsar M. 2010. *Tafonomía de micromamíferos del Pleistoceno Inferior de la Sierra de Atapuerca (Burgos): Sima del Elefante y Gran Dolina*. PhD dissertation, Departament d'Història i Història de l'art, Universitat Rovira i Virgili, Tarragona.

Bermúdez de Castro JM, Díez C, Mosquera M, *et al.* 1995. El nicho ecológico de los homínidos del Pleistoceno medio de Atapuerca. *Complutum* **6**: 9–56.

Bermúdez de Castro JM, Arsuaga JL, Carbonell E, *et al.* 1997. A hominid from the Lower Pleistocene of Atapuerca, Spain: possible ancestor to Neanderthals and modern humans. *Science* **276**: 1392–1395.

Bermúdez de Castro JM, Pérez-González A, Martinón-Torres M, *et al.* 2008. A new early Pleistocene hominin mandible from Atapuerca-TD6, Spain. *Journal of Human Evolution* **55**: 729–735.

Blain H-A. 2005. *Contribution de la Paléoherpétofaune (Amphibia et Squamata) à la connaissance de l'évolution du climat et du paysage du Pliocène supérieur au Pléistocène moyen d'Espagne*. PhD dissertation, Muséum National d'Histoire Naturelle, Paris.

Blain H-A. 2009. Contribution de la Paléoherpétofaune (Amphibia et Squamata) à la connaissance de l'évolution du climat et du paysage du Pliocène supérieur au Pléistocène moyen d'Espagne. *Treballs del Museu de Geología de Barcelona* **16**: 39–170.

Blain H-A, Bailon S, Cuenca-Bescós G. 2008. The Early–Middle Pleistocene palaeoenvironmental change based on the squamate reptile and amphibian proxies at the Gran Dolina site, Atapuerca, Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* **261**: 177–192.

Blain H-A, Bailon S, Cuenca-Bescós G, *et al.* 2009. Long-term climate record inferred from Early–Middle Pleistocene amphibian and squamate reptile assemblages at the Gran Dolina cave, Atapuerca, Spain. *Journal of Human Evolution* **56**: 55–65.

Blain H-A, Bailon S, Cuenca-Bescós G, *et al.* 2010. Climate and environment of the earliest West European hominins inferred from the amphibian and squamate reptile assemblages: Sima del Elefante Lower Red Unit, Atapuerca, Spain. *Quaternary Science Reviews* **29**: 3034–3044.

Blain H-A, Bailon S, Agustí J, *et al.* 2011. Paleoenvironmental and paleoclimatic proxies to the Early Pleistocene hominids of Barranco León D and Fuente Nueva 3 (Granada, Spain) by means of their amphibian and reptile assemblages. *Quaternary International* **243**: 44–53.

Blain H-A, Cuenca-Bescós G, Lozano-Fernández I, *et al.* 2012a. Investigating the Mid-Brunhes Event in the Spanish terrestrial sequence. *Geology* **40**: 1051–1054.

Blain H-A, Panera J, Uribelarrea D, *et al.* 2012b. Characterization of a rapid climate shift at the MIS 8/7 transition in central Spain (Valdocarros II, Autonomous Region of Madrid) by means of the herpetological assemblages. *Quaternary Science Reviews* **47**: 73–81.

Burjachs F. 2001. Paleoecología del *Homo antecessor*: Palinología de las unidades TD5, 6 y 7 de la 'Gran Dolina' de Atapuerca (Burgos, España). In *XIII Simposio de la Asociación de Palinólogos de Lengua Española (APLE). Textos completos*, Moreno S, Elvira B, Moreno JM (eds.) Universidad Politécnica de Cartagena: Cartagena; 365–372.

Carbonell E, Bermúdez de Castro JM, Arsuaga JL, *et al.* 1995. Lower Pleistocene hominids and artifacts from Atapuerca TD6 (Spain). *Science* **269**: 826–830.

Carbonell E, Bermúdez de Castro JM, Arsuaga JL, *et al.* 2005. An Early Pleistocene hominin mandible from Atapuerca-TD6, Spain. *Proceedings of the National Academy of Sciences USA* **102**: 5674–5678.

Carbonell E, Bermúdez de Castro JM, Parés JM, *et al.* 2008. The first hominin of Europe. *Nature* **452**: 465–470.

Carrascal LM, Salvador A. (eds). 2002-2012. *Enciclopedia Virtual de los Vertebrados Españoles*. Museo Nacional de Ciencias Naturales: Madrid; http://www.vertebradosibericos.org [1 September 2012].

Carrión JS, Finlayson C, Finlayson G, *et al.* 2008. A coastal reservoir of biodiversity for Upper Pleistocene human populations. *Quaternary Science Reviews* **27**: 2118–2135.

Carrión Y, Ntinou M, Badal E. 2010. *Olea europaea* L. in the North Mediterranean Basin during the Pleniglacial and the Early–Middle Holocene. *Quaternary Science Reviews* **29**: 952–968.

Cuenca-Bescós G, García N. 2007. Biostratigraphic sucession of the Early and Middle Pleistocene mammal faunas of the Atapuerca cave sites (Burgos, Spain). *Courier Forschunginstitut Senckenberg* **259**: 99–110.

Cuenca-Bescós G, Laplana C, Canudo JI. 1999. Biochronological implications of the Arvicolidae (Rodentia, Mammalia) from the Lower Pleistocene hominid bearing level of Trinchera Dolina 6 (TD6, Atapuerca, Spain). *Journal of Human Evolution* **37**: 353–373.

Cuenca-Bescós G, Rofes J, García-Pimienta JC. 2005. Early Europeans and environmental change across the Early–Middle Pleistocene transition: small mammalian evidence from Trinchera Dolina cave, Atapuerca, Spain. In *Early–Middle Pleistocene Transitions: the Land–Ocean Evidence*, Head MJ, Gibbard PL (eds). Special Publication 247, Geological Society: London; 277–286.

Cuenca-Bescós G, Straus LG, González Morales MR, *et al.* 2008. Paleoclima y paisaje del final del cuaternario en Cantabria: los pequeños mamíferos del Mirón (Ramales de la Victoria). *Revista Española de Paleontología* **23**: 91–126.

Cuenca-Bescós G, Straus LG, González Morales M, *et al.* 2009. The reconstruction of past environments through small mammals: from the Mousterian to the Bronze Age in El Miron Cave (Cantabria, Spain). *Journal of Archaeological Science* **36**: 947–955.

Cuenca-Bescós G, Rofes J, López-García JM, *et al.* 2010. Biochronology of Spanish Quaternary small vertebrate faunas. *Quaternary International* **212**: 109–119.

Cuenca-Bescós G, Melero-Rubio M, Rofes J, *et al.* 2011. The Early–Middle Pleistocene environmental and climatic change and the human expansion in Western Europe: a case study with small vertebrates (Gran Dolina, Atapuerca, Spain). *Journal of Human Evolution* **60**: 481–491.

Diego-Rasilla FJ, Ortiz-Santaliestra ME. 2009. *Los Anfibios*. Caja de Burgos, Servicio de Publicaciones: Burgos, Spain.

Díez JC, Fernández-Jalvo Y, Rosell J, *et al.* 1999. Zooarchaeology and taphonomy of Aurora stratum (Gran Dolina, Sierra de Atapuerca, Spain). *Journal of Human Evolution* **37**: 623–652.

Falguères C, Bahain J-J, Yokoyama Y, *et al.* 1999. Earliest humans in Europe: the age of TD6 Gran Dolina, Atapuerca, Spain. *Journal of Human Evolution* **37**: 343–352.

Fernández-Jalvo Y, Díez JC, Bermúdez de Castro JM, *et al.* 1996. Evidence of early cannibalism. *Science* **271**: 277–278.

Fernández-Jalvo Y, Díez C, Cáceres I, *et al.* 1999. Human cannibalism in the Early Pleistocene of Europe (Gran Dolina, Sierra de Atapuerca, Burgos, Spain). *Journal of Human Evolution* **37**: 591–622.

Finlayson C, Carrión J, Brown K, *et al.* 2011. The *Homo* habitat niche: using the avian fossil record to depict ecological characteristics of Paleolithic Eurasian hominins. *Quaternary Science Reviews* **30**: 1525–1532.

García-Antón M. 1989. *Estudio palinológico de los yacimientos mesopleistocenos de Atapuerca (Burgos): Reconstrucción paisajística y paleoclimática*. PhD dissertation, Universidad Autónoma de Madrid, Facultad de Ciencias, Departamento de Biología, Madrid.

García-Antón M. 1995. Paleovegetación del Pleistoceno Medio de Atapuerca a través del análisis polínico. In *Evolución Humana en Europa y los yacimientos de la Sierra de Atapuerca*, Bermúdez de Castro JM, Arsuaga JL, Carbonell E (eds). Junta de Castilla y León: Valladolid, Spain; 147–165.

García-Antón M, Sainz Ollero H. 1991. Pollen record from the middle Pleistocene Atapuerca site (Burgos, Spain). *Palaeoclimatology, Palaeogeography, Palaeoecology* **85**: 199–206.

García-París M, Montori A, Herrero P. 2004. Amphibia. Lissamphibia. In *Fauna Ibérica*, Vol. **24**, Ramos MA, Alba Tercedor J, Bellés i Ros X, *et al.* (eds). Museo Nacional de Ciencias Naturales: Madrid; 639 pp.

Godinho R, Teixeira J, Rebelo R, *et al.* 1999. Atlas of the continental Portuguese herpetofauna: an assemblage of published and new data. *Revista Española de Herpetología* **13**: 61–82.

Head MJ, Gibbard PL. 2005. Early–Middle Pleistocene transitions: an overview and recommendation for the defining boundary. In *Early–Middle Pleistocene Transitions: The Land–Ocean Evidence*, Head MJ, Gibbard PL (eds). Special Publication 247, Geological Society: London; 1–18.

Huguet R. 2007. *Primeras ocupaciones humanas en la Península Ibérica: Paleoeconomía en la Sierra de Atapuerca (Burgos) y la cuenca de Guadix-Baza (Granada) durante el Pleistoceno inferior*. PhD dissertation, Universidad Rovira i Virgili, Tarragona.

Laplana C, Cuenca-Bescós G. 1996. Hystricidae (Rodentia, Mammalia) del Pleistoceno de la Sierra de Atapuerca (Burgos, España). In *XII Bienal de la RSEHN: Libro de resúmenes*. Madrid; 194.

Leroy SAG, Arpe K, Mikolajewicz U. 2011. Vegetation context and climatic limits of the Early Pleistocene hominin dispersal in Europe. *Quaternary Science Reviews* **30**: 1448–1463.

Lozano-Fernández I, Agustí J, Cuenca-Bescós G, *et al.* 2013. Evolution of *Mimomys savini* (Rodentia, Mammalia) in the Iberian Peninsula during the Early Pleistocene and the origin of genus *Arvicola*. *Quaternaire* (in press).

Moreno García D. 2011. *Datation par ESR de quartz optiquement blanchis (ESR-OB) de la région de Atapuerca (Burgos, Espagne): Application au site préhistorique de Gran Dolina (contexte karstique) et aux systèmes fluviatiles quaternaires de l'Arlanzón et l'Arlanza*. PhD dissertation, Universitat Rovira i Virgili, Tarragona, and Muséum national d'Histoire naturelle, Paris.

Muttoni G, Scardia G, Kent DV. 2010. Human migration into Europe during the late Early Pleistocene climate transition. *Palaeogeography, Palaeoclimatology, Palaeoecology* **296**: 79–93.

Ninyerola M, Pons X, Roure JM. 2005. *Atlas Climático Digital de la Península Ibérica. Metodología y aplicaciones en bioclimatología y geobotánica*. Universidad Autónoma de Barcelona: Bellaterra. [Data base on CD].

Ollé A, Mosquera M, Rodríguez XP, *et al*. 2011. The Early and Middle Pleistocene technological record from Sierra de Atapuerca (Burgos, Spain). *Quaternary International* (in press).

Ortiz-Santaliestra ME, Diego-Rasilla FJ, Ayres Fernández C, *et al*. 2011. *Los Reptiles*. Caja de Burgos, Servicio de Publicaciones: Burgos, Spain.

Ozenda P. 1975. Sur les étages de végétation dans les montagnes du bassin Méditerranéen. *Documents de Cartographie Ecologique* **16**: 1–32.

Parés JM, Pérez-González A. 1995. Paleomagnetic Age for Hominid fossils at Atapuerca Archaeological site. *Nature* **269**: 830–832.

Parés JM, Pérez-González A. 1999. Magnetochronology and stratigraphy at Gran Dolina section, Atapuerca (Burgos, Spain). *Journal of Human Evolution* **37**: 325–342.

Pérez-González A, Parés JM, Carbonell E, *et al*. 2001. Géologie de la Sierra de Atapuerca et stratigraphie des remplissages karstiques de Galería et Dolina (Burgos, Spain). *L'Anthropologie* **105**: 27–44.

Pleguezuelos JM, Martínez-Rica JP. 1997. Distribución y Biogeografia de los anfibios y reptiles de España. *Monografías Revista Española de Herpetología*, Vol. **3** Universidad de Granada: Granada; 534 pp.

Pleguezuelos JM, Márquez M, Lizana M. 2004. *Atlas y libro rojo de los Anfibios y Reptiles de España*. Dirección General de Conservación de la Naturaleza e Asociación: Herpetológica Española: Madrid.

Rivas-Martínez S. 1987. *Memoria del mapa de series de vegetación de España 1:400.000*. ICONA: Madrid.

Rodríguez J, Burjachs F, Cuenca-Bescós G, *et al*. 2011. One million years of cultural evolution in a stable environment at Atapuerca (Burgos, Spain). *Quaternary Science Reviews* **30**: 1317–1333.

Rodríguez-Ariza MO, Montes E. 2005. On the origin and domestication of *Olea europaea* L. (olive) in Andalucia, Spain, based on the biogeographical distribution of its finds. *Vegetation History and Archaeobotany* **14**: 551–561.

Rofes J, Cuenca-Bescós G. 2009. A new genus of red-toothed shrew (Mammalia, Soricidae) from the Early Pleistocene of Gran Dolina (Atapuerca, Burgos, Spain), and a phylogenetic approach to the Eurasiatic Soricinae. *Zoological Journal of the Linnean Society* **155**: 904–925.

Rosell J. 2001. *Patrons d'Aprofitament de les Biomasses Animals durant el Pleistocè Inferior i Mig (Sierra de Atapuerca, Burgos) i Superior (Abric Romaní, Barcelona)*. PhD dissertation, Universitat Rovira i Virgili, Tarragona.

Roucoux KH, Tzedakis PC, de Abreu L, *et al*. 2006. Climate and vegetation changes 180,000 to 345,000 years ago recorded in a deep-sea core off Portugal. *Earth and Planetary Science Letters* **249**: 307–325.

Rubio R, Balaguer L, Manrique E, *et al*. 2002. On the historical presence of the wild olive [*Olea europaea* L. var. *sylvestris* (Miller) Lehr. (Oleaceae)] in the Eurosiberian region of the Iberian Peninsula. *Anales del Jardín Botánico de Madrid* **59**: 342–344.

Saladié P. 2009. *Mordiscos de omnívoros: Aproximación experimental y aplicación zooarqueológica en la Sierra de Atapuerca*. PhD dissertation, Universidad Rovira i Virgili, Tarragona.

Salvador A. 1997. Reptiles. In *Fauna Ibérica*, Vol. **10**, Ramos MA, Alba Tercedor J, Bellés i Ros X, *et al*. (eds.) Museo Nacional de Ciencias Naturales, CSIC: Madrid; 705 pp.

Sánchez-Marco A. 1999. Implications of the avifauna for palaeoecology in the early Pleistocene of the Iberian Peninsula. *Journal of Human Evolution* **37**: 375–388.

Tzedakis PC, Hooghiemstra H, Pälike H. 2006. The last 1.35 million years at Tenaghi Philippon: revised chronostratigraphy and long-term vegetation trends. *Quaternary Science Reviews* **25**: 3416–3430.

