UNIVERSITAT ROVIRA I VIRGILI

PALEOCOMUNIDADES DE MÚRIDOS (RODENTIA, MAMMALIA) DEL NEÓGENO SUPERIOR Y PLEISTOCENO INFERIOR DEL SURESTE DE LA PENÍNSULA IBÉRICA

Pedro Piñero Garcia

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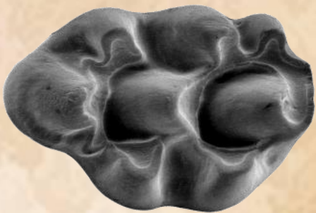
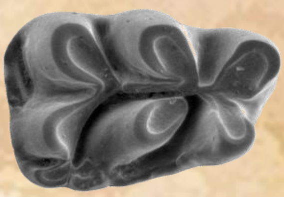
PEDRO PIÑERO GARCÍA





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Pedro Piñero García

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el Dr. Jordi Agustí Ballester

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Institut Català de Paleoecologia Humana i Evolució Social

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“Paleocomunidades de múridos (Rodentia, Mammalia) del Neógeno superior y Pleistoceno inferior del sureste de la Península Ibérica”

HAGO CONSTAR que el presente trabajo, titulado “Paleocomunidades de múridos (Rodentia, Mammalia) del Neógeno superior y Pleistoceno inferior del sureste de la Península Ibérica”, que presenta Pedro Piñero García para la obtención del título de Doctor, ha sido realizado bajo mi dirección en el Departamento de Historia e Historia del Arte de esta universidad.

Tarragona, 1 de junio de 2017

El director de la tesis doctoral

Jordi Agustí Ballester

Con el apoyo del Ministerio de Educación, Cultura y Deportes (Beca FPU)

A la persona que siempre ha contestado mis preguntas, enseñándome la magia de mirar al pasado: mi padre

Dibujo: Stefania Titton

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RESUMEN

En este trabajo, se ofrece un análisis taxonómico completo de hasta 1370 dientes de múridos procedentes de 14 niveles paleontológicos diferentes localizados en el sureste ibérico. Las distintas localidades han proporcionado asociaciones de micromamíferos de edades que van desde el Mioceno superior hasta el Pleistoceno inferior, identificándose un total de 19 especies de múridos. A partir del conjunto de taxones identificados, que incluye el resto de roedores y en algún caso también los insectívoros, se realizan correlaciones bioestratigráficas con yacimientos de otras áreas de la Península Ibérica por medio de la comparación de sus faunas. En primer lugar se han estudiado los niveles del Mioceno superior de la sección de Romerales, en la cuenca de Fortuna, incorporando un análisis paleoecológico por medio de las asociaciones de micromamíferos, que ha posibilitado inferir las condiciones ambientales reinantes durante el Mioceno superior en el sureste peninsular. En este contexto, se ha estudiado también la sección de Sifón de Librilla, localizada en la misma cuenca de Fortuna. Esta secuencia ha proporcionado un registro bioestratigráfico muy detallado desde el Mioceno superior hasta el Plioceno inferior, ligado a un marco magnetoestratigráfico bien calibrado. Esto ha permitido establecer claves para diferenciar el Mioceno superior del Plioceno inferior en depósitos continentales. La disposición de esta sección, con un registro continental de más de 2 millones de años, ha permitido también explorar un marco cronológico para las diferentes especies de roedores identificadas en los distintos yacimientos, así como revisar las relaciones filogenéticas entre especies de los géneros *Apodemus*, *Stephanomys* y *Paraethomys*. Otro de los yacimientos estudiados ha sido el de Puerto de la Cadena, localizado en la cuenca de Murcia-Carrascoy. En este caso, se ofrece una síntesis sedimentológica, magnetoestratigráfica y paleontológica con la finalidad de clarificar su edad y de realizar correlaciones entre las escalas marina y continental. Basados en la sucesión de roedores del Mioceno superior y Plioceno de la cuenca de Guadix-Baza, se presenta la primera biozonación calibrada para el Neógeno superior de esta área mediante el cruce de información magnetoestratigráfica y bioestratigráfica. Se definen así hasta nueve biozonas correlacionadas con la escala de tiempo geomagnética en base a los análisis paleomagnéticos llevados a cabo en las secciones de Negratín, Botardo-1 y Gorafe, que se suman a los ya publicados de las secciones de Zújar y Galera. En la cuenca de Guadix-Baza destaca la localidad de Baza-1, que incluye la colección de vertebrados más numerosa y diversa del Plioceno inferior de esta región. Su estudio ha permitido mejorar el conocimiento de las

asociaciones faunísticas presentes en dicha época, así como abordar una aproximación a las condiciones ambientales dominantes en el sureste ibérico durante la formación del yacimiento. Por lo que respecta al Pleistoceno inferior de esta zona, el trabajo se ha centrado en el yacimiento de Quibas, una localidad kárstica que ha librado una variada fauna de vertebrados. En esta tesis se describe por primera vez la fauna de roedores del relleno conocido como Gruta-1, que incluye cuatro especies, dos de ellas múridos. La asociación permite situar este yacimiento a finales del Pleistoceno inferior, correlacionable con los yacimientos arqueo-paleontológicos de Barranco León-5 y Fuente Nueva-3 en Orce (Granada), y la Sima del Elefante en Atapuerca (Burgos). Asimismo, se ha realizado una reconstrucción paleoambiental por medio de dicho conjunto, posibilitando el establecimiento de un contexto ambiental para la Sierra de Quibas durante el Pleistoceno inferior.

ABSTRACT

This work presents a complete taxonomic analysis of up to 1370 murid teeth collected from 14 paleontological levels of sites located in the southeastern Iberian Peninsula. The different localities have yielded micro-mammal assemblages with ages ranging from the late Miocene to the early Pleistocene, allowing for the identification of 19 murid species. From the set of taxa identified, which includes rodent species and, in one case, insectivores, biostratigraphic correlations with other sites situated in the Iberian Peninsula have been performed. Firstly, a paleoecological analysis carried out on the late Miocene levels of the Romerales section (Fortuna Basin) using micromammal associations allows to infer the dominant environmental conditions during this timeframe in the area. Secondly, the Sifón de Librilla section, a long and continuous continental sequence also located in the Fortuna Basin, was also studied, allowing to obtain a detailed biostratigraphical record extending from the latest Miocene up to the early Pliocene. Using unambiguously established magnetostratigraphical data allows to firmly establish keys with to distinguish the late Miocene from the early Pliocene in Mediterranean continental deposits. The exceptional temporal extension of this stratigraphical sequence, recording more than 2 Myr, has permitted the exploration of the chronological framework for the different rodent species identified in each site, as well as to refine the phylogenetic relationships of the *Apodemus*, *Stephanomys* and *Paraethomys* lineages. Another site is that of Puerto de la Cadena, located in the Murcia-Carrascoy Basin. In this case, a sedimentological, magnetostratigraphical and paleontological synthesis is provided to clarify its chronological situation and to offer a correlation between the marine and continental scales. Based on a rodent succession from the Guadix-Baza Basin which ranges from the latest Miocene to the latest Pliocene, the first calibrated biozonation for the late Neogene of this area is presented. This scale has been elaborated by incorporating both magnetostratigraphical and biostratigraphical information. In sum, nine biozones correlated with the geomagnetic time scale are defined based on paleomagnetic analysis performed for the Negratín, Botardo-1 and Gorafe sections, which are in addition to those already published for the Zújar and Galera sections. The Baza-1 locality in the Guadix-Baza Basin is highlighted since it has yielded the most numerous and diverse vertebrate collection dating to the early Pliocene in this region. The study of this site improves our knowledge about the faunistic associations present during this Epoch, and provides an assessment of the dominant environmental conditions in southeastern Iberia during the period of its formation. Regarding

the early Pleistocene from this area, this work focuses on the site of Quibas, a karstic locality that has yielded a diverse assemblage of vertebrate fauna. The rodent fauna from the cavity known as Gruta-1 is described for the first time. The assemblage includes four species, including two murids. Their association allows to assign the site to the late early Pleistocene and to correlate it with the nearby archeo-paleontological sites of Barranco León-5 and Fuente Nueva-3 in Orce (Granada), and also with the Sima del Elefante site at Atapuerca (Burgos). Finally, a paleoenvironmental reconstruction has been realized by means of the Quibas rodent assemblage, establishing the environmental context for the Sierra de Quibas during the early Pleistocene.

RESUM

En aquest treball s´ofereix un anàlisi taxonòmic complet de fins a 1370 dents de múrids provinents de 14 nivells paleontològics diferents localitzats al surest ibèric. Les diferents localitats han proporcionat associacions de micromamífers d´edats que van des del Miocè superior fins el Plistocè inferior, identificant-se un total de 19 espècies de múrids. A partir del conjunt de taxons identificats, que inclou la resta de rosegadors i en algun cas també els insectívors, s´han realitzat correlacions bioestratigràfiques amb jaciments d´altres àrees de la Península Ibèrica a partir de la comparació de les seves faunes. En primer lloc s´han estudiat els nivells del Miocè superior de la secció de Romerales, a la conca de Fortuna, incorporant un anàlisi paleoecològic a traves de les associacions de micromamífers, que ha possibilitat inferir les condicions ambientals imperants durant el Miocè superior al surest peninsular. En aquest context, s´ha estudiat també la secció de Sifón de Librilla, localitzada a la mateixa conca de Fortuna. Aquesta seqüència ha proporcionat un registre bioestratigràfic molt detallat des del Miocè superior fins el Pliocè inferior, lligat a un marc magnetoestratigràfic ben calibrat. Això ha permès aclarir els criteris per diferenciar el Miocè superior del Pliocè inferior en dipòsits continentals. La disposició d´aquesta secció, amb un registre continental de més de dos milions d´anys, ha permès també explorar un marc cronològic per les diferents espècies de rosegadors identificades als diferents jaciments, així com revisar les relacions filogenètiques entre espècies dels gèneres *Apodemus*, *Stephanomys* i *Paraethomys*. Un altre dels jaciments estudiats ha estat el de Puerto de la Cadena, localitzat a la conca de Murcia-Carrascoy. En aquest cas, s´ofereix una síntesi sedimentològica, magnetoestratigràfica i paleontològica amb la finalitat de clarificar la seva edat i de realitzar correlacions entre les escales marina i continental. Basada en la successió de rosegadors del Miocè superior i del Pliocè de la conca de Guadix-Baza, es presenta la primera biozonació calibrada per al Neògen superior d´aquesta àrea mitjançant el creuament d´ informació magnetoestratigràfica i bioestratigràfica. Es defineixen així fins a nou biozones correlacionades amb l´escala de temps geomagnètica en base als anàlisis paleomagnètics desenvolupats a les seccions de Negratín, Botardo-1 y Gorafe, que s´afeigeixen als ja publicats de les seccions de Zújar i Galera. A la conca de Guadix-Baza destaca la localitat de Baza-1, que inclou la col·lecció de vertebrats més nombrosa i diversa del Pliocè inferior en aquesta regió. El seu estudi ha permès millorar el coneixement de les associacions faunístiques presents en aquell moment, així com abordar una aproximació a les condiciones ambientals dominants en el surest ibèric

durant la formació del jaciment. Pel que respecta al Plistocè inferior d´aquesta zona, el treball s´ha centrat en el jaciment de Quibas, una localitat càrstica que ha lliurat una variada fauna de vertebrats. En aquesta tesis es descriu por primera vegada la fauna de rosegadors del reompliment conegut com a Gruta-1, que inclou 4 espècies, dos d´elles de la familia Muridae. La associació permet situar aquest jaciment a finals del Plistocè inferior, correlacionable amb els jaciments de Barranco León-5 i Fuente Nueva-3 a Orce, i la Sima del Elefante a Atapuerca. Així mateix, s´ha realitzat una reconstrucció paleoambiental a partir de l´esmentat conjunt, que ha permès reconstruir el context ambiental a la Serralada de Quibas durant el Plistocè inferior.