Velasco Marcos JC, Lizana Avia M, Román Sancho J, *et al*. 2005. *Guía de los Peces, Anfibios, Reptiles y Mamíferos de Castilla y León*. Náyade: Medina del Campo, Valladolid, Spain.

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PLEISTOCENE EVOLUTIONARY TRENDS IN DENTAL MORPHOLOGY OF *MIMOMYS SAVINI* (RODENTIA, MAMMALIA) FROM IBERIAN PENINSULA AND DISCUSSION ABOUT THE ORIGIN OF THE GENUS *ARVICOLA*

Iván LOZANO-FERNÁNDEZ[1,2], Jordi AGUSTÍ[2,3], Gloria CUENCA-BESCÓS[4], Hugues-Alexandre BLAIN[1,2], Juan Manuel LÓPEZ-GARCÍA[5] & Josep VALLVERDÚ[1,2]

ABSTRACT

The study of *Mimomys savini* material from the Spanish sites of Barranco León and Fuente Nueva 3 (Granada), Gran Dolina (Atapuerca), Vallparadis (Barcelona) and La Boella (Tarragona) shows evolutionary trends in the dental morphology of this species within the Lower and early Middle Pleistocene. The data obtained from each site were ordered on the basis of "absolute" datings available for the ~1.46-0.7 Ma time interval. Clearly detected trends are the size increase and a successive reduction in enamel islets on both the upper third and lower first molar, and in the *Mimomys* ridge on the lower first molar. However, the SDQ (enamel differentiation index) values of the lower first molar show no clearly directed trend within the considered time range. On the basis of these evolutionary trends observed on *Mimomys savini* in the Iberian Peninsula, the phylogenetic relationship between *Mimomys savini* and the genus *Arvicola* is discussed.

Keywords: Lower Pleistocene, Middle Pleistocene, *Mimomys savini*, Iberian Peninsula, evolutionary trends

RÉSUMÉ

TENDANCES ÉVOLUTIVES DE LA MORPHOLOGIE DENTAIRE DE *MIMOMYS SAVINI* (RODENTIA, MAMMALIA) DANS LA PÉNINSULE IBÉRIQUE DURANT LE PLÉISTOCÈNE ET DISCUSSION SUR L'ORIGINE DU GENRE *ARVICOLA*

L'étude du matériel de *Mimomys savini* des sites espagnols de Barranco León et Fuente Nueva 3 (Grenade), Gran Dolina (Atapuerca), Vallparadis (Barcelone) et La Boella (Tarragone) montre des tendances évolutives dans la morphologie dentaire de cette espèce durant le Pléistocène inférieur et le début du Pléistocène moyen. Les données obtenues pour chaque gisement ont été ordonnées selon les datations « absolues » disponibles pour l'intervalle temporel ca. 1,46-0,7 Ma. Les tendances évidentes détectées sont une augmentation de la taille et une réduction progressive des îlots d'émail aussi bien sur la troisième molaire supérieure que sur la première molaire inférieure, et du pli mimomyen sur cette dernière. Toutefois, les valeurs du rapport SDQ (indice de différenciation de l'émail) de la première molaire inférieure ne montrent aucune tendance claire pour la période considérée. Sur la base de ces tendances évolutives observées chez *Mimomys savini* dans la péninsule Ibérique, la relation phylogénétique entre *Mimomys savini* et le genre *Arvicola* est discutée.

Mots-clés : Pléistocène inférieur, Pléistocène moyen, *Mimomys savini*, péninsule Ibérique, tendances évolutives

1 - INTRODUCTION

The first appearance data (FAD) for *Mimomys savini* in Europe date to ca. 1.8 Ma (Topachevskij & Skorik, 1977; Jánossy, 1986; Rekovets, 1994; Fejfar *et al.,* 1998), and the species survived until 0.6 Ma (Fejfar *et al.,* 1998). In the Iberian Peninsula this taxon was documented for the first time around 1.6 Ma in the Guadix-Baza Basin (Agustí, 1986; Agustí *et al.*, 1987; 2010). Its earliest record coincides approximately with the first presence of hominids on the European continent, i.e. with the *Homo antecessor* remains found at Gran Dolina, Atapuerca (Bermúdez *et al.,* 1997; Carbonell *et al.*, 2008), and with the lithic industries and cut-marks at the sites in the Orce

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[1] IPHES, Institut Català de Paleoecologia Humana i Evolució Social, C/ Escorxador s/n, E-3003 TARRAGONA. *Emails:* ilozano@iphes.cat, hblain@iphes.cat

[2] Area de Prehistoria, Universitat Rovira i Virgili (URV), Avinguda de Catalunya 35, E-43002 TARRAGONA.

[3] ICREA, IPHES, Institut Català de Paleoecologia Humana i Evolució Social, C/ Escorxador s/n, E-43003 TARRAGONA. *Email:* jordi.agusti@icrea.cat

[4] Área de Paleontología, Departamento de Ciencias de la Tierra, Facultad de Ciencias, Universidad de Zaragoza, E-50009 ZARAGOZA. *Email:* cuencag@unizar.es

[5] Gruppo di Ricerca di Paleobiologia e Preistoria, Dipartimento di Studi Umanistiche, Università degli Studi di Ferrara, C.so Ercole I d'Este 32, I-44121 FERRARA. *Email:* jlopezgarcia1980@gmail.com

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region in the Guadix-Baza Basin (Martínez-Navarro *et al*., 1997; Oms *et al*., 2000; Toro *et al.,* 2010).

Mimomys savini is the oldest known representative of the so-called water vole lineage, all the members of which are characterized by rather large m1 teeth. Lower first molars of extant *Arvicola* species, which are descendants of, or at least forms closely related to, *Mimomys savini* (see discussion below), can reach lengths of as much as 4 mm.

To date, *Mimomys savini* is the last known representative of the genus *Mimomys*. The evolution of this genus shows a trend that brings its molar morphology successively closer to that of the genus *Arvicola*. *Mimomys savini* is considered by many authors to be the ancestor of *Arvicola* (Chaline & Sevilla, 1990; Viriot *et al*., 1990; Chaline *et al.,* 1999).

Due to their rapid evolutionary changes and dispersal, rodents have become a particularly useful tool in worldwide biozonation (arvicolines in the Holarctic region), separating the Pleistocene into the Villanyian, the Biharian and the Toringian stages (in the sense of Fejfar and Heinrich (1980) and Heinrich (1987) among others). The Biharian, which corresponds to the *Microtus-Mimomys* superzone (characterized by the coexistence of these two genera), is subdivided into two rodent zones: the lower is the *Mimomys savini* + *Mimomys pusillus* zone, and the upper is the *Mimomys savini* zone (fig. 1) (Fejfar *et al.,* 1998). In the biochronological subdivision defined for the Iberian Peninsula, *Mimomys savini* is present in the *Iberomys brecciensis* biozone, the *Allophaiomys chalinei* biozone, the *Allophaiomys lavocati* biozone and the *Allophaiomys pliocaenicus* biozone (Cuenca-Bescós *et al*., 2010b).

The oldest known populations of *Mimomys savini* in Europe date to the Early Pleistocene period and have been recorded at Tiligul (Topachevskij & Skorik, 1977) and Zhevakhova Gora in the Ukraine (Rekovets, 1994), Villány 5 in Hungary (Jánossy, 1986), Fuente Nueva 3 and Barranco León in Spain (Agustí, 1986; Agustí *et al*., 1987; 2010), and levels TD 3-4 (the current TD 4 was divided into TD 3 and TD 4 in the earliest papers) of Gran Dolina in Spain (Cuenca-Bescós *et al*., 1995; 1999; Cuenca-Bescós & García, 2007; Cuenca-Bescós *et al*., 2010b). The most recent populations correspond to the Early-Middle Pleistocene transition and have been recorded at several sites such as Zapadnye Kairy in the Ukraine (Markova, 1982, 2004), Kärlich E and F in Germany (von Koenigswald & van Kolfschoten, 1996), Voigtstedt in Germany (Maul, 2002), West Runton in England (Stuart, 1981), and level TD 8 of Gran Dolina in Spain (Cuenca-Bescós *et al*., 2010b).

In this article we present the results of our studies on the evolution of the molar morphology of *Mimomys savini* from the Iberian Peninsula. On the basis of these results, we discuss the phylogenetic relationship between *Mimomys savini* and the genus *Arvicola*.

2 - GEOGRAPHICAL, GEOLOGICAL AND CHRONOLOGICAL BACKGROUND

This paper is based on the data obtained from *Mimomys savini* remains from Barranco León (level D), Fuente Nueva 3, Gran Dolina (levels TD 4B, TD 5b, TD 5a, TD 6-3, TD 6-2 and TD 6-1), Vallparadis (layer 10) and La Boella (level 2) sites (fig. 2).

2.1 - FUENTE NUEVA 3 AND BARRANCO LEÓN

Fuente Nueva 3 (FN-3) and Barranco León (BL) are located within the Guadix-Baza Basin, which forms part of the Betic Mountain Range in the northern part of the province of Granada (Spain) (fig. 2). These sites fall within the *Allophaiomys lavocati* biozone for the

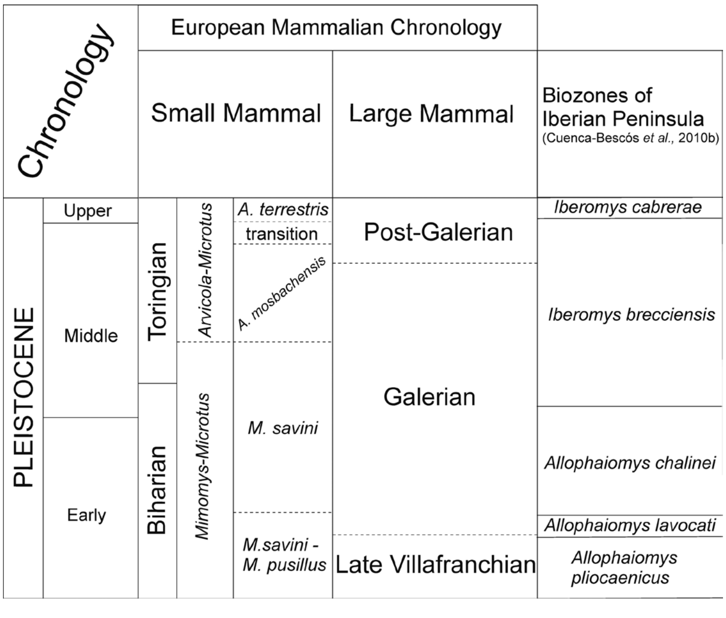

Fig. 1: European biozones (modified from Masini & Sala, 2007) and biozones of Iberian Peninsula (Cuenca-Bescós *et al.*, 2010b).
Fig. 1 : Biozones européennes (modifiées d'après Masini & Sala, 2007) et biozones de la péninsule Ibérique (Cuenca-Bescós et al.*, 2010b).*

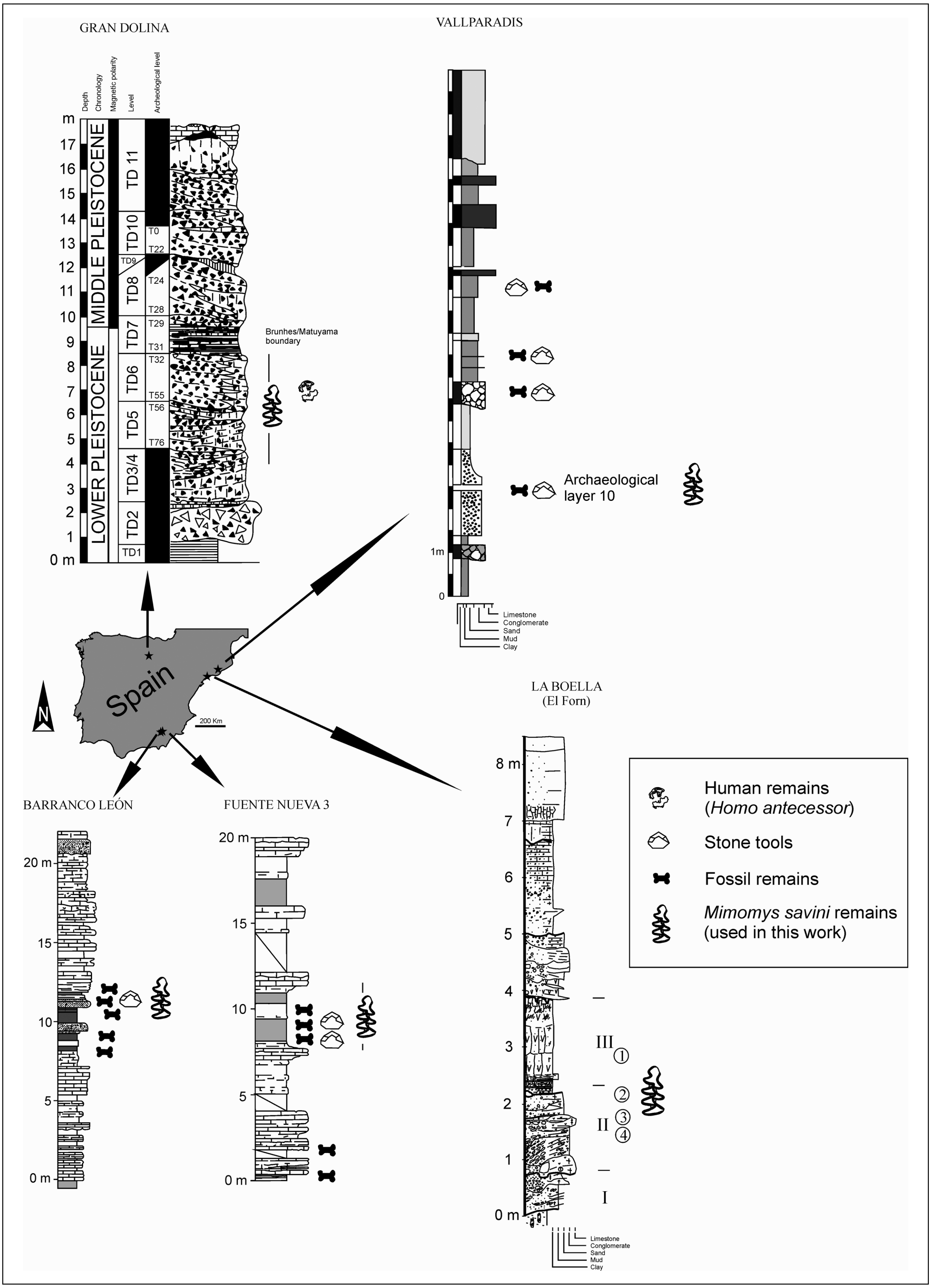

Fig. 2: Geographical location and stratigraphic columns of sites that yielded studied remains.
Gran Dolina (Parés & Pérez-González, 1995), Vallparadis (Garcia *et al.*, 2011), Fuente Nueva 3 and Barranco León (Toro *et al.*, 2010) and El Forn (stratigraphic column by Josep Vallverdú). For La Boella, Roman numerals refer to units, and circled numbers to archaeological levels.
Fig. 2 : Situation géographique et colonnes stratigraphiques des gisements ayant livré le matériel étudié. Gran Dolina (Parés & Pérez-González, 1995), Vallparadis (Garcia et al.*, 2011), Fuente Nueva 3 et Barranco León (Toro* et al.*, 2010) et El Forn (colonne stratigraphique par Josep Vallverdú). A la Boella, les chiffres romains correspondent aux unités et les nombres cerclés aux niveaux archéologiques.*

Iberian Peninsula (Agustí *et al.*, 2010; Cuenca-Bescós *et al.*, 2010b; Oms *et al.*, 2011), which corresponds to the upper part of the Early Pleistocene.

The first data on the rodent fauna of Barranco León were published by Agustí *et al.* (1987); the first on Fuente Nueva 3 by Martínez-Navarro *et al.* (1997).

The section at Fuente Nueva 3 presents a sedimentary record of some 20 meters of thickness, and the studied section of Barranco León presents a 25-m-thick sedimentary record. Both consist of a single stratigraphic unit that is Early Pleistocene in age. The samples analyzed for this article come from the layers of red and white clays of Fuente Nueva 3 and from level D of Barranco León (known in the first excavations as level 5) (fig. 2) (Toro *et al.*, 2010).

Palaeomagnetic data have revealed that these two sites date back to before the Jaramillo event (Oms *et al.*, 2000), while ESR dating has shown that level D of Barranco León dates back to 1.46 ± 0.38 Ma, and Fuente Nueva 3 to a period between 1.34 and 1.67 Ma (Duval, 2008). Recently, however, a new dating result of 1.19± 0.21 Ma was published for Fuente Nueva 3 (Duval *et al.*, 2011), thus giving a new chronological range between 1.46 ± 0.38 Ma and 1.19± 0.21 Ma.

2.2 - GRAN DOLINA

Gran Dolina is one of the sites that form part of the archaeo-palaeontological complex of Atapuerca. It is located in a cave formed as a continuation of one of the fracture planes of the Upper Cretaceous layers of the Sierra de Atapuerca. Broadly speaking, this sierra, situated approximately 15 km to the east of the city of Burgos (Spain), is a small rocky promontory situated at the north-eastern limit of the hydrographic basin of the River Duero.

The sedimentary filling of Gran Dolina is divided into 11 levels (from TD 1 to TD 11). The Matuyama-Brunhes magnetic polarity reversal has been located in level TD 7 (fig. 2). The material under study in this paper corresponds to the section between the top of TD 4 (TD 4B) and the top of TD 6 (Parés & Pérez-González, 1995).

Levels TD 5 and TD 6 are subdivided into various sublevels, of which TD 5b, TD 5a, TD 6-3, TD 6-2 and TD 6-1 provided remains of *Mimomys savini*.

Chronologically, studied levels encompass a period extending from approximately 1 Ma to 0.78 Ma (Falguères *et al.*, 1999; Berger *et al.*, 2008; Cuenca-Bescós *et al.*, 2010b).

2.3 - VALLPARADIS

The site of Vallparadis is located in the north-east of the Iberian Peninsula in the province of Barcelona (Spain). It displays a faunal association characteristic of the Lower Pleistocene. The sedimentary sequence is divided into two parts separated by an erosive discontinuity (unit 5) and is formed by the intercalation of fluvial and alluvial sedimentation (fig. 2). The palaeontological and archaeological remains are found in almost all the sequence (Madurell-Malapeira *et al.*, 2010; Martínez *et al.*, 2010; Minwer-Barakat *et al.*, 2011). The archaeological excavation focused mainly on the richest unit, unit 7 (Martínez *et al.*, 2010).

Unit 7 presents two archaeological layers: layer 10 and layer 10c.

Layer 10c has been interpreted as an accumulation produced by massive transport due to a high-density fluid with erosive capacity, whereas layer 10 has been interpreted as flood muds deposited above the previous layer (fig. 2) (Madurell-Malapeira *et al.*, 2010; Martínez *et al.*, 2010).

US-ESR dating carried out on layer 10 yielded a chronology of 0.83 ± 0.07 Ma (Martínez *et al.*, 2010).

2.4 - LA BOELLA

The site of La Boella (Barranco de la Boella, La Boella Ravine) is situated in the north-east of the Iberian Peninsula in the province of Tarragona, near the municipality of La Canonja. Two sites are currently being excavated within the ravine of La Boella, El Forn and La Mina, the first of which yielded the remains under study in this paper. The stratigraphy of the ravine is divided into 4 units (fig. 2). The material under study comes from level 2 at the top of unit 3.

The studies carried out on this site date it around 0.7 Ma (Saladié *et al.*, 2008; Vallverdú *et al.*, 2008).

3 - METHODOLOGY

The remains were recovered by water-screening the sediment with both Freudenthal tables (Daams & Freudenthal, 1988) and a tower of sieves. Which equipment was used depended on the richness of the sediment. The sediment from sites very rich in remains, such as Gran Dolina, was processed using the tower of sieves. For sediments with few remains we used the Freudenthal table, which makes it possible to wash larger samples in less time. For the washing tables, mesh sizes of 5 mm (concentrate did not contain microfaunal remains), 2 mm and 0.5 mm were used.

Remains of *Mimomys savini* were extracted from the 2-mm concentrate. Lower first molars (m1) and upper third molars (M3), from adult specimens only, were used for the study in order to prevent the high morphological variability of juvenile forms from biasing the results. We regarded m1 and M3 as belonging to adult animals when enamel-free areas were visible at the occlusal surface and roots were closed or in the process of closing (fig. 3).

On these teeth, the presence or absence of enamel islets was recorded for m1 and M3, and of the *Mimomys* ridge for m1. Measurements were taken of the length (L) and the width (W) of m1 and of the enamel thickness, as shown in figure 3. The SDQ (enamel differentiation index) was calculated as:

$$SDQ = [\ \Sigma\ (teet \times 100/leet)\ ]\ /\ N$$

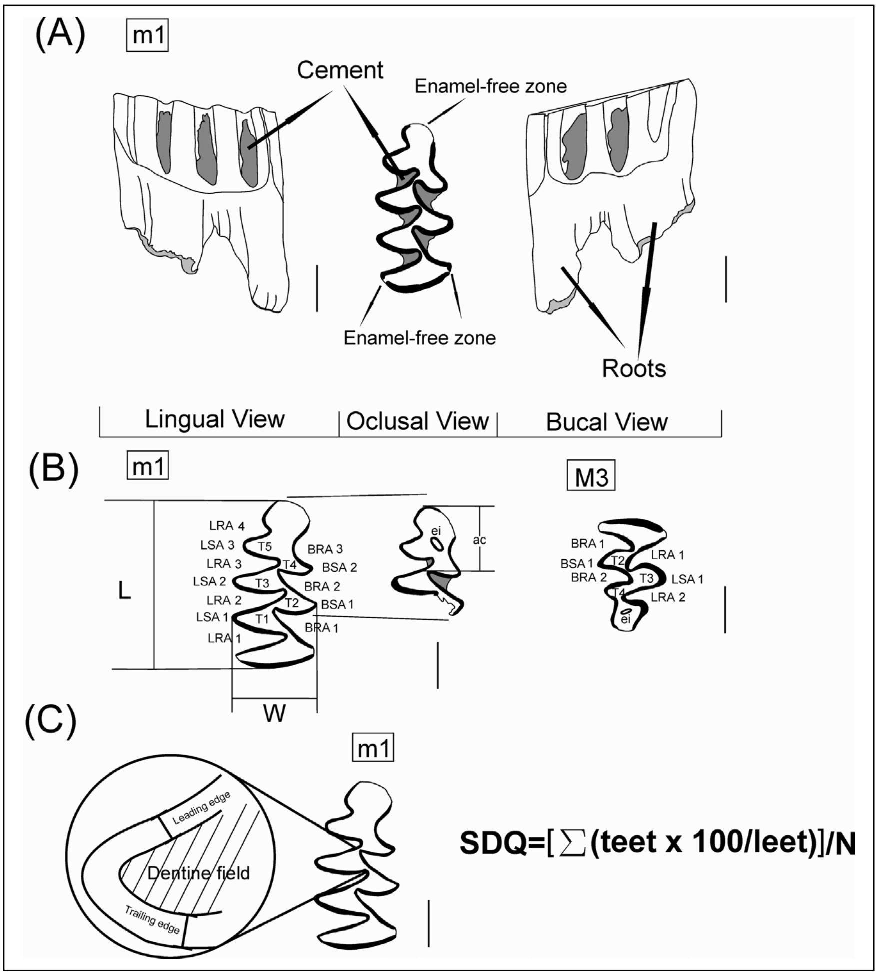

Fig. 3: (A) Different views and general characters of a m1 from *Mimomys savini*. (B) Nomenclature of the parts distinguished in the occlusal plane of a m1 and of a M3, and measurements used in this study. (C) Parts of triangles and formula for the SDQ calculation of each type of tooth. L: length; W: width; T1, T2, T3, T4 and T5: triangles composing the tooth; LRA: lingual re-entrant angles; BRA: buccal re-entrant angles; LSA: lingual salient angles; BSA: buccal salient angles; ac: anteroconid complex; ei: enamel islet (modified from van der Meulen, 1973; Heinrich, 1978; Rabeder, 1981). Formula variables: teet: trailing edge; leet: leading edge; N: total number of triangles. Scale bars = 1 mm.

Fig. 3 : (A) Différentes vues et caractéristiques générales d'une m1 de Mimomys savini. *(B) Nomenclature des parties qui se différencient en vue occlusale tant chez la m1 que chez la M3, et mesures utilisées dans ce travail. (C) Parties des triangles et formule de calcul du SDQ pour chaque type de dent. L : longueur ; W : largeur ; T1, T2, T3, T4 et T5 : triangles composant la dent ; LRA : angles reentrants ; BSA : angles sortants bucaux ; ac : complexe anteroconide ; ei : îlot d'émail (modifié d'après van der Meulen, 1973 ; Heinrich, 1978 et Rabeder, 1981). Variables de la formule : teet : bord postérieur ; leet : bord antérieur ; N : nombre total de triangles. Echelles = 1 mm.*

where N refers to the number of dentine fields of the studied tooth; teet (trailing edge enamel thickness) refers to the maximum thickness of the posterior enamel band; and leet (leading edge enamel thickness) refers to the maximum thickness of the anterior enamel band of each dentine field (Heinrich, 1978, 1987; von Koenigswald & van Kolfschoten, 1996; modified by Cuenca-Bescós *et al.*, 2010a).

All the measurements were taken on the occlusal plane of the molars with the image-treatment software Adobe PhotoShop CS5, using photographs from an Infinity X camera coupled to an Olympus SZ-40 binocular microscope. This software ensures highly reliable measurements made on flat surfaces.

4 - MATERIAL

The characters of *Mimomys savini* m1 are:

– an occlusal surface with a posterior lobe,

– five alternating triangles and an anteroconid complex,

– the presence of roots (except in the earliest stages of life),

– enamel with *Mimomys*-type differentiation (Heinrich, 1978, 1987; von Koenigswald *et al.*, 1994; von Koenigswald & van Kolfschoten, 1996),

– cement in the re-entrant angles,

– T4 and T5 widely confluent,

– depending on the age of the populations, a shallow or absent BRA3; and the neck of the head of the anteroconid complex tends to be narrow (fig. 3).

Most of the remains from Barranco León and Fuente Nueva 3 show dark coloration, and in many cases they are fractured and relatively fragile. In the absence of a detailed taphonomic study, this is interpreted as being a consequence of diagenetic processes in acid environments. It is significant that the remains come from layers showing the dark coloration characteristic of high organic matter content, which would have been responsible for the acidification of the environment. The sample from

Fuente Nueva 3 and Barranco León consists of 132 m1 and 32 M3.

The material under study from Gran Dolina was recovered in the course of a drilling carried out at the site during the 1990s (Cuenca-Bescós *et al.,* 1995, 1999). Material from more than one level of Gran Dolina was studied (TD 4B, TD 5b, TD 5a, TD 6-3, TD 6-2 and TD 6-1). The total number of remains from Gran Dolina is 364 m1 and 28 M3.

The sample from Vallparadis used in this study is made up of 22 m1. It corresponds to remains recovered between 2005 and 2007 (Martinez *et al*., 2010).

Finally, as regards the remains studied from La Boella, the sediment is very poor in microfaunal remains, and the few remains that are recovered tend to be highly fractured. Normally only remnants of enamel are recovered. For this reason, the sample used in this study was restricted to just two complete m1 recovered during the 2010 campaign.

5 - RESULTS

As the chronology of Fuente Nueva 3 includes that of Barranco León and in the light of the fact that they occur within the same geological context, the samples from these two sites were grouped together.

The data were arranged in accordance with the available physical datings, from oldest to youngest: Barranco León and Fuente Nueva 3, Gran Dolina TD 4B, Gran Dolina TD 5b, Gran Dolina TD 5a, Gran Dolina TD 6-3, Vallparadis, Gran Dolina TD 6-2, Gran Dolina TD 6-1 and La Boella.

The results show a reduction in the percentage of individuals with the *Mimomys* ridge over the evolution of the species and changing values for the percentage of the population with the enamel islet, with the maximum values associated with the oldest sites (Barranco León and Fuente Nueva 3). The enamel islet on M3 only occurs in populations older than 1 Ma (Barranco León and Fuente Nueva 3), whereas the enamel islet on m1 and the *Mimomys* ridge are retained until at least 0.78 Ma (fig. 4 and tab. 1).

The SDQ index of the species for this period does not show a clear trend. It oscillates between values of 160 and 140 (fig. 5 and tab. 2).

The length and the width of m1 show a clear trend to increase during this period, with the exception of the L values obtained from La Boella (fig. 6 and tab. 2).

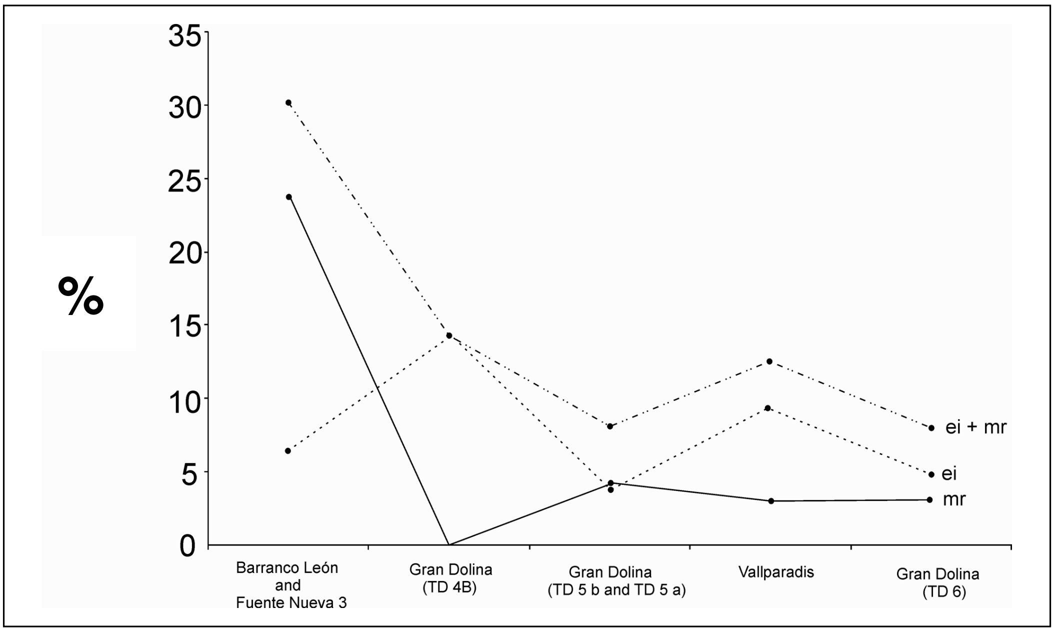

Fig. 4: Percentage of the population with m1 ancestral characters.
ei: enamel islet; mr: *Mimomys* ridge.
Fig. 4: Pourcentage de la population présentant des caractères ancestraux sur la m1. ei : îlot d'émail ; mr : pli mimomien.

	Barranco León and Fuente Nueva 3	Gran Dolina (TD 4B)	Gran Dolina (TD 5b and TD 5a)	Vallparadis	Gran Dolina (TD 6)	La Boella
% ei	6.3	14.2	3.86	9.37	4.8	50
% Mr	23.8	0	4.24	3.12	3.2	50
% ei + Mr	30.15	14.2	8.1	12.5	8	100
M3 with ei	Yes	No	No	No	No	No

Tab. 1: Percentages of the population with an enamel islet (ei), a *Mimomys* ridge (mr), archaic characters (ei + mr) and the presence of enamel islet in M3 (M3 with ei) at the various sites.
Gran Dolina encompassing a broad time interval, it is represented separately.
Tab. 1 : Pourcentages de population avec un îlot d'émail (ei), un pli mimomien (mr), des caractères archaïques (ei + mr) et la présence de l'îlot d'émail sur la M3 (M3 avec ei) dans les différents gisements. Gran Dolina englobant un large intervalle temporel, il est représenté séparément.