I. INTRODUCCIÓN

I.1. INTRODUCCIÓN GENERAL

Esta tesis se centra en el estudio sistemático de las paleocomunidades de múridos desde el Mioceno superior hasta el Pleistoceno inferior del sureste de la Península Ibérica. Estas asociaciones han sido recuperadas de varios niveles de las secciones de Sifón de Librilla y Romerales (cuenca de Fortuna), y de los yacimientos del Puerto de la Cadena (cuenca de Murcia-Carrascoy), Baza-1 (cuenca de Guadix-Baza) y Quibas (Sierra de Quibas). A partir de la identificación de las especies de múridos y teniendo en cuenta todo el conjunto de micromamíferos, se realizan correlaciones bioestratigráficas con niveles fosilíferos de otras áreas por medio de la comparación de sus faunas, tales como la región de Teruel, cuenca de Granada, cuenca de Crevillente, cuenca de Alcoy y cuenca de Cabriel, entre otras. Además, el análisis de las asociaciones de micromamíferos desde un punto de vista paleoecológico permite la realización de reconstrucciones ecológicas y climáticas de algunos de los niveles estudiados.

Otro tema importante abordado en este trabajo es el cruce de información magnetoestratigráfica con bioestratigráfica, que ha permitido llevar a cabo correlaciones entre las escalas continental y marina en varias de las secciones estudiadas. Para los casos del yacimiento del Puerto de la Cadena (cuenca de Murcia-Carrascoy) y de las secciones de Gorafe, Botardo-1 y Negratín (cuenca de Guadix-Baza) se ofrecen las primeras correlaciones magnetobioestratigráficas. A partir de la información magnetoestratigráfica obtenida para estas tres últimas secciones, y junto con la de las secciones de Zújar (Oms et al., 1999) y Galera (Garcés et al., 1997), en esta tesis se ofrece la primera escala magnetobioestratigráfica completa para el Mioceno superior y Plioceno de la cuenca de Guadix-Baza, con la propuesta de numerosas biozonas bien calibradas basadas en el registro de roedores. Como prolongación de esta biozonación, se ha añadido en el apéndice un trabajo donde se propone una escala similar para el registro continental del Pleistoceno inferior y medio de la cuenca de Guadix-Baza, donde el autor de este trabajo figura como uno de los firmantes. Ambas escalas cubren la laguna entre los yacimientos de Baza-1 y Quibas, posibilitando una continuidad bioestratigráfica desde el Mioceno superior hasta el Pleistoceno inferior.

Los trabajos sobre las secciones de Sifón de Librilla y Romerales son una continuación de las labores de investigación iniciadas en la década de los 90 por un equipo liderado por el profesor Jordi Agustí en la cuenca de Fortuna. Durante varios años se dedicaron a recoger multitud de muestras de varias secciones diferentes llevando a cabo los respectivos trabajos de lavado, tamizado y triado. De esta forma, el trabajo de campo para estas dos secciones ya estaba resuelto al inicio de esta tesis, sin embargo las colecciones no estaban montadas y la sistemática detallada de los diferentes taxones no estaba resuelta.

La sección de Sifón de Librilla ofrece un registro bioestratigráfico muy detallado, siendo excepcional para el estudio de la evolución de pequeños mamíferos desde el Mioceno superior hasta el Plioceno inferior. Se trata de una sección con un registro continental continuo de más de 2 millones de años, que además cuenta con un marco magnetoestratigráfico bien calibrado (Garcés et al., 1998, 2001). Actualmente, la magnetoestratigrafía es la herramienta más útil y ampliamente disponible para la estimación de la edad de las faunas de mamíferos (Hordijk y Bruijn, 2009). Hasta el momento, no hay muchas secciones estratigráficas que hayan proporcionado fósiles de micromamíferos y que además cuenten con datos paleomagnéticos fiables. Afortunadamente se dispone de la sección de Sifón de Librilla, que además incluye el límite Mioceno-Plioceno con una transgresión marina inmediatamente por encima de una incisión que se produjo tras la Crisis de Salinidad del Messiniense. En este caso, el nivel de SIF-413 representa el primer depósito de esta sección con contenido en microfauna formado durante el Plioceno más basal. El estudio detallado de esta sección permite por tanto analizar las implicaciones bioestratigráficas para detectar el inicio del Plioceno inferior en depósitos continentales. El hecho de que las asociaciones de los niveles de esta sección cuenten con una edad precisa permite establecer un marco cronológico para las diferentes especies encontradas a lo largo de la misma. Aparte, se proporciona un estudio completo de la taxonomía de los múridos de esta secuencia, y se revisan las relaciones filogenéticas entre especies de los géneros *Apodemus*, *Stephanomys* y *Paraethomys*.

La sección de Romerales no cuenta con un estudio de paleomagnetismo, sin embargo contiene dos de los niveles más ricos en micromamíferos de la cuenca de Fortuna. Ésto permite abordar un análisis detallado de las faunas de múridos, y de pequeños mamíferos en general, que habitaron durante el Turoliense superior en el sureste peninsular, así como establecer un marco paleoecológico para esta región antes del inicio de la Crisis de Salinidad del Messiniense.

Los fósiles de pequeños mamíferos del yacimiento del Puerto de la Cadena también se recuperaron en un momento previo al inicio de este trabajo. El proyecto para la investigación de este yacimiento, liderado por el profesor Miguel Ángel Mancheño, impulsó la recogida y procesado de gran cantidad de sedimento durante los años 2009, 2010 y 2011, labores de campo y laboratorio en las que el autor de esta tesis estuvo activamente implicado. Gracias a la colaboración de una veintena de investigadores de todo el país, en este trabajo se presenta una síntesis sedimentológica, magnetoestratigráfica y paleontológica del yacimiento del Puerto de la Cadena, permitiendo estimar su edad. En dicho trabajo no solamente se han incluido los pequeños mamíferos, sino todos los taxones de grandes y pequeños vertebrados hallados en esta localidad.

El yacimiento de Baza-1 fue descubierto por el profesor Bienvenido Martínez, iniciándose una excavación sistemática en el año 2001. Fue en este momento cuando se recogieron las muestras de sedimento de cuyo triado y puesta en colección se encargó el autor del presente trabajo. Este yacimiento ha ofrecido una de las colecciones más ricas en micromamíferos de la cuenca de Guadix-Baza, y es sin duda la colección más numerosa y diversa de su época. A pesar de que la cuenca de Guadix-Baza representa uno de los mejores registros continentales de Europa Occidental desde el Mioceno superior hasta el Pleistoceno medio, con sucesiones de microvertebrados muy completas, persiste una significativa laguna bioestratigráfica en esta parte del Plioceno inferior dada la escasez de yacimientos de esta época. Así, la localidad de Baza-1 proporciona nueva información para este intervalo de tiempo poco conocido. Aunque el yacimiento no cuenta con un estudio paleomagnético, se puede estimar su edad en base a correlaciones bioestratigráficas. Se aporta además una mejora del conocimiento de las asociaciones faunísticas del final del Rusciniense inferior en el sureste peninsular, y una aproximación a las condiciones ambientales que reinaron durante el Plioceno inferior en esta área.

La colección de roedores procedente de la Gruta-1 del yacimiento de Quibas fue recuperada en el año 2009 por Amalia Cuadros con motivo de su trabajo fin de máster, dedicado a la tafonomía de los micromamíferos de esta pequeña cavidad kárstica (Cuadros, 2010). Aunque el autor de la tesis no participó en estas labores en concreto, sí que lo hizo para la recuperación de fósiles de otros sectores de este yacimiento entre los años 2008 y 2009. A partir del año 2009, el proyecto de investigación de Quibas quedó temporalmente paralizado debido al descubrimiento del yacimiento paleontológico del Puerto de la Cadena, momento en el que se decidió concentrar el esfuerzo en el estudio de esta nueva localidad. Sin embargo, la implicación del autor en la investigación del yacimiento de Quibas no cesó en ningún momento, de forma que dedicó su trabajo fin de máster al análisis de los roedores de la Gruta-1 (Piñero, 2012), que no se encontraban clasificados ni descritos desde el trabajo de Cuadros (2010).

Siendo conscientes de la gran cantidad de información que aún puede aportar el yacimiento de Quibas, en el año 2014 se reiniciaron las labores de excavación del mismo, y es en este punto cuando el autor entra como codirector del yacimiento junto a los profesores Jordi Agustí y Antonio Rosas. El citado proyecto (Piñero, 2012) ha servido de base para la realización de los dos trabajos sobre el yacimiento de Quibas incluidos en esta tesis, donde se discute sobre la biocronología del mismo, y se ofrece un estudio paleoecológico y paleoclimático que permite reconstruir las condiciones ambientales reinantes durante el final del Pleistoceno inferior en el sureste de la península. Como complemento a estos dos estudios, se ha incluido en el apéndice una publicación sobre la cronología y el contexto ambiental del yacimiento de Barranco León-5 (cuenca de Guadix-Baza), dada su proximidad a la localidad de Quibas tanto cronológica como geográfica.

Tal y como se ha apuntado al inicio, el autor de esta tesis se ha encargado de las descripciones e identificación del conjunto de múridos, un grupo fundamental para la bioestratigrafía del Mioceno superior y el Plioceno. Sin embargo, en los sucesivos trabajos que se integran en la tesis se aporta también información acerca del resto de taxones de roedores e insectívoros. Para los glíridos, cricétidos, arvicólidos y gerbílidos se ha contado con la colaboración de Jordi Agustí, aunque en el caso concreto de los roedores del Puerto de la Cadena también han colaborado Francisco Ruiz y Samuel Mansino. Las descripciones de esciúridos y lagomorfos las ha realizado César Laplana. Los insectívoros los ha identificado y descrito Marc Furió. Los análisis paleomagnéticos de las secciones de Gorafe, Botardo-1, Negratín y Cigarrón los ha llevado a cabo Oriol Oms. Este último también se ha encargado del contexto geológico del yacimiento de Baza-1, mientras que el apartado de geología del Puerto de la Cadena ha sido realizado por Ignacio Fierro, Jesús Soria, Francisco Pérez-Valera y Juan Alberto Pérez-Valera.

El autor se ha encargado del grueso de las siete publicaciones que forman la tesis, incluyendo los análisis bioestratigráficos, magnetoestratigráficos, paleoambientales y tafonómicos, aunque naturalmente todos los firmantes que figuran en cada uno de los trabajos han participado en su elaboración.

I.2. ESTRUCTURA DE LA TESIS

Esta tesis se presenta como un compendio de siete publicaciones. De acuerdo con la regulación de la Universitat Rovira i Virgili, la tesis debe contener un índice, resumen, introducción/antecedentes/marco teórico, objetivos, métodos/resultados/discusión, conclusiones globales y bibliografía. En este caso, la introducción se corresponde al capítulo I y en él se integran además los objetivos y el marco teórico. Los capítulos II, III y IV se dedican a los antecedentes históricos, el contexto geológico y la metodología de trabajo, respectivamente. La discusión y resultados equivalen a los capítulos que van desde el V al XI, y cada uno de estos a su vez se corresponde con una publicación individual. Éstos han sido ordenados en función de la posición cronológica de los niveles paleontológicos estudiados. Las conclusiones se incluyen en el capítulo XII, tras el que figuran las perspectivas de futuro, referencias bibliográficas de los capítulos I, II, III y IV, y un apéndice. Para evitar confusión, las referencias se encuentran ordenadas de dos formas: los capítulos del V al XI tienen su propio apartado de referencias con el formato de la revista donde se han publicado o se van a publicar, mientras que al final de la tesis hay un apartado donde figuran las citas de los capítulos I al IV.

Las localidades del Mioceno superior de la sección de Romerales son de las más antiguas aquí estudiadas, por lo que su estudio inicia el conjunto de publicaciones (capítulo V). La sección de Sifón de Librilla registra una secuencia continua que contiene niveles desde el Mioceno superior hasta el Plioceno inferior, así el artículo que incluye su estudio se corresponde al capítulo VI. El capítulo VII equivale a la publicación dedicada al yacimiento del Plioceno inferior del Puerto de la Cadena. El siguiente capítulo (VIII) ofrece un estudio sobre Baza-1, otra localidad del Plioceno inferior pero más reciente que la del Puerto de la Cadena. El capítulo IX consta de una biozonación para el Mioceno superior y Plioceno de la cuenca de Guadix-Baza y sirve de nexo de unión bioestratigráfico para la inclusión de los estudios sobre la Gruta-1 de Quibas (Pleistoceno inferior), figurando en los capítulos X y XI.

Los artículos que se han utilizado para la elaboración de la tesis se muestran a continuación por orden cronológico de publicación y/o elaboración:

- P. Piñero, J. Agustí, H.-A. Blain, M. Furió, C. Laplana. **Estado: publicado (2015)**. Biochronological data for the Early Pleistocene site of Quibas (SE Spain) inferred from rodents assemblage. *Geologica Acta* 13 (3), 229–241. **Capítulo X**.