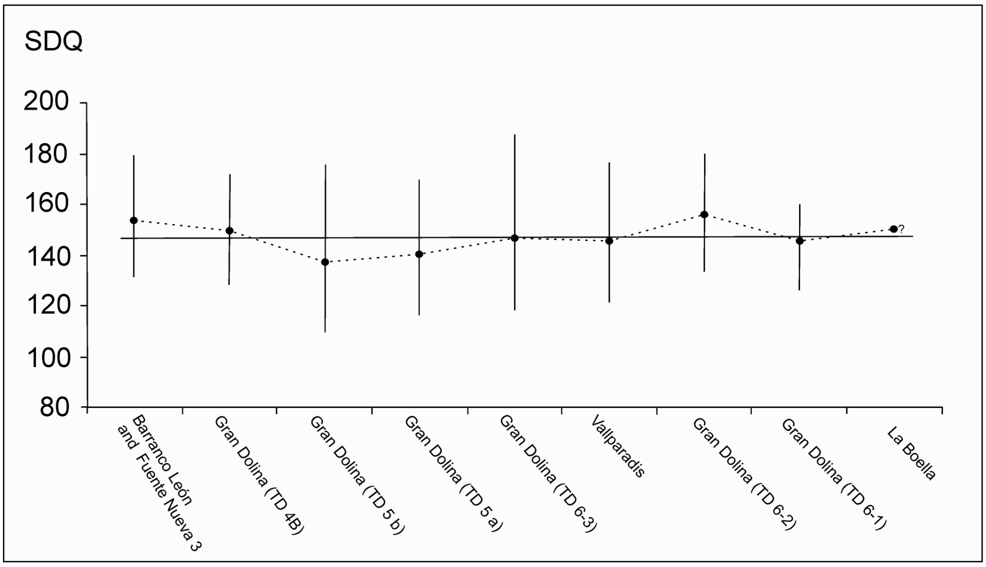

Fig. 5: Variation over time of the enamel differentiation index (SDQ) for studied Iberian populations of *Mimomys savini*.
Fig. 5 : Variation au cours du temps de l'indice de différentiation de l'émail (SDQ) chez les différentes populations ibériques étudiées de Mimomys savini.

	Barranco León and Fuente Nueva 3	Gran Dolina (TD 4B)	Gran Dolina (TD 5b)	Gran Dolina (TD 5a)	Gran Dolina (TD 6-3)	Vallparadis	Gran Dolina (TD 6-2)	Gran Dolina (TD 6-1)	La Boella
L mean	3.23	3.34	3.46	3.48	3.43	3.48	3.58	3.61	3.31
L max	3.4	3.6	3.78	3.82	3.96	3.81	3.8	3.82	3.34
L min	2.92	3.25	3.04	3.11	2.87	3.14	3.36	3.26	3.29
W mean	1.41	1.44	1.46	1.49	1.49	1.53	1.55	1.51	1.55
W max	1.6	1.52	1.67	1.67	1.63	1.69	1.69	1.64	1.63
W min	1.26	1.31	1.27	1.26	1.23	1.46	1.41	1.38	1.48
SDQ	153.4	149.6	137.34	140.2	146.3	145.2	156.1	145.3	151.9
n	132	10	137	103	102	22	4	9	2

Tab. 2: Values of m1 length (L), m1 width (W) and enamel differentiation index (SDQ), and number of m1 (n) obtained for each site.
Tab. 2 : Valeurs de la longueur de la m1 (L), de la largeur de la m1 (W) et de l'indice de différentiation de l'émail (SDQ), et nombre de m1 (n) obtenus pour chaque gisement.

6 - DISCUSSION

6.1 - EVOLUTION OF *MIMOMYS SAVINI* IN THE IBERIAN PENINSULA

This study shows that the evolution of *Mimomys savini* in the Iberian Peninsula is characterized by a gradual disappearance of ancestral characters in the m1 (*Mimomys* ridge and enamel islet) and M3 (enamel islet) and an increase in size. The specimens from La Boella have not been taken into account for the conclusions of this paper because the sample was not large enough for the statistics to be considered reliable.

The enamel islet in M3 is not present in populations dating to less than 1 Ma, while the percentage of individuals with the enamel islet in m1 shows a gradual decrease in populations. This evolutionary decrease had previously been noted for this species by Cuenca-Bescós *et al.* (1999), who ascertained that in Lower Pleistocene populations of the percentage of individuals with the enamel islet on m1 is greater than 14 %, whereas it is lower in Middle Pleistocene populations. In our study these percentages are not attained, which could be due to the different size of the sample or to the inclusion of juvenile individuals in Cuenca-Bescós *et al.* (1999). Nevertheless, the trend towards a decrease in the number of individuals with the enamel islet on m1 could be clearly made out in both cases: i.e. both the study by Cuenca-Bescos *et al.* (1999) and the present investigation. Both characteristics, the enamel islet and the *Mimomys* ridge, are lost during the individual's life (due to wear). The reduction in the population with these characteristics indicates the gradual disappearance of these characters in the evolution of the species (given that the palaeontological population is a reflection of the original biological population).

These changes constitute a progressive process over the whole stratigraphic range of *M. savini* and represent an evolution from an archaic m1 (showing similarities to the m1 of *Mimomys ostramosensis*) to a m1 which – except for the presence of roots – is very similar to the first populations of *Arvicola* (*Arvicola cantianus*) studied at Meisenheim I (van Kolfschoten, 1990) and at a number of localities of the Holsteinian, Eemian, Saalian and Weichselian of central Europe and the Pannonian Basin (Heinrich, 1982). The set of evolutionary changes undergone by *Mimomys savini* represents a clear evolutionary trend, a phenomenon noted in other arvicoline genera such as *Ondatra* (Martin, 1979), *Kislangia* and the theridomyids (Vianey-Liaud, 1972; Chaline & Sevilla, 1990; Agustí *et al.*, 1993; Chaline *et al.*, 1993).

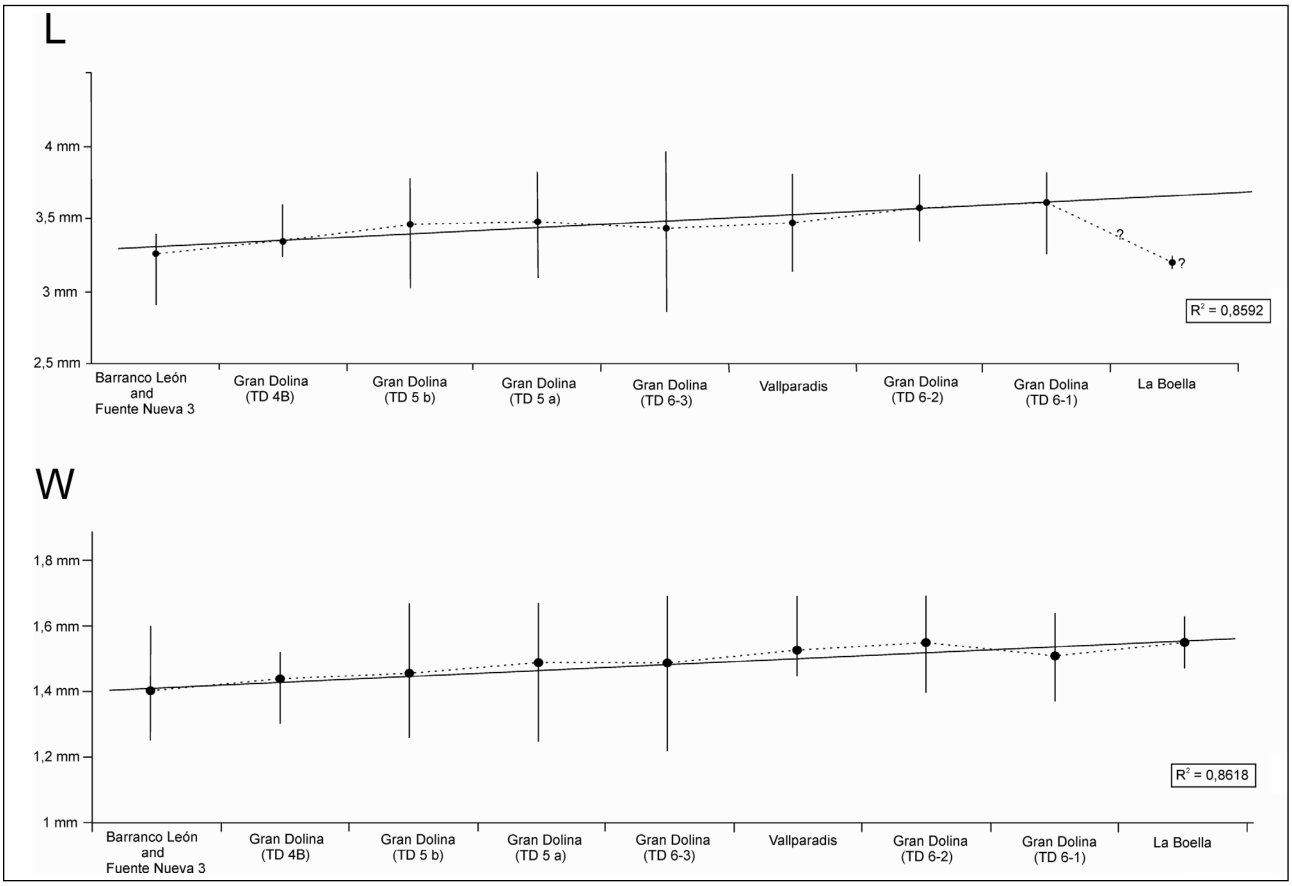

Fig. 6: Trend in evolution of size.
L: length of m1; W: width of m1. Both characters show increasing trends over time that have been underlined by regression lines.
Fig. 6 : Tendance dans l'évolution de la taille. L : longueur de la m1; W : largeur de la m1. Les deux caractères montrent une tendance à l'accroissement au cours du temps.

6.2 - RELATIONSHIP BETWEEN THE GENUS *ARVICOLA* AND *MIMOMYS SAVINI*

In arvicolines the increase in size at the lineage level has been studied for *Kislangia cappetai* - *Kislangia gusii* and *Mimomys occitanus* - *Mimomys pliocaenicus* (Agustí *et al*., 1993), as well as for *Mimomys occitanus* - *Mimomys savini* (Viriot *et al.,* 1990; Néraudeau *et al*., 1995; Chaline *et al*., 1999). As the evolution of *Mimomys savini* molars involves a loss of *Mimomys*-type characters and an increase in size that brings it closer to the size and molar morphology of the earliest populations of *Arvicola*, an evolutionary relationship between these taxa (*Mimomys savini*-*Arvicola cantianus*) seems to be clear. It is corroborated by the chronology of the records and the fact that the evolution of the genus *Arvicola* also shows an increase in size. This relationship has already been suggested by many authors (e.g. Viriot *et al*., 1990; Chaline *et al*., 1999),

However, the discovery of the new species *Arvicola jacobaeus* dated to approximately 1.2 Ma (Cuenca-Bescós *et al*., 2010a) raises a number of doubts regarding this evolutionary relationship (fig. 7). This record showed that the first representatives of *Arvicola* are similar in age to *Mimomys savini*. As this article reveals, the dental morphological characters (SDQ index, the presence of an enamel islet and *Mimomys* ridge) and size of *M. savini* are different from those of *Arvicola jacobaeus* during this period. Among *M. savini* populations, a higher percentage of individuals than in modern ones possess an enamel islet (*Arvicola jacobaeus* does not have an enamel islet), and their average length is approximately 3.2 mm, whereas in *Arvicola jacobaeus*

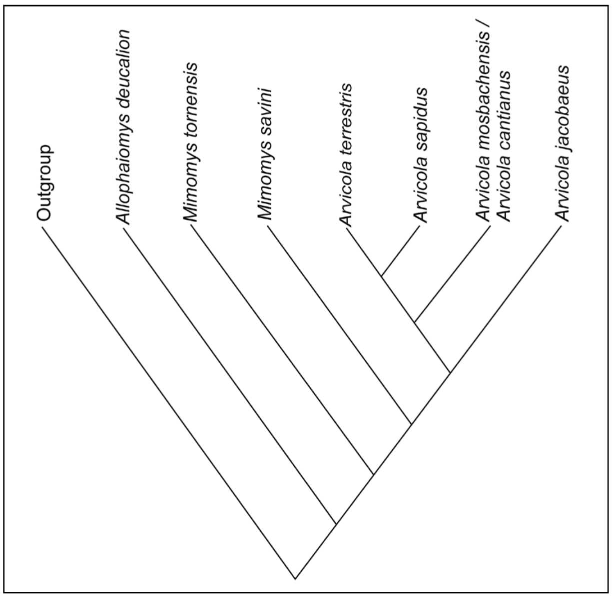

Fig. 7: Cladogram of the *Mimomys-Arvicola* relationship proposed by Cuenca-Bescós *et al*. (2010a).
Fig. 7 : Cladogramme de la relation Mimomys-Arvicola proposée par Cuenca-Bescós et al. *(2010a).*

smallest length values are 3.48 mm (Cuenca-Bescós *et al*., 2010a). The data obtained in this study, together with the classification of *A. jacobaeus*, thus force us to reconsider the evolutionary relationship between *Mimomys savini* and *Arvicola*.

Various alternatives explaining the relation between *Mimomys* and *Arvicola* have been proposed. Chaline & Sevilla (1990) and Horàček (1990) argue that *Mimomys savini* gave rise to *Arvicola terrestris*. Rabeder (1981) proposes that the origin of *Arvicola sapidus* can be traced to *Mimomys savini*, whereas *Arvicola terrestris* would be the evolutionary descendant of *Mimomys milleri*. By contrast, Ruiz Bustos (1999) proposes the existence at 1.6 Ma of the species *Arvicola deucalion*, an ancestor of *Mimomys tornensis*. This theory raises a problem, because *Arvicola deucalion* is considered as a synonym of *Allophaiomys deucalion* by most authors who also uphold the phylogenetic relationship between these two species, *Mimomys tornensis - Allophaiomys deucalion* (Rabeder, 1981; Garapich & Nadachowski, 1996; Chaline *et al*., 1999), or at least between *Mimomys* sp. and *Allophaiomys deucalion*. This phylogenetic relationship between *Mimomys tornensis* and *Allophaiomys deucalion* is defended by Chaline & Sevilla (1990), who also suggest that *Mimomys savini* is the ancestor of *Arvicola*.

As mentioned above, the increase in size during the evolution of *Mimomys savini* also occurs in *Arvicola*. Additionally, the morphological similarities between the two taxa would imply a phylogenetic relationship between them.