- P. Piñero, J. Agustí, H.-A. Blain, C. Laplana. **Estado: publicado (2016)**. Paleoenvironmental reconstruction of the Early Pleistocene site of Quibas (SE Spain) using a rodent assemblage. *Comptes Rendus Palevol* 15 (6), 659–668. **Capítulo XI**.

- P. Piñero, J. Agustí, M. Furió, C. Laplana. **Estado: publicado (2017)**. Rodents and insectivores from the late Miocene of Romerales (Fortuna Basin, Southern Spain). *Historical Biology*, DOI: 10.1080/08912963.2017.1282476. **Capítulo V**.

- P. Piñero, J. Agustí, O. Oms, I. Fierro, P. Montoya, S. Mansino, F. Ruiz-Sánchez, D.M. Alba, M.T. Alberdi, H.-A. Blain, C. Laplana, J. van der Made, A.V. Mazo, J. Morales, X. Murelaga, A. Pérez-García, F. Pérez-Valera, J.A. Pérez-Valera, P. Sevilla, J.M. Soria, G. Romero. **Estado: publicado (2017)**. Early Pliocene continental vertebrate fauna at Puerto de la Cadena (SE Spain) and its bearing on the marine-continental correlation of the Late Neogene of Eastern Betics. *Palaeogeography, Palaeoclimatology, Palaeoecology* 479, 102–114. **Capítulo VII**.

- P. Piñero, J. Agustí, O. Oms, H.-A. Blain, C. Laplana, S. Ros-Montoya, B. Martínez-Navarro. **Estado: aceptado**. Rodents from Baza-1 (Guadix-Baza Basin, SE Spain). Filling the gap of the early Pliocene succession in the Betics. *Journal of Vertebrate Paleontology*, DOI:10.1080/02724634.2017.1338294. **Capítulo VIII**.

- P. Piñero, J. Agustí. **Estado: en revisión**. The rodent succession in the Sifón de Librilla section (Fortuna Basin, SE Spain): implications for the Mio-Pliocene boundary in the Mediterranean terrestrial record. *Historical Biology*. **Capítulo VI**.

- P. Piñero, J. Agustí, O. Oms. **Estado: enviado**. The late Neogene rodent succession of the Guadix-Baza Basin (Southeastern Spain) and its correlation with Geomagnetic Time Scale. *Palaeontology*. **Capítulo IX**.

Las publicaciones que se incorporan en el apéndice y que complementan las anteriores son las siguientes:

- J. Agustí, I. Lozano-Fernández, O. Oms, P. Piñero, M. Furió, H.-A. Blain, J.M. López-García, B. Martínez-Navarro. 2015. Early to Middle Pleistocene rodent biostratigraphy of the Guadix-Baza Basin (SE Spain). *Quaternary International* 389, 139–147.
- J. Agustí, H.-A. Blain, I. Lozano-Fernández, P. Piñero, O. Oms, M. Furió, A. Blanco, J.M. López-García, R. Sala. 2015. Chronological and environmental context of the first hominin dispersal into Western Europe: The case of Barranco León (Guadix-Baza Basin, SE Spain). *Journal of Human Evolution* 87, 87–94.

I.3. LA FAMILIA MURIDAE ILLIGER, 1811

Los roedores de la familia Muridae Illiger, 1811 pertenecen al suborden Myomorpha Brandt, 1855. Se trata del grupo más abundante y diverso entre los mamíferos modernos, con 730 especies y 150 géneros (Musser y Carleton, 2005), aunque seguido de cerca por la familia Cricetidae Fischer, 1817 (681 especies y 130 géneros). Tanto los cricétidos como los múridos se incluyen dentro de la superfamilia Muroidea Illiger, 1811 (junto a Platacanthomyidae Alston, 1876; Spalacidae Gray, 1821; Calomyscidae Vorontsov y Potapova, 1979; y Nesomyidae Major, 1897). El éxito evolutivo del orden Rodentia Bowdich, 1821 (con el 40% de todos los mamíferos actuales), que integra a los múridos, puede radicar en parte en que se trata de un grupo evolutivamente joven, de forma que sus poblaciones conservan grandes reservas de variabilidad genética aún no aprovechadas. Así quedan expuestas a las fuerzas selectivas de la evolución, ya que los roedores tienen un gran número de descendientes al año, expresando combinaciones genéticas nuevas frente a diferentes condiciones ambientales (Mac Donald, 1991).

La familia Muridae consta de cinco subfamilias (Deomyinae Thomas, 1888; Leimacomyinae Musser y Carleton, 2005; Gerbillinae Gray, 1825; Otomyinae Thomas, 1897; Murinae Illiger, 1811) de las cuales los murinos (ratas y ratones del Viejo Mundo) representan la subfamilia de mamíferos más diversa, con 561 especies y 126 géneros. Debido a la dificultad para determinar relaciones sistemáticas entre los múridos, a pesar de los avances de los últimos años en este campo (Carleton y Musser, 1984; Musser y Carleton, 1993, 2005; Michaux et al., 2001), algunas autoridades consideran este grupo como una superfamilia (Muroidea) con varias subfamilias, y otras como una familia (Muridae) en cuyo caso dichas subfamilias ascienden a nivel de familia. La mayoría de paleontólogos hacen uso de esta última consideración, por lo que en este trabajo seguimos la misma fórmula.

Los múridos son nativos de Eurasia, África y Australia, pero debido a su introducción en el resto de continentes, excepto la Antártida, en la actualidad es un grupo cosmopolita. Sus especies ocupan un amplio rango de hábitats, que van desde bosques húmedos tropicales hasta desiertos áridos y tundra, con una amplia gama de estilos de vida, incluyendo formas semiacuáticas, arbóreas, trepadoras y excavadoras (Jansa y Weksler, 2004). Se trata de especies granívoras, generalistas, u oportunistas según la disponibilidad de alimento. El núcleo de mayor diversidad de géneros y especies actuales está en la India y Australia, una minoría aparece en África, y sólo unos pocos géneros son exclusivamente Paleárticos.

La fórmula dentaria de los múridos responde a 1.0.0.3 (un incisivo y tres molares) tanto para los dientes superiores como para los inferiores. Se trata de una dentición braquidonta (dientes con raíces y coronas bajas), y bunodonta (cúspides redondeadas), aunque al final de algunos linajes como en el caso de *Stephanomys* pasan a hipsodontos. Los molares de los múridos presentan un típico "plan cricétido" (Schaub, 1925), que consiste en cuatro cúspides principales y otras adicionales (anterocono o anterocónido) en la parte anterior de los primeros molares. La dentición superior se caracteriza por la presencia de una fila extra de cúspides completamente funcional que se añade a la parte lingual. Los molares inferiores pueden contar con una tercera fila de cúspides añadida labialmente, aunque en este caso las cúspides son bajas, siendo funcionales en un avanzado estado de desgaste (Freudenthal y Martín Suárez, 1999).

De forma general se acepta que los múridos derivan de los cricétidos, posiblemente de alguna forma de Cricetinae o de Cricetodontinae próxima a *Megacricetodon*. Los cricétidos *Potwarmus* y *Myocricetodon* también se han propuesto como los ancestros de los primeros múridos (Lindsay, 1988; Wessels, 2009; Patnaik, 2014). Los cricétidos fueron los roedores dominantes durante el Oligoceno y la mayor parte del Mioceno en Europa, sin embargo en el Mioceno superior ceden este dominio a los múridos, siendo el grupo hegemónico hasta el final del Plioceno. Los múridos entran en declive en Europa con la entrada de Microtidae (arvicólidos), quienes pasan a ser a finales del Plioceno los roedores dominantes (Freudenthal y Martín Suárez, 1999). La primera referencia literaria de un múrido neógeno corresponde probablemente a Forsyth Major (1873), con la cita de *Mus gaudryi* Dames, 1883.

La primera aparición de un inequívoco múrido tiene lugar en el sur de Asia, hace 13,8 Ma. Se trata de *Antemus*, hallado en las montañas de Siwalik (meseta de Potwar, Pakistán; Jacobs et al., 1990; Jacobs y Flynn, 2005). Los fósiles de múridos de Siwalik representan el mejor y mayor registro de la evolución de esta familia desde su primera aparición, contando con un preciso marco cronológico obtenido por magnetoestratigrafía (Kimura et al., 2013a; 2013b). La abundancia relativa de este grupo aumentó y se aceleró desde la primera aparición de *Antemus* hasta llegar a dominar sobre los cricétidos hace unos 11 Ma, cuando *Progonomys* hace su aparición, reemplazándolos en sus nichos ecológicos de forma exitosa (Jacobs et al., 1989). El registro fósil de los múridos de Siwalik evidencia una serie de cambios graduales en la morfología dental. Esto permite observar la presencia de dos linajes fundamentales derivados a partir de *Antemus*, como resultado de una evolución *in situ* en esta región del norte de Pakistán: el clado *Progonomys* que contiene *Progonomys* y *Mus*, y el clado *Karnimata* que contiene *Karnimata*, *Parapelomys*, y potencialmente *Rattus* (Jacobs, 1978; Jacobs y Downs, 1994; Kimura et al., 2013b; Patnaik, 2014).

En Europa Occidental, el Vallesiense superior se caracteriza por un gran aumento en la diversidad de múridos, aunque los más antiguos de esta región ya se encuentran en el Vallesiense inferior, estando ya algo diversificados. Así, Freudenthal y Martín Suárez (1999) reconocen tres líneas en ese momento: "*Mus*", *Apodemus* y Muridae indet. (éste último de Can Llobateres; Hartenberger y Thaler, 1963; Michaux, 1971; Mein et al., 1993). Aunque la línea de *Progonomys* ya está presente en Turquía durante el Vallesiense inferior, en Europa aparece algo más tarde. El género *Occitanomys* está constatado en el Vallesiense superior (*Occitanomys hispanicus*). En este momento, *Progonomys* da lugar a *Huerzelerimys*. El género "*Mus*" no se conoce en Europa durante el Turoliense, pero sí en otros lugares. En el Turoliense inferior se distinguen al menos dos líneas de *Apodemus*, que derivarán en varios géneros (*Castromys*, *Rhagapodemus*, *Mikrotia*). Durante el Turoliense, *Occitanomys sondaari* da lugar a *Occitanomys adroveri*, que a su vez es el origen del género *Stephanomys*. Al inicio del Turoliense superior, migra a Europa la especie *Occitanomys alcalai*. Hacia mitad del Turoliense superior *Paraethomys* alcanza la Península Ibérica, mientras que hacia el final de este período aparece *Micromys*. *Castillomys* probablemente hace su aparición durante el Rusciniense inferior (Freudenthal y Martín Suárez, 1999).

En la figura I.1 se muestra la evolución de los múridos europeos del Mioceno de acuerdo al esquema de Freudenthal y Martín Suárez (1999). Lo cierto es que este esquema queda algo anticuado en base a nuestros resultados, ya que por medio del estudio de las sucesiones de múridos de la sección de Sifón de Librilla, se proponen algunas variaciones respecto a las relaciones filogenéticas entre miembros de los géneros *Stephanomys* y *Apodemus*, y se adelanta la primera aparición de algunos taxones como *Occitanomys alcalai* y *Apodemus gorafensis* (ver capítulo VI).

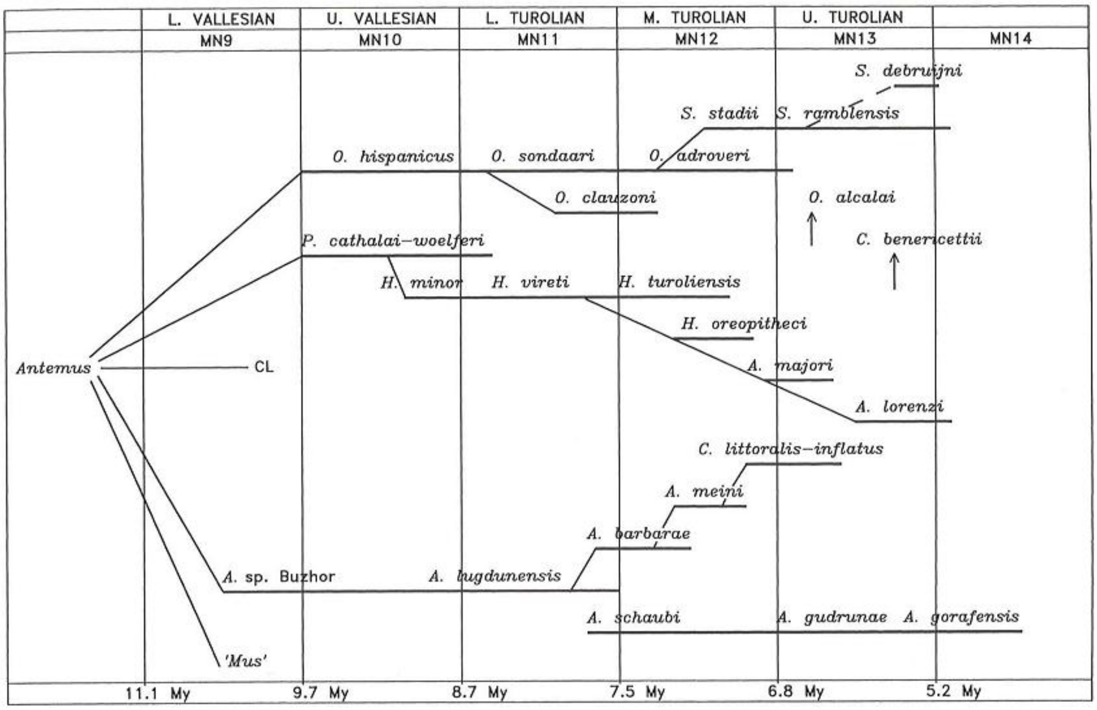

Figura I.1: Evolución de la familia Muridae del Mioceno europeo. Las flechas indican migraciones. Tomado de Freudenthal y Martín Suárez (1999).

I.4. IMPORTANCIA DE LOS MÚRIDOS EN PALEONTOLOGÍA

El análisis de los múridos permite llevar a cabo múltiples estudios en paleontología. Esto se debe a que dicha familia (y los pequeños mamíferos en general) presentan ciertas características que permiten extraer información muy valiosa del pasado: rápida evolución, requerimientos climáticos y ambientales específicos, amplia distribución geográfica, y alta representación en los yacimientos. Para su análisis se hace uso principalmente de dientes, ya que los restos craneales y mandibulares son los que más información presentan a nivel de especie. Se trata además del elemento que mejor y en más cantidad se suele conservar. Al mismo tiempo, la morfología dental registra perfectamente los cambios a lo largo de la evolución de los linajes.

Los múridos son fundamentales para la bioestratigrafía del Mioceno superior y el Plioceno, el intervalo de tiempo mejor estudiado en esta tesis. Este grupo ofrece también pistas importantes sobre los intercambios faunísticos entre Asia, Europa y África, como es el caso de la dispersión de *Paraethomys* desde África a Europa poco antes del inicio de la Crisis de Salinidad del Messiniense (Bruijn, 1974; Jaeger et al., 1975; Agustí et al., 2006; Gibert et al., 2013). Su diversidad además es útil para las reconstrucciones paleoambientales (ver capítulos V, VIII y XI). Los micromamíferos en general presentan un triple valor en el estudio paleontológico (Chaline y Alcalde, 1983):

1. Marcadores estratigráficos. Permiten el establecimiento de una cronología relativa (especialmente los roedores) con un alto grado de resolución.

2. Indicadores paleoecológicos y paleoambientales. Ante cambios ambientales, responden a través de la adaptación, de lo contrario, supone la extinción.

3. Valor evolutivo. A lo largo de una serie estratigráfica es posible el estudio de la evolución de los micromamíferos.

I.4.1. Marcadores estratigráficos

Los múridos constituyen una herramienta imprescindible para el estudio bioestratigráfico de medios continentales del Mioceno superior y Plioceno, y por tanto para la datación de sedimentos de este intervalo temporal (van de Weerd, 1976; Mein et al., 1990; Martín Suárez y Freudenthal, 1998; García-Alix, 2008a; Minwer-Barakat et al., 2012a; Mansino et al., 2017). Además de las altas tasas evolutivas y rapidez de diversificación de este exitoso grupo de roedores, su cosmopolitismo y presencia en una amplia variedad de terrenos les convierte en excelentes herramientas de correlación bioestratigráfica, permitiendo establecer dataciones relativas en las secuencias donde se encuentran. Estos cambios evolutivos quedan plasmados en su dentición. Así, la variación de la dentición a través de una secuencia estratigráfica permite determinar y calibrar la evolución de las especies y de sus poblaciones (Cuenca-Bescós et al., 1998).

I.4.2. Indicadores paleoecológicos y paleoambientales

De forma general, los micromamíferos son más efectivos que los macromamíferos para llevar a cabo inferencias paleoambientales. Esto es así porque presentan unos requerimientos ecológicos más específicos que los de los grandes mamíferos, tienen un alto grado de especialización como consecuencia de sus restricciones energéticas y fisiológicas, y además suele haber una mayor abundancia de restos fósiles (Hernández Fernández, 2001). Los pequeños mamíferos son muy sensibles a las condiciones climáticas, presentando una alta adaptabilidad a hábitats concretos, de forma que ante cambios climáticos se pueden ver obligados a migrar a otras zonas (Guillem, 1995). Su pequeño tamaño (sensibilidad hacia cambios de temperatura) y alta tasa metabólica se traducen en unas necesidades energéticas y fisiológicas concretas, y puesto que la competencia interespecífica puede llegar a ser muy compleja por el gran número de especies, el rango de distribución geográfica puede ser limitado. Con ello, el estudio de las asociaciones de pequeños mamíferos permite realizar una inferencia sobre las características climáticas y de vegetación del lugar donde se encuentra la muestra en el momento de la formación del yacimiento (Minwer-Barakat, 2005); así como una reconstrucción de los cambios climáticos y paisajísticos a lo largo de la secuencia estratigráfica como ya se ha comentado.

Los roedores en particular se han usado ampliamente como indicadores paleoclimáticos y paleoecológicos (Martín-Suárez et al., 2001; Minwer-Barakat et al., 2005; Montuire et al., 2006; García-Alix et al., 2008b; entre otros). No obstante, tal y como ponen de manifiesto García-Alix (2015), García-Alix et al. (2013) y Freudenthal et al. (2014), en ocasiones las inferencias paleoecológicas y paleoambientales (especialmente las condiciones de humedad) se pueden ver afectadas por la paleogeografía del área, registrando en muchos casos cambios físicos del paisaje y no tanto tendencias climáticas globales o regionales.

I.4.3. Valor evolutivo

Los múridos, y los pequeños mamíferos en general, evolucionan a un ritmo rápido, gradual, y más o menos constante. Estos cambios evolutivos se muestran en su morfología, y en el caso de los múridos y resto de roedores, en su dentición. La evolución de las especies y sus poblaciones puede estudiarse y calibrarse por medio de los mencionados cambios en los dientes a lo largo de una secuencia estratigráfica (Cuenca-Bescós et al., 1998). En este caso, la potente y continua sección de Sifón de Librilla, con hasta ocho niveles ricos en microfauna extendidos a lo largo de más de 2 Ma, nos ofrece una oportunidad única para establecer relaciones filogenéticas entre diferentes taxones (capítulo VI).

I.5. CARACTERES DIAGNÓSTICOS DE LOS MÚRIDOS

A continuación se expone una serie de caracteres que se consideran diagnósticos para la identificación de los múridos (para la nomenclatura consultar el capítulo IV):

1. Talla. El uso de la talla como carácter diagnóstico ha sido en general limitado por razones obvias. No obstante, la talla ha jugado un papel importante en la definición de algunas líneas, por ejemplo en el caso de *Huerzelerimys*. En general, una talla elevada es un carácter derivado, aunque disminuciones en la talla se han descrito dentro de géneros como *Occitanomys* (van de Weerd, 1976).

2. Anchura relativa de los molares. En diversas líneas se observa una tendencia a desarrollar molares superiores más anchos. Este es el caso, por ejemplo, de algunas especies incluidas en el género *Huerzelerimys*. La condición primitiva parece ser la posesión de molares estrechos, tal y como se observa en *Progonomys* o en *Apodemus* primitivos.

3. Posición del t1. Durante mucho tiempo se consideró que la posición adelantada del t1, tal y como se observa en *Progonomys cathalai*, constituía la condición primitiva. Ello convertía a *Occitanomys*, *Stephanomys*, etc. en géneros con una morfología derivada. Jacobs (1978) ha sido uno de los primeros en mostrar que por el contrario la posición retrasada del t1 es la condición primitiva. La posición adelantada del t1, tal como se

observa en *Progonomys cathalai*, *Huerzelerimys vireti* y *Apodemus lugduniensis,* constituye por tanto un carácter derivado.

4. Forma del t1. Un t1 de forma redondeada sin conexión con el t4 constituye un carácter que en general se encuentra en la mayor parte de las especies de múridos. La presencia de un pequeño espolón posterior dirigido hacia el t4 constituye por tanto un carácter derivado que se encuentra en algunas especies incluidas en *Huerzelerimys* y en todas las formas relacionadas con *Occitanomys*.

5. Conexión t6-t9. A la conexión entre el t6 y el t9 se le da una importancia fundamental en la clasificación de los múridos europeos. Sin embargo, en una serie de especies constituye un carácter altamente variable. Se trata de un carácter sobrevalorado que ha aparecido independientemente en diferentes líneas (*Parapodemus, Huerzelerimys,* etc.).

6. Anchura tubérculos centrales. En algunas especies de géneros como *Huerzelerimys* se observa la tendencia a un gran desarrollo de los tubérculos centrales del M1.

7. t12. Un t12 bien desarrollado constituye una simplesiomorfía de los géneros *Progonomys, Apodemus* y *Castromys.* La tendencia a reducir esta cúspide se observa en mayor o menor grado en diferentes especies de los géneros *Occitanomys, Huerzelerimys* y *Paraethomys.*

8. Cúspides oblicuas. En el género *Golunda* y en formas relacionadas con *Occitanomys*, las cúspides suelen ser más oblicuas que en otros taxones.

9. Talla del t9 en el M2. La reducción del t9 aparece ligada a la reducción del t12 en los M2 de *Paraethomys*.

10. Forma del t8 en el M3. Se observan dos estadios, sencillo y doble. El estadio sencillo es general en la mayor parte de formas europeas. Por el contrario, el estadio doble aparece en algunos representantes asiáticos.

11. Tubérculo medio anterior. El desarrollo del tma se observa en algunas especies de los géneros *Progonomys, Karnimata, Huerzelerimys,* aparte de los géneros *Parapodemus* y *Apodemus*.

12. Cresta longitudinal. El desarrollo de la cresta longitudinal se observa especialmente en las formas derivadas de *Occitanomys*, pero también aparece tímidamente en otros géneros como *Huerzelerimys* y *Castromys*.

13. Cíngulo labial. Este carácter aparece desarrollado en mayor o menor grado en la mayor parte de formas europeas, especialmente *Parapodemus* y *Apodemus*, y falta o es reducido en *Castromys* y *Paraethomys.*

14. Forma del tubérculo posterior. Este cíngulo es voluminoso en la mayor parte de géneros y tiende a reducirse en *Paraethomys*. Se ha usado además para diferenciar líneas evolutivas de *Stephanomys*.

I.6. LOCALIZACIÓN GEOGRÁFICA

En las siguientes líneas se detalla la situación geográfica de aquellas localidades cuyas asociaciones de múridos se han descrito en el presente trabajo (figura I.2).

I.6.1. Sección de Sifón de Librilla

La sección de Sifón de Librilla (cuenca de Fortuna) se localiza en la Sierra del Cura. El acceso a su parte más baja se sitúa a unos 2 km al norte de Librilla (Murcia), en el cruce entre la carretera C-2 y unas instalaciones del canal del trasvase Tajo-Segura. De base a techo, la serie discurre desde este punto hacia el noreste. Las coordenadas del punto de partida corresponden a 37° 54′ 18″ N, 1° 21′ 41″ O.

I.6.2. Sección de Romerales

La serie de Romerales (cuenca de Fortuna) tenía su acceso a través de una carretera en dirección a Fortuna, poco después de abandonar Molina de Segura (Murcia). Desafortunadamente, tras la extracción del sedimento a finales de la década de los 90, la mayor parte de la sección desapareció como consecuencia de la construcción de un puente durante las obras de la autovía A30. Las coordenadas de localización geográfica son 38° 4′ 21″ N, 1° 12′ 10″ O.

I.6.3. Yacimiento del Puerto de la Cadena

El yacimiento del Puerto de la Cadena (cuenca de Murcia-Carrascoy) se encuentra a unos 8 km al SSO de Murcia capital y a 2,5 km al sur de la pedanía de El Palmar, muy próximo al lugar denominado como Venta de La Paloma y dentro del Parque Regional de Carrascoy-El Valle. Para acceder a él se debe tomar la autovía de Murcia (A-30) en dirección a Cartagena y desviarse por la salida La Paloma-Nonduermas que conecta con la nacional N-301 (Carretera de Madrid-Cartagena). Una vez tomada la salida se debe pasar por debajo de dicha autovía. Las coordenadas de localización son 37° 55' 9" N, 1° 9' 41" O, con una altitud de 160 m.s.n.m.