When the SDQ values obtained in this study are compared with those from various populations of *Arvicola* throughout Europe (fig. 8), both *Arvicola jacobaeus*

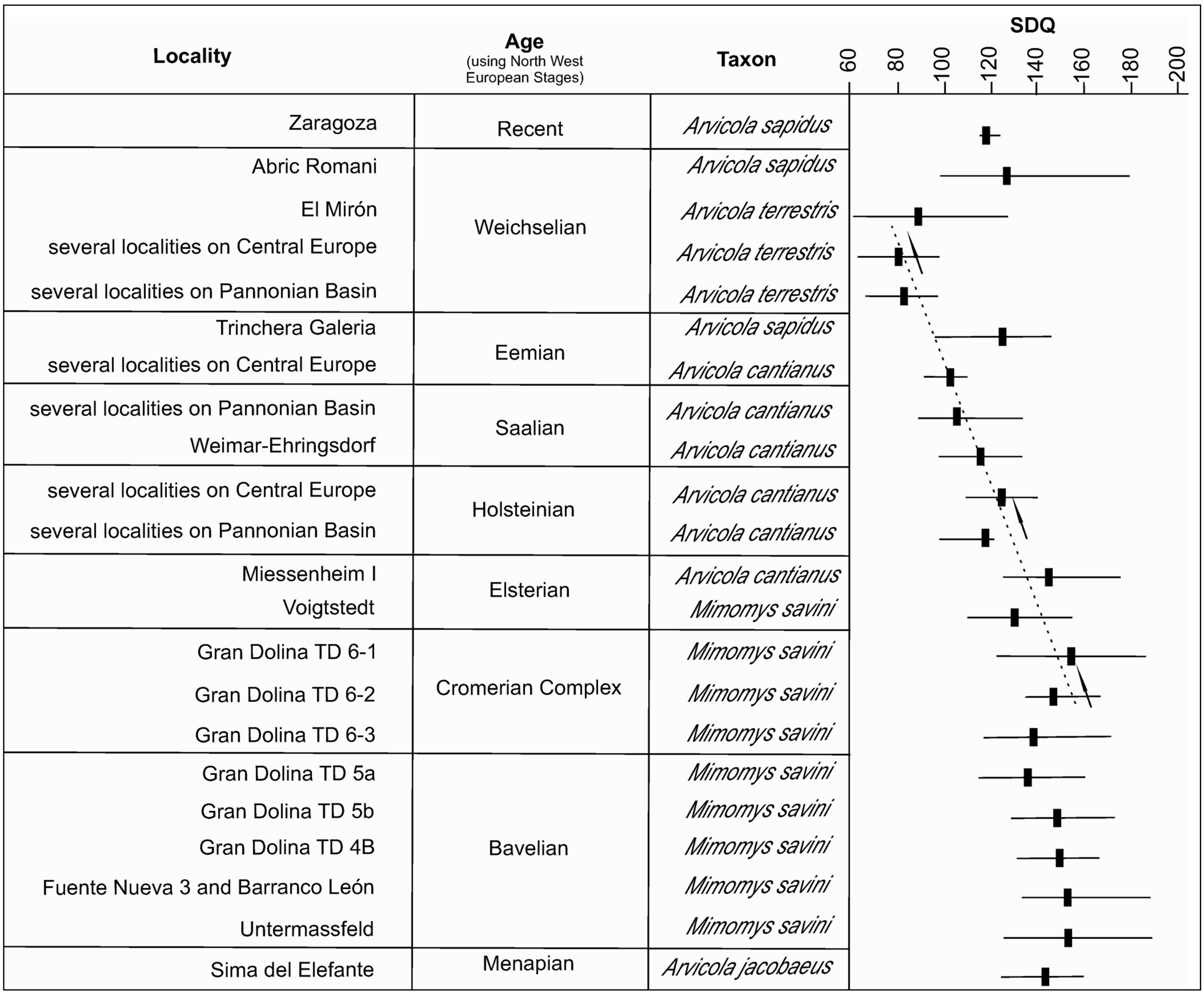

Fig. 8: Comparison of various populations of *Mimomys savini*, *Arvicola cantianus*, *Arvicola sapidus*, *Arvicola terrestris* and *Arvicola jacobaeus*. Sima del Elefante (Cuenca-Bescós *et al*., 2010a), Untermassfeld (Maul *et al*., 1998), Fuente Nueva 3, Barranco León, Gran Dolina TD 4B, TD 5b, TD 5a, TD 6-3, TD 6-2 and TD 6-1 (this study), Voigtstedt (Maul *et al*., 1998), Meisenheim I (Kolfschoten, 1990), localities in the Pannonian Basin, Central Europe and Weimar-Ehringsdorf (Heinrich, 1982), Trinchera Galeria (Atapuerca) (Cuenca-Bescós *et. al*., 2010a), El Mirón (Cantabria) and Abric Romani (Tarragona) (Cuenca-Bescós *et. al*., 2010a), and finally current data from populations in Zaragoza (Cuenca-Bescós *et. al*., 2010a). A decreasing trend in SDQ starts in late populations of *Mimomys savini* and continues in *Arvicola* ones.

Fig. 8 : Comparaison entre différentes populations de Mimomys savini*,* Arvicola cantianus*,* Arvícola sapidus*,* Arvícola terrestris *et* Arvícola jacobaeus. *Sima del Elefante (Cuenca-Bescós* et al.*, 2010a), Untermassfeld (Maul* et al.*, 1998), Fuente Nueva 3, Barranco León, Gran Dolina TD 4B, TD 5b, TD 5a, TD 6-3, TD 6-2 and TD 6-1 (cette étude), Voigstedt (Maul* et al.*, 1998), Meisenheim I (Kolfschoten, 1990), localités du Bassin Pannonien, d'Europe Centrale et de Weimar Ehringsdorf (Heinrich, 1982), Trinchera Galeria (Atapuerca) (Cuenca-Bescós* et al.*, 2010a), El Mirón (Cantabrie) et Abric Romani, (Tarragone) (Cuenca-Bescós* et al.*, 2010a), et finalement données actuelles de populations de Saragosse (Cuenca-Bescós* et al.*, 2010a). Une tendance décroissante de la valeur du SDQ commence dans les dernières populations de* Mimomys savini *et continue chez* Arvicola.

and the oldest populations of *Arvicola cantianus* display similar values to those of *Mimomys savini*. Moreover, the most modern populations of *Mimomys savini* (Gran Dolina TD 6-2, TD 6-1 and Voigtstedt) show a trend towards a reduction in this index, which is continued in *Arvicola* populations up to recent times. The continuous evolution of this character would be an indicator that *Mimomys savini* is the ancestor of *Arvicola cantianus*, as proposed by Chaline *et al.* (1999). Taking into account that the youngest populations of *M. savini* have length and SDQ values similar to the earliest *A. cantianus* populations, both species follow the same evolutionary trend for these characters (Abbassi & Desclaux, 1996; Escudé *et al*., 2008a, 2008b), the morphology of their m1 is similar, and they are only clearly distinguished by the absence of roots.

7 - CONCLUSION

In the Iberian Peninsula, *Mimomys savini* displays clear evolutionary trends: the successive reduction or loss of archaic characters in stratigraphically consecutive samples, such as the enamel islet on M3, which is only present in populations older than 1 Ma, and the enamel islet and the *Mimomys* ridge on m1.

In the course of its evolution, this species also undergoes an increase in size. The only character that seems not to follow a clearly directed evolutionary trend in *M. savini* is the SDQ value, which only shows oscillatory variations.

The occurrence of *Arvicola jacobaeus* during similar periods to *Mimomys savini* requires the assumption of a common ancestor shared by *Mimomys savini* and the genus *Arvicola*, as already argued by Cuenca-Bescós *et al.* (2010a). However, this paper has demonstrated that the youngest populations of *Mimomys savini* show a trend towards a decrease in the SDQ index, which is continued by the oldest *Arvicola* populations. The evolution of this character supports *Mimomys savini* as a possible ancestor of the *Arvicola* genus, as proposed by Chaline *et al*. (1999), or at least of *Arvicola cantianus*. However, the origin of *Arvicola jacobaeus* still remains unexplained.

Everything seems to indicate that two groups with different origins have been classified as *Arvicola*: on the one hand *Arvicola jacobaeus*, which shares a common ancestor with *Mimomys savini*, and on the other hand *Arvicola cantianus* and descendants, whose ancestor would be *Mimomys savini*.

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REFERENCES

ABBASSI M. & DESCLAUX E., 1996 - *Arvicola* Lacépède, 1799 (*Rodentia, Mammalia*) de quatre sequences du sud-est de la France et de Ligurie datant de la fin du Pléistocène moyen et du début du Pléistocène supérieur. *Quaternaire*, **7** (1), 29-37.

AGUSTÍ J., 1986 - Synthèse biostratigraphique du plio-pleistocène de Guadix-Baza (Province de Granada, Sud-Est de l'Espagne). *Geobios*, **19** (4), 505-510.

AGUSTÍ J., ARBIOL S. & MARTÍN SUÁREZ E., 1987 - Roedores y Lagomorfos (Mammalia) del Pleistoceno inferior de Venta Micena (depresión de Guadix-Baza, Granada). *Paleontologia i Evolució, Memòria especial*, **1**, 95-107.

AGUSTÍ J., CASTILLO C. & GALOBART A., 1993 - Heterochronic evolution in the late pliocene-early pleistocene arvicolids of the Mediterranean area. *Quaternary International*, **19**, 51-56.

AGUSTÍ J., BLAIN H-A., FURIÓ M., DE MARFÁ R. & SANTOS-CUBEDO A., 2010 - The early Pleistocene small vertebrate succession from the Orce region (Guadix-Baza Basin, SE Spain) and its bearing on the first human occupation of Europe. *Quaternary International*, **223-224**,162-169.

BERGER G.W., PÉREZ-GONZÁLEZ E., CARBONELL E., ARSUAGA J.L., BERMÚDEZ DE CASTRO J.-M. & KU T.-L., 2008 - Luminescence chronology of cave sediments at the Atapuerca paleoanthropological site, Spain. *Journal of Human Evolution*, **55** (2), 300-311.

BERMÚDEZ DE CASTRO J.M., ARSUAGA J.L., CARBONELL E., ROSAS A., MARTINEZ I. & MOSQUERA M., 1997 - A hominid from lower Pleistocene of Atapuerca, Spain: Possible ancestor to Neanderthals and modern humans. *Science*, **276** (5317), 1392-1395.

CARBONELL E., BERMÚDEZ DE CASTRO J.M., PARÉS J.M., PÉREZ- GONZÁLEZ A., CUENCA-BESCÓS G., OLLÉ A., MOSQUERA M., HUGUET R., VAN DER MADE J., ROSAS A., SALA R., VALLVERDÚ J., GARCÍA N., GRANGER D.E., MARTINÓN-TORRES M., RODRÍGUEZ X.P., STOCK G.M., VERGÈS J.M., ALLUÉ E., BURJACHS F., CÁCERES I., CANALS A., BENITO A., DÍEZ C., LOZANO M., MATEOS A., NAVAZO M., RODRÍGUEZ J., ROSELL J., ARSUAGA J.L., 2008 - The first hominin of Europe. *Nature*, **452** (7186), 465-469.

CHALINE J. & SEVILLA P., 1990 - Phyletic gradualism and developmental heterochronies in a European Plio-Pleistocene *Mimomys* linage (Arvicolidae, Rodentia). *In* O. Fejfar & W.-D. Heinrich (eds.), *International Symposium on the Evolution, Phylogeny and Biostratigraphy of Arvicolids, Rohanov, May 1987*. Geological Survey, Prague, 85-98.

CHALINE J., LAURIN B., BRUNET-LECOMTE P. & VIRIOT L., 1993 - Morphological trends and rates of evolution in arvicolids (Arvicolidae, Rodentia): Towards a punctuated equilibria/disequilibria model. *Quaternary International*, **19**, 27-39.

CHALINE J., BRUNET-LECOMTE P., MONTUIRE S., VIRIOT L. & COURANT F., 1999 - Anatomy of the arvicoline radiation (Rodentia): palaeogeographical, palaecoecological history and evolutionary data. *Annales Zoologici Fennici*, **36**, 239-267.

CUENCA-BESCÓS G., LAPLANA C. & CANUDO J.I. ,1995 - Los Arvicólidos (Rodentia, Mammalia) de los niveles inferiores de Gran Dolina (Pleistoceno Inferior, Atapuerca, Burgos, España). *Revista Española de Paleontología*, **10** (2), 202-218.

CUENCA-BESCÓS G., LAPLANA C. & CANUDO J.I., 1999 - Biochronological implications of the Arvicolidae (Rodentia, Mammalia) from the Lower Pleistocene hominid-bearing level of Trinchera Dolina 6 (TD6, Atapuerca, Spain). *Journal of Human Evolution*, **37** (3-4), 353-373.

CUENCA-BESCÓS G. & GARCÍA N., 2007 - Biostratigraphic succession on the Early and Middle Pleistocene mammal faunas of the Atapuerca cave sites (Burgos, Spain). *Courier Forschungsinstitut Senckenberg*, **259**, 99-110.

CUENCA-BESCÓS G., AGUSTÍ J., LIRA J., MELERO M. & ROFES J., 2010a - A new species of water vole from the Early Pleistocene of Southern Europe. *Acta Palaeontologica Polonica*, **55** (4), 565-580.

CUENCA-BESCÓS G., ROFES J., LÓPEZ-GARCÍA J.M., BLAIN H-A., DE MARFÁ R.J., GALINDO-PELLICENA M.A., BENNÁSAR-SERRA M.L., MELERO-RUBIO M., ARSUAGA J.L., BERMÚDEZ DE CASTRO J.M. & CARBONELL E., 2010b - Biochronology of Spanish Quaternary small vertebrate faunas. *Quaternary International*, **212** (2), 109-119.

DAAMS R. & FREUDENTHAL M., 1988 - Synopsis of the Dutch-Spanish collaboration program in the Neogene of Calatayud-Teruel Basin. 1976-1986. *Scripta Geologica, Special Issue*, **1**, 3-18.

DUVAL M., 2008 - *Evaluation du potentiel de la méthode de datation par Résonance de Spin Electronique (ESR) appliquée aux gisements du Pléistocène inférieur : étude des gisements d'Orce (bassin de Guadix-Baza, Espagne) et contribution à la connaissance des premiers peuplements de l'Europe*. Thèse de Doctorat, Muséum national d'Histoire naturelle, Paris, 522 p.

DUVAL M., AUBERT M., HELLSTROM J. & GRÜN R., 2011 - High resolution LA-ICP-MS mapping of U and Th isotopes in an Early Pleistocene equid tooth from Fuente Nueva-3 (Orce, Andalusia, Spain). *Quaternary Geochronology*, **6** (5), 458-467.

ESCUDÉ E., MONTUIRE S. & DESCLAUX E., 2008a - Variabilité morphologique de l'espècie *Arvicola cantiana* (Arvicolinae, Rodentia) du Pléistocène moyen au Pléistocène Supérieur de France et de Liguire (Italie). *Quaternaire*, **19** (1), 31-41.

ESCUDÉ E., MONTIUIRE S., DESCLAUX E., QUÉRÉ J.-P., RENVOISÉ E. & JEANNET M., 2008b - Reappraisal of 'chronospecies' and the use of *Arvicola* (Rodentia, Mammalia) for biochronology. *Journal of Archaelogical Science*, **35** (7), 1867-1879.

FALGUÈRES C., BAHAIN J.-J., YOKOYAMA Y., ARSUAGA J.L., BERMÚDEZ DE CASTRO J.M., CARBONELL E., BISCHOFF J.L. & DOLO J.M., 1999 - Earliest humans in Europe: the age of TD6 Gran Dolina, Atapuerca, Spain. *Journal of Human Evolution*, **37** (3-4), 343-352.

FEJFAR O. & HEINRICH W.-D., 1980 - Zur biostratigraphischen Abgrenzung und Gliederung des kontinentalen Quartärs in Europa anhand von Arvicoliden (Mammalia, Rodentia). *Časopis pro Mineralogii a Geologii*, **25** (2), 185-189.

FEJFAR O., HEINRICH W.-D. & LINDSAY E.H., 1998 - Updating the Neogene Rodent biochronology in Europe. *Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen Toegepast Natuurwetenschappelijk Onderzoek*, **60**, 533-554.

GARAPICH A. & NADACHOWSKI A., 1996 - A contribution to the origin of *Allophaiomys* (Arvicolidae, Rodentia) in Central Europe: the relationship between *Mimomys* and *Allophaiomys* from Kamyk (Poland). *Acta Zoologica Cracoviensia*, **39** (1), 179-184.

GARCIA J., MARTÍNEZ K. & CARBONELL E., 2011 - Continuity of the first human occupation in the Iberian Peninsula: Closing the archaeological gap. *Comptes Rendus Palevol*, **10** (4), 279-282.

HEINRICH W.-D., 1978 - Zur biometrischen Erfassung eines Evolutiontrends bei *Arvicola* (Rodentia, Mammalia) aus dem Pleistozän Thüringens. *Säugetierkundliche Informationen*, **1** (2), 3-21.

HEINRICH W.-D., 1982 - Zur Evolution und Biostratigraphie von *Arvicola* (Rodentia, Mammalia) im Pleistozän Europas. *Zeitschrift für Geologische Wissenschaften*, **10**, 683-735.

HEINRICH W.-D., 1987 - Neue Ergebnisse zur Evolution und Biostratigraphie von *Arvicola* (Rodentia, Mammalia) im Quartär Europas. *Zeitschrift für Geologische Wissenschaften*, **15**, 389-406.