I.6.4. Yacimiento de Baza-1

El yacimiento de Baza-1 (cuenca de Guadix-Baza) se localiza muy cerca del casco urbano de la ciudad de Baza (Granada), en el barranco conocido como Seguidillas-Cuesta del Francés (Las Arrodeas), a escasos 50 m de un depósito de agua (Ros-Montoya, 2010; Martínez-Navarro et al., 2015; Piñero et al., 2016). Las coordenadas geográficas corresponden a 37° 29' 00" N, 2° 47' 05" O.

I.6.5. Yacimiento de Quibas

El yacimiento paleontológico de Quibas está situado en la ladera sureste del extremo oriental de la Sierra de Quibas, en el paraje denominado Collado del Rey, al pie de una cantera abandonada (municipio de Abanilla, Murcia). El núcleo urbano más importante de la zona de estudio es la pedanía de Barinas, a 5 km al sureste del yacimiento. Otras pedanías próximas son Cañada de la Leña al SE, Cañada del Trigo al NE, La Zarza al NO y Peña Zafra al O. Las coordenadas geográficas del yacimiento son 1° 4' 42" O, 38° 18' 51" N; mientras que la cota está en 669 m.s.n.m.

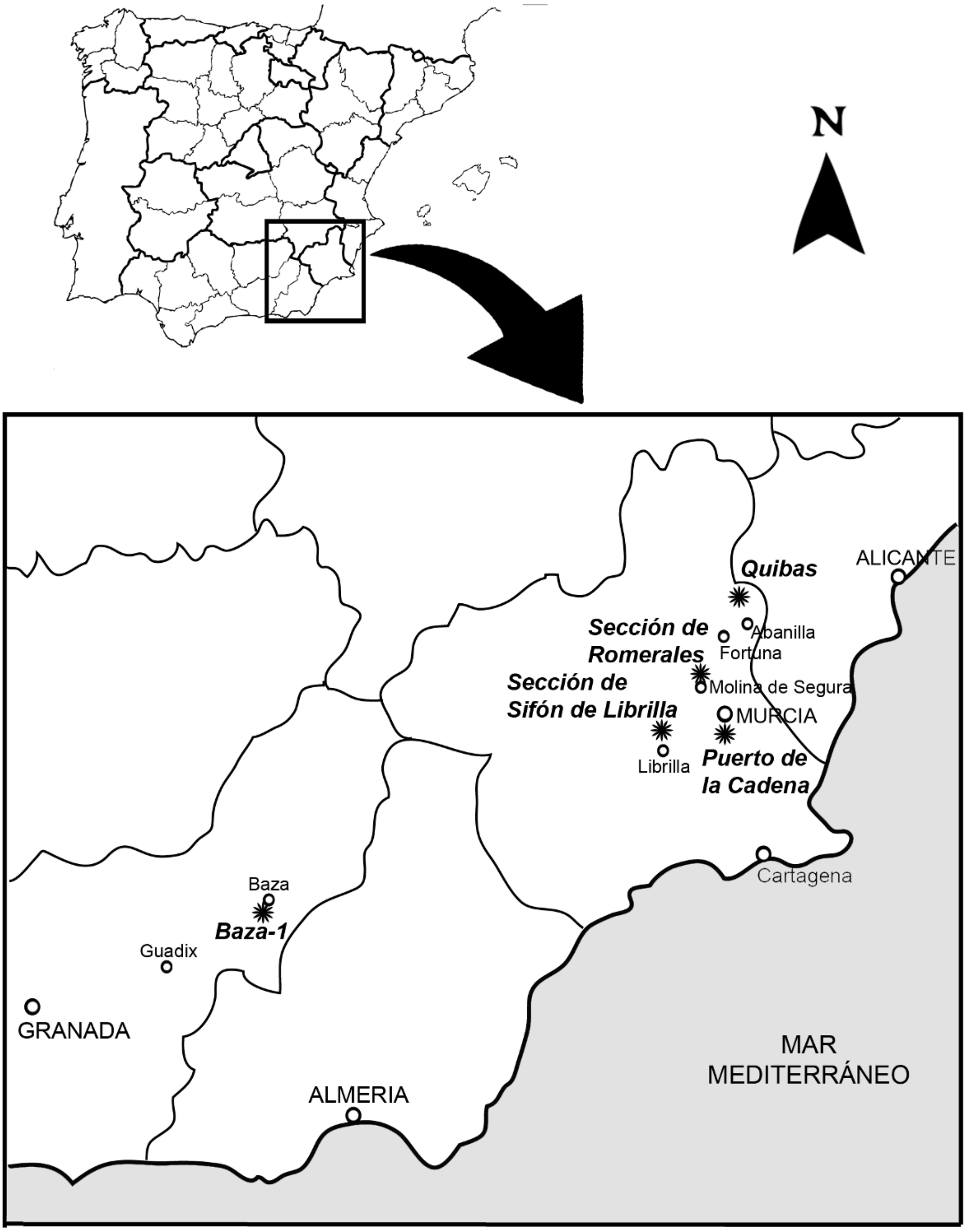

Figura I.2: Localización geográfica de los yacimientos y secciones estudiados.

I.7. OBJETIVOS

El principal objetivo de esta tesis se centra en la Paleontología Sistemática de las paleocomunidades de múridos del Mioceno superior, Plioceno y Pleistoceno inferior del sureste de la Península Ibérica (cuenca de Fortuna, cuenca de Guadix-Baza, cuenca de Murcia-Carrascoy y Sierra de Quibas). La finalidad por tanto es proporcionar un estudio taxonómico completo de los miembros de esta familia, actualizando en la medida de lo posible las relaciones filogenéticas de las especies identificadas. Este propósito principal se complementa con otra serie de metas considerando las asociaciones completas de roedores que han proporcionado los niveles estudiados, y en algunos casos teniendo en cuenta también los representantes de insectívoros y lagomorfos:

1. Datación relativa de las localidades estudiadas en base a su contenido faunístico, y realización de correlaciones bioestratigráficas con otros yacimientos de la Península Ibérica por comparación de las asociaciones de micromamíferos.

2. Realización de correlaciones magnetobioestratigráficas para aquellas secciones que disponen de un análisis paleomagnético, por medio de la conjunción con la bioestratigrafía.

3. Ajuste de la distribución temporal de los roedores que aparecen en secciones con información magnetoestratigráfica.

4. Establecer un esquema magnetobioestratigráfico para el Mioceno superior y Plioceno de la cuenca de Guadix-Baza por medio de la propuesta de biozonas bien calibradas basadas en asociaciones de roedores.

5. Reconstrucción de las condiciones ambientales (hábitat, temperatura, humedad) dominantes en el momento de la formación de algunos yacimientos.

II. ANTECEDENTES HISTÓRICOS

II.1. CUENCA DE FORTUNA

El primer estudio sobre el registro continental en la cuenca de Fortuna lo llevan a cabo Montenat y Crusafont (1970), donde se da a conocer la localidad de Librilla (Turoliense superior). Tras el descubrimiento de este yacimiento, se publicaron una serie de trabajos sobre sus restos fósiles de vertebrados (Montenat, 1973; Bruijn et al., 1975; Montenat et al., 1975; Alberdi et al., 1981).

Otra localidad clásica de la cuenca de Fortuna es Casa del Acero, muy próxima a la sección del Chícamo (Garcés et al., 2001; Agustí et al., 2006). Este yacimiento del Turoliense medio (MN12, Tortoniense superior) se publicó por primera vez en Agustí et al. (1981), trabajo al que le siguieron otra serie de publicaciones (Agustí, 1986a; Pons-Moyà, 1987a). La primera síntesis geológica y bioestratigráfica de los depósitos continentales de la cuenca de Fortuna la realizó Agustí et al. (1983a), trabajo en el que se incluye la serie de Molina de Segura (Salinas de Molina en Agustí et al., 2006).

La cuenca de Fortuna presenta un registro de depósitos evaporíticos sobre una serie regresiva marina y bajo una secuencia continental. La datación de estos paquetes de evaporitas ha sido objeto de una amplia discusión, concluyendo finalmente que se trata de depósitos del Tortoniense y no del Messiniense (Santisteban, 1981; Santisteban y Taberner, 1983; Muller y Hsu, 1987; Muller y Schrader, 1989; Ortí et al., 1993; Mankiewicz, 1995; Playà et al., 1995, 1999; Dinarès-Turell et al., 1999; Krijgsman et al., 2000; Tent-Manclús et al., 2008).

Garcés et al. (1998, 2001) establecen un marco cronológico para el relleno sedimentario de la cuenca de Fortuna. Para ello se ofrece un detallado estudio magnetoestratigráfico en el que se incluyen los paquetes continentales desde el Turoliense medio (MN12) hasta el Rusciniense inferior (MN14). En estos, se estudian las secciones de Barranco de la Salada, Río Chícamo, El Chorrico, Salinas de Molina y Sifón de Librilla.

En base al registro de vertebrados fósiles y la información magnetoestratigráfica obtenida en los trabajos anteriores, Agustí et al. (1999a, 2006) ofrecen una cronología bastante precisa de los principales eventos de mamíferos (MME, *Messinian Mammalian Event*) que tuvieron lugar en el Mediterráneo occidental entre hace 4,5 y 7,6 Ma. Estos autores publican además listas faunísticas de muchos niveles localizados en la cuenca de Fortuna. Sin embargo, la información taxonómica es muy limitada.

Hasta el momento, hay muy pocos trabajos que ofrezcan una información taxonómica precisa sobre los fósiles de pequeños mamíferos de la cuenca de Fortuna. Bajo este precepto, se realizan los capítulos V y VI. Entre los trabajos con descripciones sistemáticas se cuenta con Agustí et al. (1981), quienes estudian la fauna de microvertebrados de Casa del Acero; Agustí (1986a) que examina los cricétidos de esta misma localidad, definiendo las especies *Kowalskia meini* e *Hispanomys adroveri*; Agustí y Llenas (1996) que definen el género *Parasaidomys* para la nueva especie *P. kowalskii* en Molina de Segura-1; y Furió y Agustí (2017) que incluyen el estudio de los insectívoros de las series de Sifón de Librilla y El Chorrico – Salinas de Molina.

II.2. CUENCA DE GUADIX-BAZA

Desde los primeros trabajos geológicos con enfoque científico llevados a cabo en la cuenca de Guadix-Baza (Fallot et al., 1950, 1967) se han publicado multitud de estudios enfocados en esta región. De hecho, de entre las áreas estudiadas, es con diferencia la que mayor producción científica ha proporcionado hasta el momento. Entre los trabajos estratigráficos y sedimentológicos se deben citar Vera (1969, 1970a, 1970b), Marín (1971), Bruijn (1974), López-Garrido y Vera (1974), Peña (1975, 1979, 1985), Rodríguez Fernández (1976, 1982), Rodríguez Fernández et al. (1984), García Aguilar (1986), Soria et al. (1987), Alonso Diago (1989, 1991), Viseras y Fernández (1988), Viseras (1991), Pla (2009, 2010), García Aguilar (2010a), y Pla et al. (2011). Otros trabajos que cabe mencionar sobre la estratigrafía y evolución paleogeográfica de la cuenca son Fernández et al. (1996a), Soria et al. (1998, 1999) y Viseras et al. (2004, 2005).

Se han realizado también estudios sobre los modelos sedimentarios de los sistemas deposicionales que rellenan la cuenca (Fernández et al., 1991, 1993; Viseras y Fernández, 1994, 1995; Viseras et al., 1998, 2003; Soria et al., 2003; García-García et al., 2006), así como otra serie de trabajos sobre magnetoestratigrafía (Garcés, 1993; Garcés et al., 1996, 1997; Oms, 1998; Oms et al., 1996, 1999, 2000a, 2003, 2010, 2011; Agustí et al., 1999b; Agustí y Oms, 2002; Queralt et al., 2003; Gibert et al., 2006, 2007; Scott et al., 2007; Álvarez et al., 2015) y otros métodos de datación basados en técnicas radiométricas y de resonancia de spin electrónico (Duval, 2008; Duval et al., 2011, 2012a, 2012b).

La evolución de la cuenca de Guadix-Baza durante la etapa de sedimentación continental, con atención a la ciclicidad lacustre, se ha estudiado en García Aguilar (1997, 2010b), García Aguilar y Martín (2000), y García Aguilar y Palmqvist (2012). Discusiones sobre el momento de continentalización de la cuenca corresponden a Hüsing et al. (2010, 2012) y Minwer-Barakat et al. (2012b). También hay un grupo de contribuciones sobre geomorfología y tectónica (Estévez et al., 1976; Estévez y Sanz de Galdeano, 1983; Goy et al., 1989; Calvache et al., 1996; Calvache y Viseras, 1997; Heddi et al., 1999; Soria, 1999; Vandekerckhove et al., 2000, 2003; Espigares et al., 2003; Gibert et al., 2005; Díaz-Hernández y Julià, 2006; entre otros) y sobre geoquímica de los sedimentos continentales (Sebastián, 1979; Anadón y Juliá, 1990; Anadón et al., 1994).

No obstante, la paleontología es la rama que mayor interés científico ha despertado en la cuenca de Guadix-Baza, especialmente la disciplina referida al estudio de los vertebrados. De hecho, la cuenca cuenta con más de 100 yacimientos paleontológicos de mamíferos (Agustí, 1986b; Agustí y Moyá-Solá, 1991), formando parte de potentes secciones que se superponen estratigráficamente. Así, esta zona presenta uno de los mejores registros de mamíferos continentales de Europa desde el Mioceno superior hasta el Pleistoceno (especialmente para este último).

Los primeros estudios sobre mamíferos fósiles de esta área vieron la luz con Fallot et al. (1950) y Aguirre (1963). El primer trabajo monográfico sobre restos de mamíferos de la zona corresponde a Ruiz Bustos (1976), estudiando la fauna de Cúllar de Baza I. En los años 80 se descubrieron numerosos yacimientos con fósiles de grandes mamíferos que propiciaron la publicación de varios trabajos (Cuevas et al., 1984; Mazo et al., 1985; Alonso Diago, 1986; Martín Penela, 1987). Hacia finales de esta década, se publica una monografía dedicada al estudio geológico y paleontológico del yacimiento de Venta Micena (Moyá-Solá et al., 1987). Dos años más tarde, se edita otra monografía (Alberdi y Bonadonna, 1989) recopilando una gran cantidad de información sobre los fósiles de la cuenca de Guadix-Baza conocidos hasta esa fecha. Posteriormente, vieron la luz otros yacimientos como Barranco León-5 y Fuente Nueva-3 (Turq et al., 1996) que presumen de haber ofrecido las evidencias de ocupación humana más antiguas de Europa Occidental (Martínez-Navarro et al., 1997; Oms et al., 2000a; Toro et al., 2011; Duval et al., 2012a), incluyendo un diente de leche humano recuperado de Barranco León-5 (Toro et al., 2013). La importante información ofrecida por estos yacimientos motivó la publicación de dos monografías recopilando la información sedimentológica, estratigráfica, faunística y arqueológica conocida hasta el momento (Toro et al., 2003, 2010). Otro de los yacimientos de vertebrados que ha propiciado la publicación de numerosos trabajos es Fonelas P-1 (Arribas et al., 2001, 2004, 2008; Viseras et al., 2006 Garrido, 2006; Arribas y Garrido, 2007).

Tras el descubrimiento de Venta Micena, con el polémico hallazgo de restos óseos asignados al género *Homo* (Gibert et al., 1983, 1994), se sucedieron multitud de trabajos discutiendo la identificación de estos fragmentos (Agustí y Moyà-Solà, 1987; Campillo, 1989; Gibert et al., 1989, 1998; García-Olivares et al., 1989; Borja et al., 1992, 1997; Martínez-Navarro, 2002, 2008; Campillo et al., 2006; entre otros). También hay numerosas investigaciones sobre la fauna tanto de macromamíferos como de micromamíferos (Moyà-Solà et al., 1981; Agustí et al., 1983b, 1987a; Alberdi y Ruiz Bustos, 1985; Marín, 1987; Menéndez, 1987; Moyà-Solà, 1987; Pons-Moyà, 1987b; Santafé-Llopis y Casanovas-Cladellas, 1987; Martín Suárez, 1988; Martínez Navarro, 1991; Palmqvist et al., 1996, 1999, 2003; Arribas y Palmqvist, 1998, 1999; Guerrero-Alba y Palmqvist, 1998; Palmqvist y Arribas, 2001; Martínez-Navarro et al., 2009). Espigares (2010) y Ros-Montoya (2010) elaboran sus tesis doctorales centrándose el primero en el estudio tafonómico de yacimientos de la cuenca de Guadix-Baza, y el segundo en el análisis de proboscídeos, incorporando ambos trabajos material de Fuente Nueva-3, Barraco León-5 y Venta Micena, entre otros yacimientos. El yacimiento de La Solana del Zamborino también ha sido objeto de interés de muchos investigadores (Botella et al., 1975a, 1975b; Casas et al., 1975; Porta, 1975; García-García y Rosino-Sánchez, 1983; Martín-Penela, 1983, 1987, 1988; Martínez-Fernández y López-Reyes, 1998; Toro et al., 2007). Van der Made y Morales (2012) contribuyen al conocimiento del jiráfido de Huélago. Recientemente, Martínez-Navarro et al. (2015) presentan el yacimiento de Baza-1, mientras que Ros-Montoya et al. (en prensa) publican la fauna de grandes mamíferos librada por el mismo.

Las primeras referencias sobre fósiles de micromamíferos en la cuenca de Guadix-Baza son los trabajos de Bruijn (1973, 1974), donde se da a conocer la presencia de varios roedores en las localidades de Gorafe-1, Gorafe-2 y Baza. Éste último nivel, a pesar de haber sido denominado como Baza, no se corresponde con la localidad de Baza-1 estudiada en esta tesis, sino que probablemente se corresponde con alguno de los niveles de la sección de Zújar (comunicación personal, Bruijn). A estas publicaciones se suma un importante número de trabajos llevados a cabo durante la década de los 80 en los que se analiza la fauna de nuevos yacimientos (Agustí, 1983, 1986b, 1986c, 1990; Agustí et al., 1983b, 1986, 1987a, 1987b, 1987c; Agustí y Martín Suárez, 1984; Ruiz Bustos, 1990a; Ruiz Bustos et al., 1984). Sin embargo, el estudio más extenso del momento sobre los micromamíferos de esta cuenca corresponde a la tesis doctoral de Martín Suárez (1988). En ésta se hacen descripciones de las faunas fósiles procedentes de varias secciones de la cuenca (Botardo, Cañada del Castaño, Galera, Alquería, Orce, Venta Micena, Loma Quemada y Gorafe), se aporta un esquema bioestratigráfico completo de la cuenca y se ofrece la primera interpretación paleoecológica de esta región basada en micromamíferos. Al año siguiente de la publicación de esta tesis, Sesé (1989) incluye nueva información sobre las localidades de micromamíferos de esta cuenca. A este trabajo le sigue la tesis de Castillo Ruiz (1990), donde se incluye un análisis detallado de roedores fósiles procedentes de una serie de rellenos kársticos del margen occidental de la subcuenca de Guadix. Se trata del yacimiento de Moreda, aunque efectivamente dado su origen kárstico no se puede considerar parte del relleno sedimentario de esta cuenca. A parte de Castillo Ruiz (1990), otros trabajos incluyen en sus análisis piezas procedentes de esta localidad (Bruijn, 1973; Cordy, 1976; Gmelig-Meyling y Michaux, 1983; Ruiz Bustos, 1986; entre otros).

Ya entrada la década de los 90, se descubren nuevas localidades con fósiles de micromamíferos en esta región (Ruiz Bustos, 1991, 1992; Soria y Ruiz Bustos, 1991, 1992; Guerra Merchán y Ruiz Bustos, 1991, 1992; Guerra Merchán et al., 1991). Se aportan interpretaciones paleoambientales (Sesé, 1991; Ruiz Bustos, 1990b) y revisiones de las biozonaciones basadas en pequeños mamíferos (Agustí y Martín Suárez, 1994; Ruiz Bustos, 1995). También se estudian nuevos niveles en las secciones de Galera y Zújar (Garcés et al., 1997; Agustí et al., 1997, 2001; Oms et al., 1999; Agustí et al., 2001).

Una vez entrado el presente siglo, se publican revisiones de las asociaciones faunísticas de esta región (Sesé et al., 2001; Ruiz Bustos, 2002). Se publican trabajos sobre los pequeños vertebrados de Fuente Nueva-3 y Barranco León-5 (Agustí y Madurell, 2003; Blain, 2003; Furió, 2003, 2010; Blain y Bailón, 2010; Agustí et al., 2010a). Blain et al. (2011) aportan una reconstrucción paleoambiental y paleoclimática de Barranco León-5 y Fuente Nueva-3 basándose en el estudio de la paleoherpetofauna. Agustí et al. (2015a) establecen una biozonación del Pleistoceno de esta cuenca calibrada mediante correlaciones magnetoestratigráficas. Agustí et al. (2015b) ofrecen un contexto ambiental y cronológico del yacimiento de Barranco León en base a la fauna de microvertebrados.

Los trabajos de Minwer-Barakat et al. (2004, 2005) suponen un adelanto a los contenidos de la tesis de Minwer-Barakat (2005), la cual constituye un trabajo en profundidad sobre las faunas de micromamíferos del sector central de la subcuenca de Guadix. Hasta el momento, la mayor parte de los estudios sobre micromamíferos se basaban principalmente en yacimientos del sector oriental de la cuenca (subcuenca de Baza), de acuerdo a su mayor registro fósil. El sector occidental (subcuenca de Guadix) sin embargo, es generalmente más pobre en contenido fósil por el predominio de sedimentos fluviales. En este contexto, Minwer-Barakat (2005) ofrece un análisis completo sobre las faunas de pequeños mamíferos procedentes de varias secciones (Negratín, Rambla de Chimeneas, Loma de las Yeguas y Tollo de Chiclana), aportando además un esquema bioestratigráfico de la subcuenca de Guadix, un estudio paleoecológico, e información sobre los primeros niveles con fósiles tras la continentalización de la cuenca (Negratín-1, Rambla de Chimeneas-3). A partir de datos tomados de esta tesis, hubo una aportación de numerosos trabajos científicos (Minwer-Barakat et al., 2007, 2008a, 2008b, 2008c, 2009a, 2009b, 2010, 2012b; García-Alix et al., 2007, 2008c).

Las tesis de Furió (2007) y De Marfá (2009) ofrecen descripciones de restos de insectívoros y lagomorfos respectivamente de varios yacimientos de la cuenca de Guadix-Baza. Furió et al. (2007) contribuyen al conocimiento de *Myosorex* fuera de África incorporando datos de Tollo de Chiclana. Laplana y Blain (2008) aportan información acerca de los microvertebrados de Fonelas P-1. Blain (2009) incluye en su tesis el análisis de la herpetofauna fósil de multitud de localidades de esta cuenca. Martín-Suárez et al. (2012) presentan un análisis detallado de la microfauna del Cortijo de la Piedra. Agustí et al. (2010b) sintetizan la sucesión de pequeños vertebrados de la región de Orce. Los pequeños vertebrados del yacimiento de Barranco Conejos se estudian en Agustí et al. (2013). Anchelergues Tarraco et al. (2015) contribuyen al conocimiento de los múridos de Loma Quemada-1.

Por último Piñero et al. (2016) publican por primera vez un listado de los micromamíferos del yacimiento de Baza-1, que sirve de preámbulo para la realización del capítulo VIII de esta tesis. De forma paralela, Piñero y Agustí (2015) presentan una biozonación del Mioceno superior y Plioceno de la cuenca de Guadix-Baza basada en asociaciones de roedores que actúa como adelanto del capítulo IX. La abundancia de yacimientos convierte a la cuenca de Guadix-Baza en un objetivo prioritario para el establecimiento de escalas bioestratigráficas del Plio-Pleistoceno en Europa (Oms et al., 1999). De hecho, se han propuesto numerosas biozonaciones para dicha cuenca, habiendo sido la mayoría definidas en base al estudio de micromamíferos de diferentes yacimientos (Agustí, 1986b, 1990; Agustí et al., 1987a; Martín Suárez, 1988; Ruiz Bustos, 1990; Agustí y Martín Suárez, 1994; Oms et al., 2000b; Gibert et al., 2007; Minwer-Barakat et al., 2012a; Agustí et al., 2015a).