HORÀČEK I., 1990 - On the context of Quaternary arvicolid evolution: changes in community development. *In* O. Fejfar & W.-D. Heinrich (eds.), *International Symposium on the Evolution, Phylogeny and Biostratigraphy of Arvicolids, Rohanov, May 1987*. Geological Survey, Prague, 201-222.

JÁNOSSY D., 1986 - *Pleistocene vertebrate faunas of Hungary*. Akadémiai Kiadó, Budapest, 208 p.

MADURELL-MALAPEIRA J., MINWER-BARAKAT R., ALBA D.M., GARCES M., GOMEZ M., AURELL-GARRIDO J., ROS-MONTOYA S., MOYA-SOLA S. & BERASTEGUI X., 2010 - The Vallparadís section (Terrassa, Iberian Peninsula) and the latest Villafranchian faunas of Europe. *Quaternary Science Reviews*, **29** (27-28), 3972-3982.

MARKOVA A.K., 1982 - *Pleistotsenovye gryzuny Russkoi ravniny* [Pleistocene Rodents of the Russian Plain]. Nauka, Moscow, 184 p. [in Russian]

MARKOVA A.K., 2004 - Pleistocene mammal faunas of Eastern Europe. *In* V.N. Konishchev & G.A Safyanov (eds.), *Structure, dynamics and evolution of natural geosystems*. Gorodets, Moscow, 583-597.

MARTIN L.D., 1979 - The biostratigraphy of arvicoline rodents in North America. *Transactions of the Nebraska Academy of Sciences*, **7**, 91-100.

MARTÍNEZ K., GARCIA J., CARBONELL E., AGUSTÍ J., BAHAIN J.-J., BLAIN H.-A., BURJACHS F., CÁCERES I., DUVAL M., FALGUÈRES C., GÓMEZ M. & HUGUET R., 2010 - A new Lower Pleistocene archeological site in Europe (Vallparadís, Barcelona, Spain). *Proceeding of the National Academy of Sciences*, **107** (13), 5762-5767.

MARTÍNEZ-NAVARRO B., TURQ A., AGUSTÍ J. & OMS, O., 1997 - Fuente Nueva 3 (Orce, Granada, Spain) and the first human occupation of Europe. *Journal of Human Evolution*, **33** (5), 611-620.

MASINI F. & SALA B., 2007 - Large and small mammal distribution patterns and chronostratigraphic boundaries from the Late Pliocene to the Middle Pleistocene of the Italian peninsula. *Quaternary International*, **160** (1), 43-56.

MAUL L.C., 2002 - The Quaternary small mammal faunas of Thuringia (Central Germany). *In* R.A. Meyrick, D.C. Schreve (eds.), *The Quaternary of Central Germany (Thuringia and surroundings)*. Quaternary Research Association, London, 79-96.

MAUL L., MASINI F., ABBAZZI L. & TURNER A., 1998 - The use of different morphometric data for absolute age calibration of some South and Middle European arvicolid populations. *Palaeontographia Italica*, **85**, 111-151.

MINWER-BARAKAT R., MADURELL-MALAPEIRA J., ALBA D., AURELL- GARRIDO J., ESTEBAN-TRIVIGNO S. & MOYÀ-SOLÀ S., 2011 - Pleistocene rodents from the torrent de Vallparadis section (Terrassa, northeastern Spain) and biochronological implications. *Journal of Vertebrate Paleontology*, **31** (4), 849-865.

NÉRAUDEAU D., VIRIOT L., CHALINE J., LAURIN B. & VAN KOLFSCHOTEN T., 1995 - Discontinuity in the Plio-Pleistocene Eurasian water vole lineage. *Palaentology*, **38** (1), 77-85.

OMS O., PARÉS J.M., MARTÍNEZ-NAVARRO B., AGUSTÍ J., TORO I., MARTÍNEZ FERNÁNDEZ G. & TURQ A., 2000 - Early human occupation of Western Europe: Paleomagnetic dates of two paleolithic sites in Spain. *Proceeding of the National Academy of Sciences*, **97** (19), 10666-10670.

OMS O., ANADÓN P., AGUSTÍ J. & JULIÀ R., 2011 - Geology and chronology of the continental Pleistocene archeological and paleontological sites of the Orce area (Baza basin, Spain). *Quaternary International*, **243** (1), 33-43.

PARÉS J.M. & PÉREZ-GONZÁLEZ A., 1995 - Paleomagnetic age for hominid fossils at Atapuerca archaeological site, Spain. *Science*, **269** (5225), 830-832.

RABEDER G., 1981 - Die Arvicoliden (Rodentia, Mammalia) aus dem Pliozän und dem älteren Pleistozän von Niederösterreich. *Beiträge zur Paläontologie von Österreich*, **8**, 1-373.

REKOVETS L., 1994 - *Melkie mlekopitayushchie Antropogena yuzhnoy chaste vostochnoi Evropy* [Small mammals from the Anthropogene of the southern part of East Europe]. Naukova Dumka, Kiev, 371 p. [in Russian]

RUIZ BUSTOS A., 1999 - The role of the water voles (*Arvicola*, Rodentia) in the Quatenary. *Estudios Geologicos*, **55** (1-2), 89-95.

SALADIÉ P., VALLVERDÚ J., BENNÀSAR L.L., CABANES D., MANCHA E., MENÉNDEZ L., BLAIN H.-A., OLLÉ A., MOSQUERA M., VILALTA J., CÁCERES I., EXPOSITO I., ESTEBAN M., HUGUET R., ROSAS A., SOLÉ A., LÓPEZ-POLÍN L., GARCIA A.B., MARTÍNEZ B., CARBONELL E. & CAPDEVILA R., 2008 - Resultats preliminars del nivell 2 del sondeig al Centre de Convencions del barranc de la Boella. *Cota Zero*, **23**, 13-19.

STUART A.J., 1981 - A comparison of the Middle Pleistocene Mammal Faunas of Voigstedt (Thuringia, GDR) and West Runton (Norfolk, England). *Quartärpaläontologie*, **4**, 155-163.

TOPACHEVSKIJ V.A. & SKORIK A.F., 1977 - *Gryzuny rannetamanskoj fauny tiligul'skogo razreza* [Rodents of Early Tamanian faunas of the Tiligul section]. Naukovo Dumka, Kiev, 250 p. [in Russian]

TORO I., MARTÍNEZ-NAVARRO B. & AGUSTÍ, J. (eds.), 2010 - *Ocupaciones Humanas en el Pleistoceno inferior y medio de la Cuenca de Guadix-Baza*. Arqueología. Serie Monografías. .Junta de Andalucía & Consejería de Cultura, Seville, 582 p.

VALLVERDÚ J., SALADIÉ P., BENNÀSAR L.L., CABANES D., MANCHA E., MENÉNDEZ L., BLAIN H.-A., OLLÉ A., VILALTA J., MOSQUERA M., CÁCERES I., EXPOSITO I., ESTEBAN M., HUGUET R., ROSAS A., SOLÉ A., LÓPEZ-POLIN L., MARTINELL J., BARBO A., BIENVENIDO MARTÍNEZ B., AGUSTÍ J., ROS S., CARBONELL E & CAPDEVILA R., 2008 - El barranc de la Boella de la Canonja

(Tarragonès) revisitat en la intervenció arqueològica preventiva de l'any 2007. *Tribuna d'Arqueologia*, **2008-2009**, 7-28.

VAN DER MEULEN A.J., 1973 - Middle Pleistocene smaller mammals from the Monte Peglia (Orvieto, Italy), with special reference to the phylogeny of Microtus (Arvicolidae, Rodentia). *Quaternaria*, **17**, 1-144.

VAN KOLFSCHOTEN T., 1990 - The evolution of the mammal fauna in the Netherlands and the Middle Rhine area (Western Germany) during the late Middle Pleistocene. *Mededelingen Rijks Geologische Dienst*, **43** (3), 1-69.

VIANEY-LIAUD M., 1972 - Un cas de parallélisme intragénérique : l'évolution du genre *Therydomys* (Rodentia, Theridomyidae) à l'Oligocène moyen. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences. Série D, Sciences Naturelles*, **174** (1), 1007-1010.

VIRIOT L., CHALINE J. & SCHAAF A., 1990 - Quantification du gradualisme phylétique de *Mimomys occitanus* à *Mimomys ostramosensis* (Arvicolidae, Rodentia) à l'aide de l'analyse d'images. *Comptes Rendus de l'Académie des Sciences. Série 2, Mécanique, Physique, Chimie, Sciences de l'Univers, Sciences de la Terre*, **310**, 1755-1760.

VON KOENIGSWALD W., SANDER M.P., LEITE M.B., MÖRS T. & SANTEL W., 1994 - Functional symmetries in the schmelzmuster and morphology of rootless rodent molars. *Zoological Journal of the Linnean Society*, **110** (2), 141-179.

VON KOENIGSWALD W. & VAN KOLFSCHOTEN T., 1996 - The *Mimomys-Arvicola* boundary and the enamel thickness quotient (SDQ) of Arvicola as stratigraphic markers in the Middle Pleistocene. *In* C. Turner (ed.), *The early Middle Pleistocene in Europe: proceedings of the SEQS Cromer Symposium, Norwich, 3-7 September 1990*. A.A. Balkema, Rotterdam, 211-226.

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Mimomys savini size evolution in the Early Pleistocene of south-western Europe and possible biochronological implications

Iván Lozano-Fernández[a,b,*], Gloria Cuenca-Bescós[c], Hugues-Alexandre Blain[a,b], Juan Manuel López-García[d], Jordi Agustí[e]

[a] IPHES, Institut Català de Paleoecologia Humana i Evolució Social, C/ Escorxador s/n, E-43003 Tarragona, Spain
[b] Area de Prehistoria, Universitat Rovira i Virgili (URV), Avinguda de Catalunya 35, E-43002 Tarragona, Spain
[c] Área de Paleontología-EIA-IUCA, Dpto. Ciencias de la Tierra, Facultad de Ciencias, Universidad de Zaragoza, E-50009 Zaragoza, Spain
[d] Gruppo di Ricerca di Paleobiologia e Preistoria, Dipartimento di Studi Umanistici, Università degli Studi di Ferrara, C.so Ercole I d'Este 32, I-44121 Ferrara, Italy
[e] ICREA. IPHES, Institut Català de Paleoecologia Humana i Evolució Social, C/ Escorxador s/n, E-43003 Tarragona, Spain

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ABSTRACT

Over the course of their evolutionary history, some species of mammals have undergone variations in size, with a general trend towards increased morphometry. This effect can be seen very clearly in the fossil record of rodents because their high rate of reproduction that generates a high fossil record, which allows this phenomenon to be studied in detail. Furthermore, the rapid geographic distribution of rodents means that their evolution can be studied on a continental scale.

If a relationship can be established between the size of individuals and their chronology, and the trend that governs a species' increase in size can be determined, then the chronologies of different sites can be estimated based on the size of the individuals of that species recovered at those particular sites. The correlation between morphometric data of micromammal fossils and age was already used by other authors.

This article studies the rate at which the length of the first lower molar (m1) of *Mimomys savini* (a species of Palearctic arvicoline present in Europe between approximately 1.8 and 0.6 Ma ago) increased over the course of its evolution in Iberian Peninsula (south-western Europe). Because this increase in length occurred at a constant rate, a direct relationship can be established between average length of m1 and chronology, which allows us to set numerical dates to Pleistocene sites containing *Mimomys savini* remains.

1. Introduction

The existence of evolutionary trends has held the interest of the scientific community ever since the theory of evolution was first put forward (Darwin, 1859). An evolutionary trend is essentially a directional change within a single lineage or parallel changes in several lineages or, in other words, a situation in which several lineages undergo the same types of changes. To be considered an evolutionary trend, this directional change has to be maintained over time and may affect one or more taxa within the lineages in which it occurs.

The origin of these evolutionary trends in nature or their causes remains a topic of debate for which there have classically been two different schools of thought: orthogenesis (a biological hypothesis according to which life has an innate tendency to evolve in a unilinear fashion due to some 'guiding force', whether it be internal or external (Marsh, 1874)) and directional selection or orthoselection (a particular modality of natural selection (Simpson, 1944)). In any case, starting from the basic assumption that species evolve in a chain-like fashion and are constantly changing, the existence of evolutionary trends is a completely logical consequence of evolution, and is patently obvious in the fossil record (Simpson, 1944).

The genus *Mimomys* was present in Europe during the Pliocene that disappeared at the beginning of the Middle Pleistocene (about 4 to 0.6 Ma ago [Chaline and Laurin, 1986; Chaline and Sevilla, 1990; Chaline et al., 1993; Agustí, 1995]). The first representative of this genus in Europe was *Mimomys occitanus* and the last was *Mimomys*

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* Corresponding author. IPHES, Institut Català de Paleoecologia Humana i Evolució Social, C/ Escorxador s/n, E-43003 Tarragona, Spain.
E-mail address: ilozano@iphes.cat (I. Lozano-Fernández).

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savini (Chaline and Laurin, 1986; Agustí, 1995). Features of the evolution of the lineage include an increase in size, the appearance of cement in the re-entrant angles in molars and a progressive increase in crown height (Agustí, 1995). The last representative of the genus *Mimomys* (*Mimomys savini*) lived from about 1.8 to about 0.6 Ma ago (Fejfar et al., 1998) and exhibits a series of evolutionary trends such as a progressive increase in size (Viriot et al., 1990; Chaline et al., 1999; Lozano-Fernández et al., 2013), a gradual loss of 'mimomyian' traits (mimomys-ridge and enamel islet in m1) and variations in tooth enamel thickness (Koenigswald, 1973, 1982; Heinrich, 1978; Koenigswald and Kolfschoten, 1996; Cuenca-Bescós et al., 1999; Lozano-Fernández et al., 2013).

This work investigates the correlation between size and age of *Mimomys savini* at the Gran Dolina site in order to ascertain whether this trend followed a linear pattern over time and, if so, to evaluate its use as a method for the numerical dating of archaeological sites. If validated, this method would constitute yet another tool with which to study the first human populations in Europe on the Iberian Peninsula (Bermúdez de Castro et al., 1997; Martínez-Navarro et al., 1997; Oms et al., 2000; Carbonell et al., 2008; Toro et al., 2010) during the late Early Pleistocene.

2. Geological and chronological setting

This study was conducted based on data obtained from the *Mimomys savini* remains recovered during the excavation carried out at the Gran Dolina site (Atapuerca, Spain) between levels TD4 and TD6 in the 1990's.

The Sierra de Atapuerca is ~1080 m above sea level, dominating the now-flat landscape of the Castilian grain-growing plains irrigated by the River Arlanzón near the village of Ibeas de Juarros, located 14 km east of the city of Burgos (Fig. 1).

The Gran Dolina is one of the caves of the Railway Trench of the Atapuerca Hill. The Trinchera Dolina represents one of the longest stratigraphic sequences at Atapuerca. It comprises 18–19 m of surface filling which is divided into 11 stratigraphic levels. Nine of these levels (TD3–TD11, numbered from bottom to top) are rich in faunal remains and artefacts (Carbonell et al., 1995, 1999; Bermúdez de Castro et al., 1997; Cuenca-Bescós et al., 2005; Rodríguez et al., 2011).

The archaeological and paleontological excavations in Gran Dolina, or Trinchera Dolina (TD), cave have been conducted every year since 1976, and have revealed a long, culturally and paleontologically rich sequence dated at between ca 1 Ma and 250 Ka ago by means of biostratigraphy, electron spin resonance, electron spin resonance on optically bleached quartz dating, U-series, thermoluminescence, infrared-stimulated-luminescence analysis, and paleomagnetic dating (Cuenca-Bescós et al., 2011; Moreno García, 2011 [Fig. 1]).