Las escalas bioestratigráficas establecidas para el Plioceno de esta cuenca son relativamente antiguas, de forma que algunos de los taxones usados para la definición de las mismas han sido revisados con posterioridad. Esto dificulta el uso de estas escalas locales para asignar algunos yacimientos descubiertos más recientemente, con la excepción de la biozonación de Minwer-Barakat et al. (2012a), que sin embargo se centra exclusivamente en el sector central de la subcuenca de Guadix. Este escenario ha motivado la realización del capítulo IX en el que por primera vez se establece un esquema bioestratigráfico del Mioceno superior y Plioceno calibrado en base a correlaciones magnetoestratigráficas para toda la cuenca.

II.3. ENTORNO DEL PUERTO DE LA CADENA

En este apartado se resume la información que se conoce acerca de los yacimientos paleontológicos de vertebrados hallados en el entorno más próximo al yacimiento del Puerto de la Cadena. En primer lugar, cabe mencionar que el yacimiento se descubrió en el año 2008 como consecuencia de la construcción de la autovía MU-31, en las proximidades del Puerto de la Cadena. En ese momento se pudo recuperar una gran cantidad de restos de vertebrados fósiles gracias a la colaboración entre el Ministerio de Fomento, la empresa adjudicataria de la obra y un equipo de paleontólogos formados por personal de la Universidad de Murcia y de la Fundación Cidaris-Museo Paleontológico de Elche. Posteriormente, en los años 2009, 2010 y 2011, se realizaron varias campañas de excavación sistemática en el marco de un proyecto de investigación de la Fundación Séneca, dirigido por el Dr. Mancheño, y en las que se recuperaron más de 2000 fósiles. En julio del año 2013, el yacimiento del Puerto de la Cadena se declara como Bien de Interés Cultural (BIC) bajo la categoría de Zona Paleontológica, poniendo de manifiesto la excepcionalidad del mismo (Fierro et al., 2015).

Los primeros hallazgos de vertebrados fósiles continentales en el área del Puerto de la Cadena los llevó a cabo el geólogo francés Christian Montenat, a finales de los años 60, durante la realización de su tesis doctoral sobre las formaciones del Neógeno y Cuaternario del Levante Español (Provincias de Alicante y de Murcia). Así, se dieron a conocer los yacimientos de La Alberca y La Paloma (Montenat, 1973). Los primeros datos publicados aparecen en Montenat y Crusafont (1970) y, posteriormente, en Montenat (1973) y en Mein et al. (1973). En estos trabajos, se atribuye una posición estratigráfica que oscila entre el Vallesiense (Mioceno superior) y la base del Plioceno. Pero trabajos posteriores (Aguirre et al., 1974 y Bruijn et al., 1975) sitúan su edad en la parte final del Mioceno, correlacionándola con el yacimiento de El Arquillo (Teruel).

Los antecedentes son importantes y muy cercanos. No obstante, se deben cuidar las extrapolaciones de información puesto que las relaciones estratigráficas entre los yacimientos de La Alberca, La Paloma y el Puerto de la Cadena no están claras. Aún así, las facies que describen Montenat y Crusafont (1970), parecen corresponderse con las afectadas por las obras de la autovía MU-31. La relación es aún más clara con los materiales de la serie del Barranco del Cigarrón (Mancheño et al., 2001), correspondiendo a la misma unidad sedimentaria (Unidad del Cigarrón).

En relación al yacimiento de La Paloma, Gibert et al. (1987) ofrecen su localización a 1 km al sur de la localidad de El Palmar y a 4 km al SO de Murcia. Estos escasos datos hacen muy difícil la ubicación del lugar, ya que además no cuadran correctamente (si la localización fuese a 1 km al sur de El Palmar, la distancia desde Murcia no podría ser de tan sólo 4 km puesto que entre El Palmar y Murcia ya existe una distancia de 5,5 km). La descripción de Montenat (1973) sitúa este lugar al sur de la Venta de la Paloma, en la Rambla del Puerto. Montenat y Crusafont (1970) indican la presencia de dos especies de artiodáctilos, por una parte restos de dentición de cérvido (Cervidae indet.) y por otra una mandíbula de jirafa del grupo de los sivaterinos, atribuida a la especie *Decennatherium pachecoi*.

La ubicación del yacimiento de La Alberca vuelve a ser incierta. Gibert et al. (1987) lo sitúan justo al sur de la pedanía con el mismo nombre y a 1500 m del yacimiento de La

Paloma. Comentarios personales del Dr. Agustí lo sitúan cerca del caserío del Tío Calavera. Se trata de un yacimiento con mucha más riqueza faunística que el yacimiento de La Paloma. Montenat y Crusafont (1970) ofrecen el primer listado taxonómico, que ha sido revisado posteriormente (Morales, 1984; López Martínez, 1989; Freudenthal et al., 1998; Pérez-García et al., 2011): *Cricetus kormosi* (=*Apocricetus alberti*), *Stephanomys medius* (=*Stephanomys dubari*, *Stephanomys cordii*), *Ruscinomys lasallei*, *Paraethomys miocaenicus* (=*Paraethomys meini*), *Castillomys* sp., *Eliomys* sp., *Hispanolagus crusafonti* (=*Trischizolagus crusafonti*), *Prolagus michauxi*, *Percrocuta minor*, *Plioviverrops guerini*, *Hipparion concudense*, *Dicerorhinus schleiermacheri*, *Birgerbohlinia* sp., Cervidae indet., Bovidae indet., *Titanochelon* cf. *bolivari*, y Trionychinae indet. En base a la asociación faunística, tanto La Alberca como La Paloma se correlacionaron con la MN13 (Aguirre et al., 1976; Morales, 1984), y más recientemente con el Ventiense (Morales et al., 2013).

Además del caparazón de tortuga gigante recuperado de la localidad de La Alberca (reasignado por Adán Pérez en el capítulo VII a *Titanochelon* sp.), se han recuperado otros especímenes en los alrededores del Puerto de la Cadena. Los primeros restos fueron hallados en la década de los 90 por miembros de la Asociación Cultural Paleontológica Murciana, aunque no tuvieron repercusión científica. Otro ejemplo es el caparazón de un espécimen adulto recuperado del Barranco del Cigarrón (localizado al oeste del yacimiento del Puerto de la Cadena), y que Mancheño et al. (2001) lo asigna preliminarmente a '*Testudo*' *bolivari*, lo cual se discute también en el capítulo VII. Mancheño et al. (2001) incluye además un estudio estratigráfico y micropaleontológico del Barranco del Cigarrón.

Otro caso es el caparazón incompleto recuperado del yacimiento de Autovía, hasta el momento inédito (Murelaga et al., 2007; Romero et al., 2007a, 2007b). En 2005, miembros de la Asociación Cultural Paleontológica Murciana, localizan este gran ejemplar de tortuga gigante seccionado (debido a las obras en el talud de un ramal de la autovía Murcia-Cartagena) en la pedanía de El Palmar. Se situaba en la cuneta del carril de incorporación a la autovía A-30 dirección Murcia, en la salida Nonduermas-La Paloma. Este lugar se encuentra cercano al Barranco del Cigarrón, y forma parte de las intervenciones en las obras de la autovía MU-31. Tras la restauración del fósil, se comprobó que podría tratarse del mismo taxón de La Alberca (Murelaga et al., 2007). En el yacimiento de Autovía, no sólo se recuperó el caparazón de tortuga, sino también varias piezas dentarias y fragmentos de huesos largos y otros restos óseos que por su mal estado de conservación no han podido ser identificados

(Romero et al., 2007a). Los primeros resultados sobre las intervenciones paleontológicas en el entorno del Puerto de la Cadena como consecuencia de las obras de la autovía se sintetizan en Romero y Fierro (2010). El último trabajo previo a la publicación que se presenta en esta tesis es Mancheño et al. (2013), que ofrece un listado preliminar de la fauna de vertebrados hallada en el yacimiento del Puerto de la Cadena.

II.4. YACIMIENTO DE QUIBAS

El Grupo cultural Paleontológico de Elche "Cidaris", a finales del año 1994 recibió una serie de restos óseos fósiles, que fueron descubiertos por casualidad en una pequeña cantera abandonada en la Sierra de Quibas por parte de unos excursionistas (Mancheño et al., 2003a). Por lo tanto se decidió llevar a cabo una prospección en la zona en la que participaron miembros de esta asociación, investigadores de la Universidad de Valencia, e investigadores del Museo Nacional de Ciencias Naturales (CSIC, Madrid), localizando el yacimiento. Los materiales recogidos de la superficie fueron estudiados dos años después, y publicados en los trabajos Montoya et al. (1999, 2001).

En el año 1999, este hallazgo se comunicó a la Dirección General de Cultura de la Comunidad Autónoma de Murcia. Un año después, el Departamento de Química Agrícola, Geología y Edafología de la Universidad de Murcia solicitó un permiso de actuación paleontológica en el yacimiento (Mancheño et al., 2003a), asumiendo la dirección el Dr. Miguel Ángel Mancheño. De esta forma se iniciaron las primeras excavaciones sistemáticas. Junto con la mayoría de investigadores de la primera etapa y nuevas incorporaciones, la Fundación Séneca de la Comunidad Autónoma de Murcia concedió dos Proyectos de Investigación para los trienios 2002-2004 y 2005-2007, lo que facilitó el proceso de investigación.

Debido a la indiscutible importancia del yacimiento de Quibas para el conocimiento del Pleistoceno inferior, así como su accesibilidad (se sitúa en torno a diversas canteras, facilitando su estudio), la Dirección General de Cultura de la Comunidad Autónoma de Murcia decidió catalogarlo en agosto de 2005 como Bien de Interés Cultural (BIC) bajo la denominación de Zona Arqueológica, incluido dentro de la Ley de Patrimonio Histórico de 1985. Este hecho impulsó el interés por avanzar en la investigación de este yacimiento desde diferentes perspectivas: estudios en paleontología sistemática; estudios en tafonomía; un estudio geológico de toda la sierra de Quibas y del yacimiento en sí; un estudio geofísico de los alrededores del yacimiento; un estudio paleomagnético; un estudio polínico; y otro de isótopos estables de carbono y oxígeno para obtener datos paleoclimáticos.

En el año 2009, el proyecto de estudio del yacimiento de Quibas quedó paralizado. No obstante, tras cinco años de inactividad, en el año 2014 se llevó a cabo una valoración del estado del yacimiento para analizar las posibilidades de estudio. Con esto se da comienzo a una nueva etapa de trabajo, con un equipo formado por personal del Institut de Paleoecologia Humana i Evolució Social (IPHES), Museo Nacional de Ciencias Naturales (MNCN), Universidad Complutense de Madrid (UCM) y Museo Arqueológico Regional de la Comunidad de Madrid (MAR). Así, se inician una serie de campañas de excavación dirigidas por el Dr. Jordi Agustí, el Dr. Antonio Rosas y el autor de la presente tesis, contando con muy buenas perspectivas de continuidad futura.

Como se ha citado, los primeros trabajos publicados relativos al yacimiento de Quibas fueron Montoya et al. (1999, 2001), donde se analiza la fauna del yacimiento y se elaboran las listas de los taxones identificados. Montoya et al. (2001) numeran hasta 61 especies diferentes. La mayor parte de los estudios que se han realizado posteriormente, se han centrado en el análisis taxonómico de macromamíferos. De esta forma, Carlos-Calero et al. (2004) incrementan la lista faunística incorporando un cánido, asignándose en Carlos-Calero (2006a) a *Vulpes praeglacialis*. Carlos-Calero et al. (2006b) y Van der Made et al. (2008) analizan la presencia de *Capra alba* en Quibas. Alba et al. (2008, 2011) estudian la presencia de *Macaca sylvanus*, identificándose como *Macaca sylvanus florentina*. Crégut-Bonnoure (2002) describe una nueva especie, *Praeovibos mediterraneus*, identificándola en el yacimiento de Quibas. Piñero y Alberdi (2015) hacen un estudio de los caballos que aparecen en el yacimiento diferenciando por primera vez dos especies: *Equus altidens* y *Equus suessenbornensis*. Pérez-García et al. (2015) confirman la presencia de *Testudo hermanni*, posicionándose como el representante más antiguo de esta especie en la Península Ibérica. En relación a la microfauna, Blain et al. (2014) determinan la última aparición de agámidos de Europa Occidental en Quibas. El yacimiento de Quibas también ha ofrecido dos trabajos fin de máster: Cuadros (2010) y Piñero (2012). Este último sirvió de preámbulo para la realización de los capítulos X y XI del presente trabajo.