3. Material and methods

We studied 372 lower first molars (m1), all of them from adult individuals (Table 1). In other words, these molars all had defined areas free of enamel on the occlusal plane and fully developed roots (Fig. 2). In other published works, both variations in the length and the width of the occlusal plane of the m1 have been used as a reflection of size-related changes among individuals from different paleontological populations (Viriot et al., 1990; Chaline et al., 1999; Lozano-Fernández et al., 2013). The size of the individuals in this

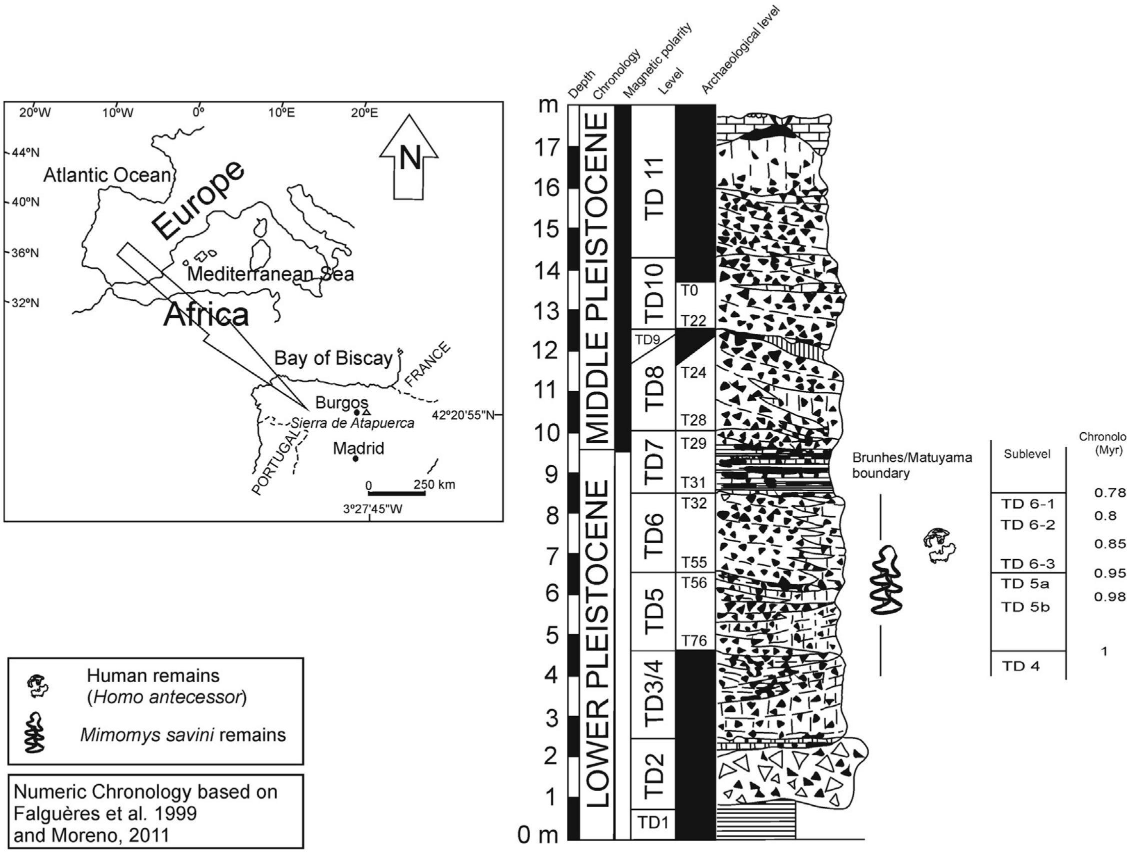

Fig. 1. Geographical location of the Sierra de Atapuerca archaeological sites complex, and Stratigraphic log of Gran Dolina (Modified from Parés and Pérez-González, 1995).

Table 1
Measurements for the first lower molar of *Mimomys savini* in the different sublevels of Gran Dolina cave. The age of the levels corresponds to the mean between the upper and lower ages of each level given by Falguères et al. (1999) and Moreno García, (2011). Abbreviations: *n*: number of remains per level; sd: standard deviation.

Sublevel	Age (Myr)		Length m1 (mm)				
			n	Min	Mean	Max	sd
TD6-1	0.8	(Mean error ± 110 ka)	9	3.26	3.62	3.82	0.17
TD6-2	0.83		10	3.36	3.59	3.81	0.17
TD6-3	0.86		101	2.87	3.43	3.96	0.17
TD5a	0.96		103	3.11	3.49	3.82	0.14
TD5b	0.99		137	3.04	3.46	3.78	0.14
TD4	1.01		12	3.22	3.43	3.68	0.14

study was interpreted based on the length (*L*) of the occlusal plane (Fig. 2).

Once these data were recorded, the average length and the standard deviation were calculated to define the populations of the different sublevels of TD4 and TD6 containing m1s of *Mimomys savini*. This allowed us to characterize each population by a point (average length) and by the associated dispersal. Finally, the populations were put in order and arranged chronologically for each sublevel and each population was assigned to the average chronology between the bottom and the top of the sublevels in order to detect any possible patterns in how these animals evolved in terms of size. We assumed a maximum error in chronology of ±120 ka, corresponding to the error in the dating at the top of TD6-1 and an average error of ±110 ka based on the datings performed by Falguères et al. (1999) and Moreno García, 2011.

4. Results

Of the various sublevels in the sequence between TD4 and TD6, m1s of *Mimomys savini* were only found at the top of TD4, in TD5a, TD5b, TD6-3, TD6-2 and TD6-1. Although remains from *M. savini* were recovered from sublevels TD5c and TD5d, m1s from adult individuals were not among them.

The first relevant piece of data we found is that the standard deviation of the different populations always ranges between 0.14 and 0.17. In other words, the distribution values are similar for the populations and therefore the populations are comparable (Table 1).

The relationship between size and chronology can only be approximated by means of a linear, logarithmic or exponential trend. When the populations are put in chronological order, a clear increase in size can be seen over time. However there is no constant acceleration or deceleration in this increase, which rules out exponential and logarithmic models as possible approaches to the evolutionary trend of this trait. That leaves the linear trend model (linear regression) as the best fit for approximating the reality of the situation.

Using all of the data from the TD4–TD6 sequence, the trend towards size increase over the course of time is governed by the equation:

$$Y = 838.86X - 3847.6$$

(where X corresponds to the length of the occlusal plane of the m1s in millimeters and Y to the chronology in ka).

The correlation coefficient and the determination coefficient for this relationship are not statistically representative ($r = 0.7555$; $R^2 = 0.5708$) due to the value obtained in level TD6-3 (Fig. 3). Level TD6-3 contains a higher diversity of microvertebrate species as well as central European fauna input (Cuenca-Bescós and García, 2007; Cuenca-Bescós et al., 2011) and a possible mixture of *M. savini* populations from Iberian Peninsula with populations from Central Europe, which may be responsible for this anomalous value.

Obviating this value, the trend towards size increase over the course of time is governed by the equation:

$$Y = 1178.6X - 5064.3$$

(where X corresponds to the length of the occlusal plane of the m1s in millimeters and Y to the chronology in ka).

In this case, both the correlation coefficient and the determination coefficient are statistically representative ($r = 0.9958$; $R^2 = 0.9917$), which allows us to conclude that the trend towards an increase in size among *Mimomys savini* is linear and governed by the equation $Y = 1178.6X - 5064.3$ (Fig. 3).

Therefore, using this equation allows us to assign numerical dates based on the size of the *M. savini* remains recovered as long as the standard deviation of individual size in the population is equal to or less than 0.17. We assume a margin of error of ±120 ka for these dates because this is the maximum error for the datings of the sequence used to obtain the relationship between size and chronology for this species, as well as the margin at which the error generated by the regression analysis is less than 1%, thereby encompassing everything within ±120 ka.

In populations with a standard deviation in individual size of more than 0.17, because they are outside of the range used in this

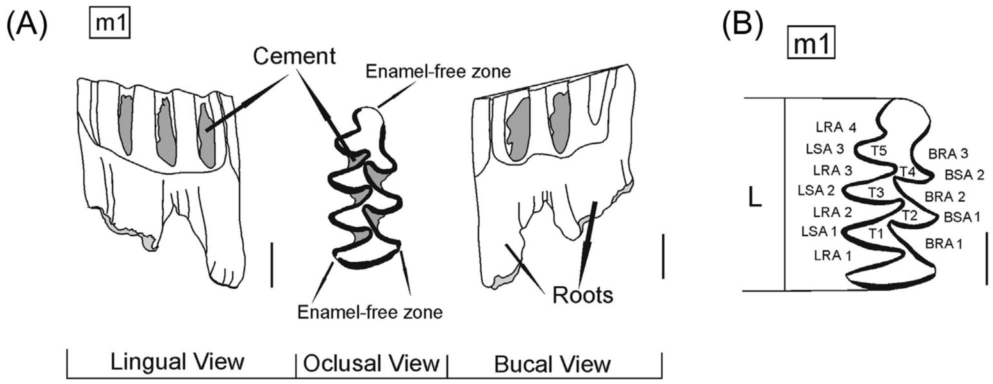

Fig. 2. A: Schema of the buccal, labial and occlusal views of a right inferior, first lower molar of *Mimomys savini* and its different parts. The characteristics defining adult specimens are indicated (enamel-free zones and presence of roots). Scale = 1 mm. B: Nomenclature of the parts distinguished in the occlusal plane of an m1, and the measurement used in this study: *L* refers to the length; T1, T2, T3, T4 and T5 are the various triangles that make up the tooth; LRA refers to the various lingual re-entrant angles, and BRA to the buccal re-entrant angles; LSA refers to the lingual salient angles, and BSA to the buccal salient angles (modified from Meulen, 1973; Heinrich, 1978; Rabeder, 1981).

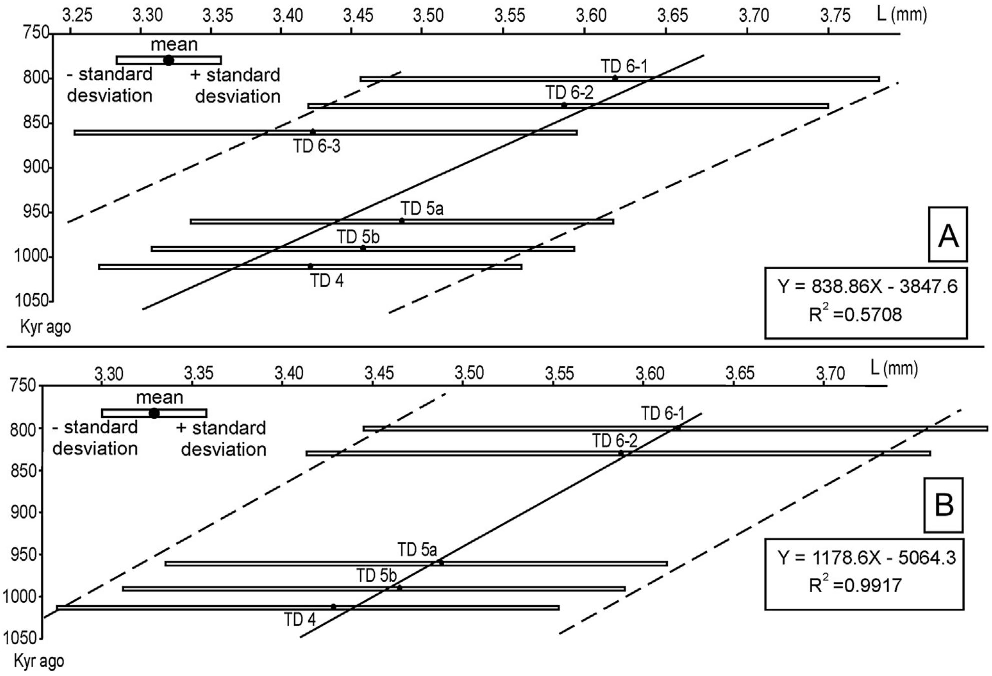

Fig. 3. Relationship between the length of the m1 of *Mimomys savini* from Gran Dolina cave and the chronology according to the age of each level given by Falguères et al. (1999) and Moreno García (2011). In graph A we observe the presence of one population with values deviating significantly from the tendency line (TD6-3) and resulting in a relatively low determination coefficient ($R^2 = 0.5708$). In graph B we observe that when TD6-3 is removed, we obtain a tendency with a very good determination coefficient ($R^2 = 0.9917$). The populations of each level are characterized by the mean length (L) and its associated standard deviation.

study, the difference may affect the central size trend in the sample. To correct this possible uncertainty, the margin of error was governed by the formula:

$$\pm(120 + (f(x+\sigma) - f(x)))\ \text{kyr with } f(x) = 1178.6X - 5064.3$$

(where X corresponds to the average length of the occlusal plane of the m1s of the population in millimeters and σ to the standard deviation).

5. Discussion

Both in central Europe and on the Iberian Peninsula, *M. savini* exhibits the same evolutionary trends, including an increase in size (Maul, 1990; Viriot et al., 1990; Maul et al., 1998a,b; Chaline et al., 1999; Lozano-Fernández et al., 2013). However, the Iberian individuals (those studied here) are systematically larger (as seen in the comparison of values obtained in this work with those previously published (Maul, 1990; Maul et al., 1998a,b). This is explained by a separate evolution of the populations of Iberian Peninsula and Central Europe. This phenomenon would have been similar to what was seen in islands where different to the evolutive rhythms of the continents is observed (Millien, 2006).

Foster (1964) found that in island systems the body size of micromammals tends to be larger. This is due to their isolation from the continent, which means there are fewer predators and less interspecies competition (Heaney, 1978; Sondaar, 1991; Damuth, 1993; Dayan and Simberloff, 1998). Lister (1996), Sondaar (1991) and Millien (2006, 2011) observed that what actually caused these characteristics of less competition and less predation was first of all the acceleration of the trend towards a larger size and subsequently the stability of the rate of growth, which resulted in larger individuals on islands than on the continents.

It is possible that the size difference of the individuals observed within Central Europe and Iberian Peninsula was also due to the issue that the populations of the Iberian Peninsula have suffered the acceleration-stabilization process of evolutive tendency when separating from the central European populations.

The evolutive tendency of the size increase is also observed in the *Arvicola* genus (Maul et al., 2000; Agadzhanyan, 2012), descendent of *M. savini* (Chaline and Sevilla, 1990; Viriot et al., 1990; Chaline et al., 1999)). If we compare the data published on *Arvicola* of the Iberian Peninsula with the data of Central Europe, it can be observed that the individuals of Iberian Peninsula are bigger for the similar chronologies of Central Europe (Maul et al., 2000; López-García, 2008; Sesé and Villa, 2008; López-García et al., 2011; Agadzhanyan, 2012) as it occurs with *M. savini.*

The specific characteristic of the islands which facilitates this acceleration in the evolutionary trends of micromammal species is isolation from the rest of the continent. In our case, the Iberian Peninsula is isolated to a certain extent by the biogeographical barrier of the Pyrenees. This mountain chain that separates the peninsula from the rest of the continent certainly also separated the continental populations of *M. savini* from the Iberian populations of the species. Therefore, a phenomenon similar to the island-effect phenomenon occurred on the Iberian Peninsula.

Putting the Atapuerca data in order by numerical datings (Falguères et al., 1999; Cuenca-Bescós et al., 2011; Moreno García, 2011) reveals that all of the levels except TD6-3 show a highly pronounced linear trend in size increase. In other words, if it were not for TD6-3, the conclusion could be drawn that there is a direct relationship between the size of the individuals and their chronology. Millien and Damuth (2004) found that the island effect has a more marked impact than climatic variations on the evolution of rodents and therefore on their increase in size. Because the incidence of the island effect does not change over time, what we have here is a highly pronounced linear evolutionary trend in size increase, or in other words, a direct relationship between the size of the individual animals of a population and their chronology.

Upon studying level TD6-3 in detail in an attempt to understand this apparently anomalous result, it became clear that in TD6-3 the evolutionary trend of the species would have been affected by environmental circumstances: an increase in the biodiversity of micromammals (Cuenca-Bescós et al., 2011) and lower average annual temperatures (Blain et al., 2009, 2012). The increase in biodiversity would have meant an increase in interspecies competition and the resulting deceleration in the pace of evolutionary changes (Heaney, 1978; Sondaar, 1991; Damuth, 1993; Dayan and Simberloff, 1998), but would not have changed the evolutionary trend itself. Meanwhile, lower temperatures may have favored an increase in size (Bergmann, 1847) or, on the other hand, they may have slowed down the evolution of the size of individual animals due to a reduction in trophic resources, which would have affected the pace of growth. But in no case would the evolutionary trends have been reversed. Therefore, the explanation for this decrease in size in the individuals recovered from TD6-3 must lie in a combination of these two factors.

As seen with large mammals, in the period corresponding to the transition between TD5 and TD6-3 the Iberian Peninsula was affected by the addition of new European fauna to the pre-existing fauna on the peninsula (Cuenca-Bescós and García, 2007; Cuenca-Bescós et al., 2011), which was very likely due to the decrease in temperatures experienced in the region at the time. This is reflected in the increased biodiversity of micromammals in level TD6-3. The appearance of more northern species also meant the arrival of populations of *M. savini* from central Europe, where individuals were smaller (Maul, 1990; Maul et al., 1998a,b). So, the decrease in size of the individuals in TD6-3 may be the result of the mixing of populations. Subsequently, the system returned to species diversity values similar to those found in TD5a and TD5b, going back to the evolutionary trend seen prior to TD6-3. This process of reacceleration and return to a stable pace in evolutionary trends would have happened relatively quickly, as in island effect processes (Sondaar, 1991; Lister, 1996), which is why we see the values for TD6-2 return to fit within the theoretical trend.

6. Conclusions

The significance of conducting this study using data from the Gran Dolina stratigraphic sequence lies in the fact that this is a relatively continuous, well-dated sequence in which ecological and climatic variations have been exhaustively studied (Cuenca-Bescós et al., 1999, 2001, 2005, 2011; Blain et al., 2008, 2009, 2012). This allows us to determine whether external factors may have had an influence on the evolutionary trends documented in this species.

The stratigraphic sequence studied here, TD4-TD-6 of Gran Dolina (Atapuerca, Spain), has yielded evidence of the existence of an evolutionary trend towards increased size in the species *M. savini* in south-western Europe. This trend is very close to a linear model with very good correlation and determination coefficients and can therefore be defined as linear. This means that this characteristic can be used to extrapolate chronologies outside of the TD4–TD6 range using the size of individuals to provide datings in the chronological framework between the FAD and LAD of *M. savini*.

The application of this method can provide clarity in the dating of the sites that have diverse opinions about the chronologies as it is the case for the sites of Orce (Cuenca Guadix-Baza, Granada, Spain).

This chronological tool yields results with error ranges similar to radiometric methods, but it is relatively faster and less destructive to the sample. Furthermore, it can be used as a complement to radiometric methods to increase the precision of datings.

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References

Agadzhanyan, A.K., 2012. Timing of the *Mimomys-Arvicola* transition on the Russian Plain. Quaternary International 271, 38–49.

Agustí, J., 1995. Ritmo y modalidades de la evolución. Innovación y Ciencia 4, 70–79.

Bergmann, C., 1847. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. Göttinger Studien 3, 595–708.

Bermúdez de Castro, J.M., Arsuaga, J.L., Carbonell, E., Rosas, A., Martínez, I., Mosquera, M., 1997. A hominid from Lower Pleistocene of Atapuerca, Spain: possible ancestor to Neanderthals and modern humans. Science 276, 1392–1395.

Blain, H.-A., Bailon, S., Cuenca-Bescós, G., 2008. The Early–Middle Pleistocene palaeoenvironmental change based on the squamate reptile and amphibian proxies at the Gran Dolina site, Atapuerca, Spain. Palaeogeography, Palaeoclimatology, Palaeoecology 261, 172–192.

Blain, H.-A., Bailon, S., Cuenca-Bescos, G., Arsuaga, J.L., Bermudez de Castro, J.M., Carbonell, E., 2009. Long-term climate record inferred from early-middle Pleistocene amphibian and squamate reptile assemblages at the Gran Dolina Cave, Atapuerca, Spain. Journal of Human Evolution 56, 55–65.

Blain, H.-A., Cuenca-Bescós, G., Lozano-Fernández, I., López-García, J.M., Ollé, A., Rosell, J., Rodríguez, J., 2012. Investigating the Mid-Brunhes event in the Spanish terrestrial sequence. Geology 40, 1051–1054.

Carbonell, E., Bermúdez de Castro, J.M., Arsuaga, J.L., Díez, J.C., Rosas, A., Cuenca, G., Sala, R., Mosquera, M., Rodríguez, J., 1995. Lower Pleistocene hominids and artifacts from Atapuerca-TD6 (Spain). Science 269, 826–830.

Carbonell, E., Esteban, M., Nájera, A.M., Mosquera, M., Rodríguez, X.P., Ollé, A., Sala, R., Vergès, J.M., Bermúdez de Castro, J.M., Ortega, A.I., 1999. The Pleistocene site of Gran Dolina, Sierra de Atapuerca, Spain: a history of the archaeological investigations. Journal of Human Evolution 37, 313–324.

Carbonell, E., Bermúdez de Castro, J.M., Parés, J.M., Pérez-González, A., Cuenca-Bescós, G., Ollé, A., Mosquera, M., Huguet, R., van der Made, J., Rosas, A., Sala, R., Vallverdú, J., García, N., Granger, D.E., Martinón-Torres, M., Rodríguez, X.P., Stock, G.M., Vergés, J.M., Allué, E., Burjachs, F., Cáceres, I., Canals, A., Benito, A., Díez, C., Lozano, M., Mateos, A., Navazo, M., Rodriguez, J., Rosell, J., Arsuaga, J.L., 2008. The first Hominin of Europe. Nature 452, 465–469.

Chaline, J., Brunet-Lecomte, P., Montuire, S., Viriot, L., Courant, F., 1999. Anatomy of the arvicoline radiation (Rodentia): palaeogeographical, palaecoecological history and evolutionary data. Annales zoologici fennici 36, 239–267.

Chaline, J., Laurin, B., 1986. Phyletic gradualism in a European Plio-Pleistocene *mimomys* lineage (Arvicolidae, Rodentia). Paleobiology 12, 203–216.

Chaline, J., Laurin, B., Brunet-Lecomte, P., Viriot, L., 1993. Morphological trends and rates of evolution in arvicolids (Arvicolidae, Rodentia): towards a punctuated equilibria/disequilibria model. Quaternary International 19, 27–39.

Chaline, J., Sevilla, P., 1990. Phyletic gradualism and developmental heterochronies in a European Plio-Pleistocene *Mimomys* linage (Arvicolidae, Rodentia). In: International Symposium on the Evolution, Phylogeny and Biostratigraphy of Arvicolids, pp. 85–98.

Cuenca-Bescós, G., García, N., 2007. Biostratigraphic succession of the early and middle Pleistocene mammal faunas of the Atapuerca cave sites (Burgos, Spain). Courier Forschunginstitut Senckenberg 259, 99–100.

Cuenca-Bescós, G., Canudo, J.I., Laplana, C., 2001. La séquence des rongeurs (Mammalia) des sites du Pléistocène inférieur et moyen d'Atapuerca (Burgos, Espagne). L'Antropologie 105, 115–130.

Cuenca-Bescós, G., Laplana, C., Canudo, J.I., 1999. Biochronological implications of the Arvicolidae (Rodentia, Mammalia) from the Lower Pleistocene hominid-bearing level of Trinchera Dolina 6 (TD6, Atapuerca, Spain). Journal of Human Evolution 37 (3–4), 353–373.

Cuenca-Bescós, G., Melero-Rubio, M., Rofes, J., Martínez, I., Arsuaga, J.L., Blain, H.-A., López-García, J.M., Carbonell, E., Bermúdez de Castro, J.M., 2011. The Early–Middle Pleistocene environmental and climatic change and the human expansion in Western Europe: a case study with small vertebrates (Gran Dolina, Atapuerca, Spain). Journal of Human Evolution 60, 481–491.

Cuenca-Bescós, G., Rofes, J., Garcia-Pimienta, J., 2005. Environmental Change across the Early–Middle Pleistocene Transition: Small Mammalian Evidence from the Trinchera Dolina Cave, Atapuerca, Spain. In: Geological Society, London, Special Publications, vol. 247, pp. 277–286.

Damuth, J., 1993. Cope's rule, the island rule and the scaling of mammalian population density. Nature 365, 748–750.

Darwin, C., 1859. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life, 1a ed. John Murray, London.

Dayan, T., Simberloff, D., 1998. Size patterns among competitors: ecological character displacement and character release in mammals, with special reference to island populations. Mammal Review 28, 99–124.

Falguères, C., Bahain, J.J., Yokoyama, Y., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., Bischoff, J.L., Dolo, J.M., 1999. Earliest humans in Europe: the age of TD6 Gran Dolina, Atapuerca, Spain. Journal of Human Evolution 37, 343–352.

Fejfar, O., Heinrich, W.-D., Lindsay, E.H., 1998. Updating the Neogene rodent biochronology in Europe. In: Van Kolfschoten, T., Gibbard, P.L. (Eds.), The Dawn of the Quaternary. Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen, pp. 60,533–60,554.

Foster, J.B., 1964. The evolution of mammals on islands. Nature 202, 234–235.

Heaney, L.R., 1978. Island area and body size of insular mammals: evidence from the tri-colored squirrel (*Callosciurus prevosti*) of southeast Asia. Evolution 32, 29–44.

Heinrich, W.-D., 1978. Zur biometrischen Erfassung eines Evolutionstrends bei *Arvicola* (Rodentia, Mammalia) aus dem Pleistozän Thüringens. Säugetierkundliche Informationen 2, 3–21.

Koenigswald, W. Von, 1973. Veränderungen in der Kleinsäugerfauna von Mitteleuropa zwischen Cromer und Eem (Pleistozän). Eiszeitalter und Gegenwart 23/24, 159–167.

Koenigswald, W.Von, 1982. Zum Verständnis der Morphologie der Wühlmausmolaren (Arvicolidae, Rodentia, Mammalia). Zeitschrift für Geologische Wissenschaften 10, 951–962.

Koenigswald, W.Von, Kolfschoten, T.Van, 1996. The *Mimomys–Arvicola* boundary and the enamel thickness quotient (SDQ) of *Arvicola* as stratigraphic markers in the Middle Pleistocene. In: Turner, C. (Ed.), Proceedings of the SEQS Cromer Symposium. Norwich/United Kingdom, The Early–Middle Pleistocene in Europe, Norwich, pp. 211–226.

Lister, A.M., 1996. Dwarfing in island elephants and deer: processes in relation to time of isolation. Symposia of the Zoological Society of London 69, 277–292.

López-García, J.M., 2008. Evolución de la diversidad taxonómica de los micromamíferos en la Península Ibérica y cambios Paleoambientales durante el Pleistoceno Superior (Ph.D. thesis). Universitat Rovira i Virgili, Tarragona, p. 407.

López-García, J.M., Blain, H.-A., Cuenca-Bescós, G., Alonso, C., Alonso, S., Vaquero, M., 2011. Small vertebrates (Amphibia, Squamata, Mammalia) from the late Pleistocene–Holocene of the Valdavara-1 cave (Galicia, northwestern Spain). Geobios 44, 253–269.

Lozano-Fernández, I., Agustí, J., Cuenca-Bescós, G., Blain, H.-A., López-García, J.M., Vallverdú, J., 2013. Pleistocene evolutionary trends in dental morphology of *Mimomys savini* (Rodentia, Mammalia) from Iberian Peninsula and discussion about the origin of the genus Arvicola. Quaternaire 24, 179–190.

Marsh, O.C., 1874. Notice of new Equine mammals from the Tertiary Formation. American Journal of Sciences and Arts 7 (39), 250.

Martínez-Navarro, B., Turq, A., Agustí, J., Oms, O., 1997. Fuente Nueva 3 (Orce, Granada, Spain) and the first human occupation of Europe. Journal of Human Evolution 33, 611–620.

Maul, L., 1990. Biharische Kleinsäugerfunde von Untermaßfeld, Voigtstedt und Süßenborn und ihre chronologische Stellung im Rahmen der biharischen Micromammalia-Faunen Europas (Ph.D. thesis). Humboldt-University, Berlin, p. 138. +20 pp.

Maul, L., Masini, F., Abbazzi, L., Turner, A., 1998a. The use of different morphometric data for absolute age calibration of some South and Middle European arvicolid populations. Palaeontographia Italica 85, 111–151.

Maul, L., Masini, F., Abbazzi, L., Turner, A., 1998b. Geochronometric application of evolutionary trends in the dentition of fossil Arvicolidae. In: van Kolfschoten, T., Gibbard, P.L. (Eds.), The Dawn of the Quaternary. Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen, pp. 565–572. TNO 60.

Maul, L., Rekovets, L., Heinrich, W.-D., Keller, T., Storch, G., 2000. *Arvicola mosbachensis* (SCHMIDTGEN 1911) of Mosbach 2: a basic sample for the early evolution of the genus and a reference for further biostratigraphical studies. Senckenbergiana lethaea 80, 129–147.

Meulen, A.J. van der, 1973. Middle Pleistocene Smaller Mammals from the Monte Peglia (Orvieto, Italy) with special Reference to the Phylogeny of Miocrotus (Arvicolidae, Rodentia). Quaternaria 17, 1–144.

Millien, V., 2006. Morphological evolution is accelerated among island mammals. Plos Biology 4, 1863–1868.

Millien, V., 2011. Mammals evolve faster on smaller islands. Evolution 65, 1935–1944.

Millien, V., Damuth, J., 2004. Climate change and size evolution in an island rodent species: new perspectives on the island rule. Evolution 58, 1353–1360.

Moreno García, D., 2011. Datation par ESR de quartz optiquement blanchis (ESR-OB) de la région de Atapuerca (Burgos, Espagne). Application au site préhistorique de Gran Dolina (contexte karstique) et aux systèmes fluviatiles quater- naires de l'Arlanzón et l'Arlanza (Ph.D. thesis). Universitat Rovira i Virgili and Paris, Muséum National d'Histoire Naturelle, Tarragona, p. 304.

Oms, O., Parés, J.M., Martínez-Navarro, B., Agustí, J., Toro, I., Martínez Fernández, G., Turq, A., 2000. Early human occupation of Western Europe: paleomagnetic dates of two paleolithic sites in Spain. Proceeding of the National Academy of Science 97 (19), 10666–10670.

Parés, J.M., Pérez-González, A., 1995. Paleomagnetic age for hominid fossils at Atapuerca archaeological site, Spain. Science 269, 830–832.

Rabeder, G., 1981. Die Arvicoliden (Rodentia, Mammalia) aus dem Pliozän und dem älterren Pleistozän von Niederösterreich. Beiträge zur Paläontologie 8 (1), 343.

Rodríguez, J., Burjachs, F., Cuenca-Bescós, G., García, N., van der Made, J., Pérez González, A., Blain, H.-A., Expósito, I., López-García, J.M., García Antón, M., Allué, E., Cáceres, I., Huguet, R., Mosquera, M., Ollé, A., Rosell, J., Parés, J.M., Rodríguez, X.P., Díez, C., Rofes, J., Sala, R., Saladié, P., Vallverdú, J., Bennasar, M.L., Blasco, R., Bermúdez de Castro, J.M., Carbonell, E., 2011. One million years of cultural evolution in a stable environment at Atapuerca (Burgos, Spain). Quaternary Science Reviews 30, 1396–1412.

Sesé, C., Villa, P., 2008. Micromammals (rodents and insectivores) from early Late Pleistocene cave site of Bois Roche (Charente, France): systematics and paleoclimatology. Geobios 41, 399–414.

Simpson, G.G., 1944. Tempo and Mode in Evolution. Columbia University Press, New York.

Sondaar, P.Y., 1991. Island mammals of the past. Science Progress 75, 249–264.

Toro, I., Martínez-Navarro, B., Agustí, J. (Eds.), 2010. Ocupaciones Humanas en el Pleistoceno inferior y medio de la Cuenca de Guadix-Baza: Memoria Científica. Junta de Andalucía. Consejería de Cultura. E.P.G. Arqueología Monográfico, p. 582.

Viriot, L., Chaline, J., Schaaf, A., 1990. Quantification du gradualisme phylétique de *Mimomys occitanus* à *Mimomys ostramosensis* (Arvicolinae, Rodentia) à l'aide de l'analyse d'image. Comptes Rendus de l'Académie des Sciences 310, 1755–1760.