No obstante, se han realizado otra serie de trabajos cuyo objetivo se centra en el propio yacimiento. Así, Mancheño et al. (2003a) hacen un análisis sobre el interés patrimonial del yacimiento y establecen una valoración. Rodríguez-Estrella et al. (2004) determinan las características geológicas de la sierra de Quibas, y su relación con el yacimiento. Durán et al. (2004) estudian una secuencia espeleotemática del mismo. Por otra parte, se ha colaborado en diferentes ediciones de las Jornadas de Patrimonio Histórico y Arqueología de la Región de Murcia (Mancheño et al., 2003b, 2004 y 2006), Jornadas de Patrimonio Cultural de la Región de Murcia (Romero et al., 2009), Sociedad Española de Paleontología (Carlos-Calero et al., 2004), así como en el Encuentro de Jóvenes Investigadores en Paleontología (Piñero et al., 2015). También se ha participado en congresos con Mancheño et al. (2003c) y Mancheño et al. (2009).

III. CONTEXTO GEOLÓGICO

III.1. CONTEXTO GEOLÓGICO REGIONAL

El sur de la Península Ibérica está constituido en su mayor parte por la Cordillera Bética, con una longitud de unos 600 km y una anchura de 200 km. Es en esta cordillera donde se localizan todos los yacimientos estudiados en este trabajo. Junto con la del Rift y la del Tell (Marruecos, Argelia, Túnez) forman el segmento más occidental del orógeno Alpino mediterráneo. Esta cadena montañosa se formó tras el cierre del océano Thetys por la convergencia de las placas Euroasiática, Africana e Ibérica (Dewey et al., 1989; Sanz de Galdeano, 1990; Soria et al., 1999).

Los materiales sedimentarios marinos del margen sur de la meseta se plegaron debido al choque de la Microplaca de Alborán, que cabalgó sobre ellos, de forma que dichos materiales sedimentarios constituyeron las Zonas Externas de la Cordillera Bética (Fontboté, 1970; Comas y García-Dueñas, 1988), y los materiales del Dominio de Alborán formaron las Zonas Internas (Andrieux et al., 1971; Balanyá y García-Dueñas, 1987). De esta forma, en la Cordillera Bética se pueden diferenciar dos dominios estructurales:

1. Zonas Externas o Dominio Sudibérico. Están situadas al norte y se encuentran en posición parautóctona. Se trata de materiales mesozoicos y cenozoicos cabalgados y plegados sin metamorfizar que proceden del margen meridional de la placa Ibérica. Representan el paleomargen Sudibérico deformado (Comas y García Dueñas, 1988), y se estructuran en tres subdominios paleogeográficos (García Hernández et al., 1980): la Zona Subbética al sur, la Zona Prebética al norte, y las Unidades Intermedias entre ambas.

2. Zonas Internas o Dominio de Alborán. Se encuentran al sur y están formadas por un apilamiento alóctono de unidades mayores formado a base de materiales fundamentalmente metamórficos (de base a techo, complejos Nevado-Filábride, Alpujárride y Maláguide-Dorsal), que se separan por cabalgamientos.

Las Zonas Internas y las Zonas Externas sufrieron procesos de colisión y convergencia que finalizaron en el Mioceno inferior engrosando significativamente la corteza. Cabe citar también otro dominio alóctono, el denominado Complejo del Campo de Gibraltar (o Surco de los "Flysch") que se encuentra rodeando gran parte de las Zonas Internas (Martín Algarra, 1987).

Después de la colisión entre las Zonas Externas y las Zonas Internas se originaron numerosas cuencas durante el Mioceno medio en las que se dio lugar a rellenos de depósitos correspondientes al Mioceno superior, Plioceno y Pleistoceno. El relleno se inicia en el Tortoniense con materiales marinos, y durante el Messiniense y Plioceno la retirada del mar dio paso al depósito de una gran cantidad de sedimentos continentales. De acuerdo a la posición estructural de las diferentes cuencas neógeno-cuaternarias de la Cordillera Bética (Viseras et al., 2004), se distingue una cuenca de antepaís (cuenca del Guadalquivir) y una serie de cuencas intramontañosas asentadas en el interior de la cordillera, entre las que se encuentran las cuencas de Guadix-Baza, Fortuna y Murcia-Carrascoy (figura III.1).

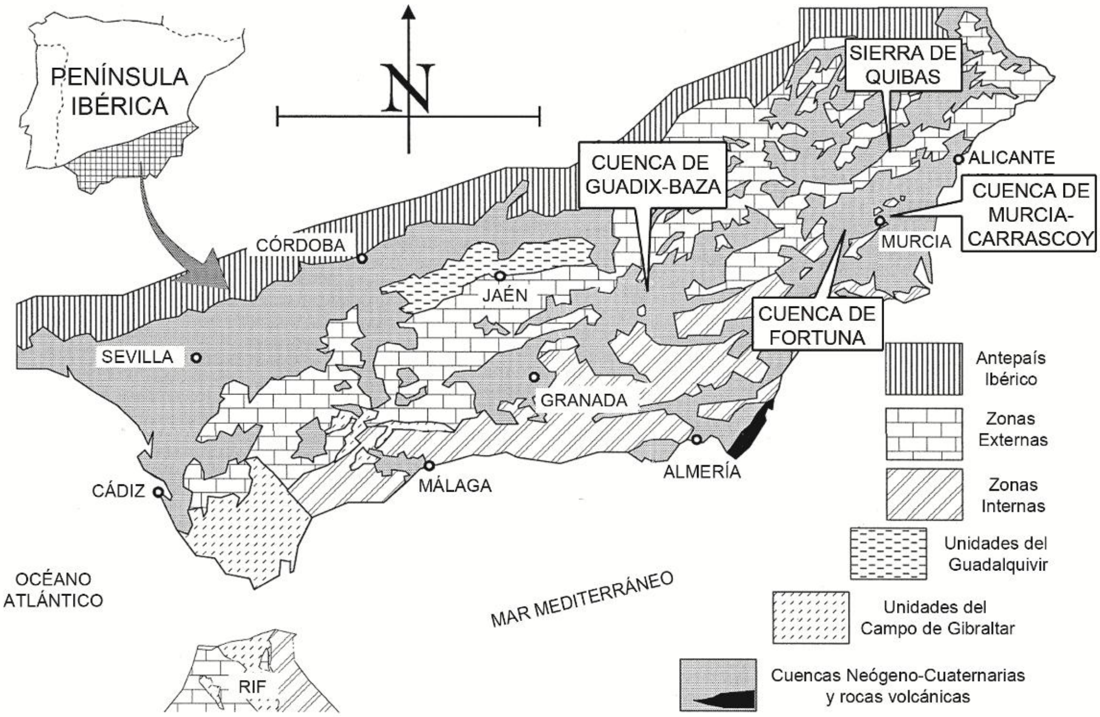

Figura III.1: Mapa geológico de la Cordillera Bética. Tomado de Soria et al. (1999).

Desde el punto de vista tectónico, durante el Mioceno inferior comienza una fase extensiva que resulta en un adelgazamiento de la corteza dando lugar a la formación de la cuenca de Alborán (Comas et al., 1992; García Dueñas et al., 1992). Esta fase es seguida durante el Mioceno medio y la parte basal del Mioceno superior (Tortoniense) por una etapa de *rifting* con dirección NE-SO (oblicua al mar de Alborán). Posteriormente, aunque también durante el Tortoniense, comienza una contracción generalizada de dirección N-S (Martínez del Olmo et al., 2006). No obstante, lo más probable es que la extensión acaecida durante el

Mioceno medio y superior fuese más responsable de la creación e individualización de cuencas que la compresión posterior, cuyo papel más llamativo es la actual topografía, los accidentes de desgarre y la elevación de las Zonas Internas.

Las cuencas neógeno-cuaternarias de las Cordilleras Béticas ofrecen un marco privilegiado para el estudio de la evolución de la cuenca Mediterránea occidental durante el Mioceno superior y el Plioceno. Durante el Mioceno superior, el Mediterráneo estaba conectado con el océano Atlántico a través de dos corredores: el Corredor Nord-Bético y el Corredor del Rift (norte de Marruecos). La conjunción de procesos neotectónicos y procesos paleoclimáticos ligados a fluctuaciones glacio-eustáticas del nivel global de los océanos, contribuyeron progresivamente al cierre de ambos corredores durante el Messiniense. Esto llevó al completo aislamiento de la cuenca Mediterránea resultando en una serie de acontecimientos que cambiaron la paleogeografía de dicha cuenca. El evento más importante es la llamada Crisis de Salinidad del Messiniense, que tuvo lugar entre hace 5,33 y 5,97 Ma (Krijgsman et al., 1999) y que desencadenó la práctica desecación del mar Mediterráneo hasta su transformación en un desierto salino. Los mecanismos que desencadenaron la desconexión entre el Mediterráneo y el Atlántico, así como la reinundación posterior de la cuenca Mediterránea, son aún hoy objeto de controversia (Clauzon et al., 1996; Riding et al., 1998; Krijgsman et al., 1999; Braga et al., 2006; Manzi et al., 2013; Pérez-Asensio et al., 2013).

III.2. CUENCA DE FORTUNA

La cuenca de Fortuna constituye una de las numerosas depresiones intramontañosas originadas durante la formación de la Cordillera Bética. Esta cuenca se localiza en la zona de contacto entre las Zonas Externas y las Zonas Internas de la Cordillera Bética oriental (figura III.2), y su origen se remonta al Tortoniense superior. La cuenca está delimitada por dos zonas de cizalla importantes: la falla Norbética y la falla de Alhama de Murcia, cuya actuación a partir del Tortoniense generó un espacio de acomodación a lo largo de un surco estrecho de orientación NO-SE, en el contexto de la convergencia entre las placas Africana e Ibérica (De Larouzière et al., 1988; Montenat et al., 1990; Sanz de Galdeano, 1990; Sanz de Galdeano y Vera, 1992; Garcés et al., 2001; Agustí et al., 2006). El relleno sedimentario de la cuenca de Fortuna se puede agrupar en tres unidades principales (Garcés et al., 1998; 2001):

1. Unidad marina inferior. Se trata de una sucesión marina de aproximadamente 500 m de espesor. En las zonas centrales de la cuenca está representada por potentes unidades de margas pelágicas y turbiditas, mientras que en las zonas marginales del sur y este de la cuenca pasan a calizas arrecifales y bioclásticas así como a sucesiones siliciclásticas aluviales deltaicas. Datos magnetoestratigráficos de las cuencas de Lorca y Fortuna (Krijgsman et al., 2000) confirman una edad Tortoniense superior para esta unidad, tal y como sugirió Montenat (1973).

2. Unidad marina transicional evaporítica. Sobre las margas de la unidad anterior, se asienta una secuencia regresiva de unos 200 m de espesor. Está formada por margas yesíferas, diatomitas, yesos masivos y depósitos terrígenos, variando su grado de desarrollo en los diferentes sectores de la cuenca. Así, en la Formación Río Chícamo (sur de Abanilla) se distinguen dos tramos (Ortí et al., 1993): una unidad de yesos inferior (Yesos Chícamo) y una secuencia superior de ciclos diatomíticos-evaporíticos (Ciclos Chícamo). Las evaporitas de la cuenca de Fortuna se han correlacionado generalmente con la Crisis de Salinidad del Messiniense (Müller y Hsü, 1987; Lukowski, 1988; Dinarès-Turrel et al., 1999). Sin embargo, Krijgsman et al. (2000) demostraron que realmente corresponden a una fase Tortoniense local de restricción de la cuenca, afectando tanto a la cuenca de Fortuna como a la de Lorca.

3. Unidad continental superior. Se trata de una sucesión aluvial-lacustre de más de 1000 m de espesor. Su parte inferior es lutítica, intercalándose tramos con yesos y calizas, mientras que hacia la parte superior pasa progresivamente a ser más conglomerática. En la parte media de esta secuencia se intercalan sedimentos marinos someros como consecuencia de una transgresión muy efímera hacia el Plioceno basal. Los niveles inferiores de estas unidades continentales han aportado fósiles de vertebrados del Turoliense medio (MN12) en la localidad de Casa del Acero (Agustí et al., 1981), y Barranco de la Salada-141 (Garcés et al., 2001; Agustí et al., 2006). El resto de unidades contienen un registro rico en vertebrados fósiles del Turoliense superior (MN13) e incluso Rusciniense inferior (MN14), tal y como se analiza en los capítulos V y VI para las secciones de Romerales y Sifón de Librilla.

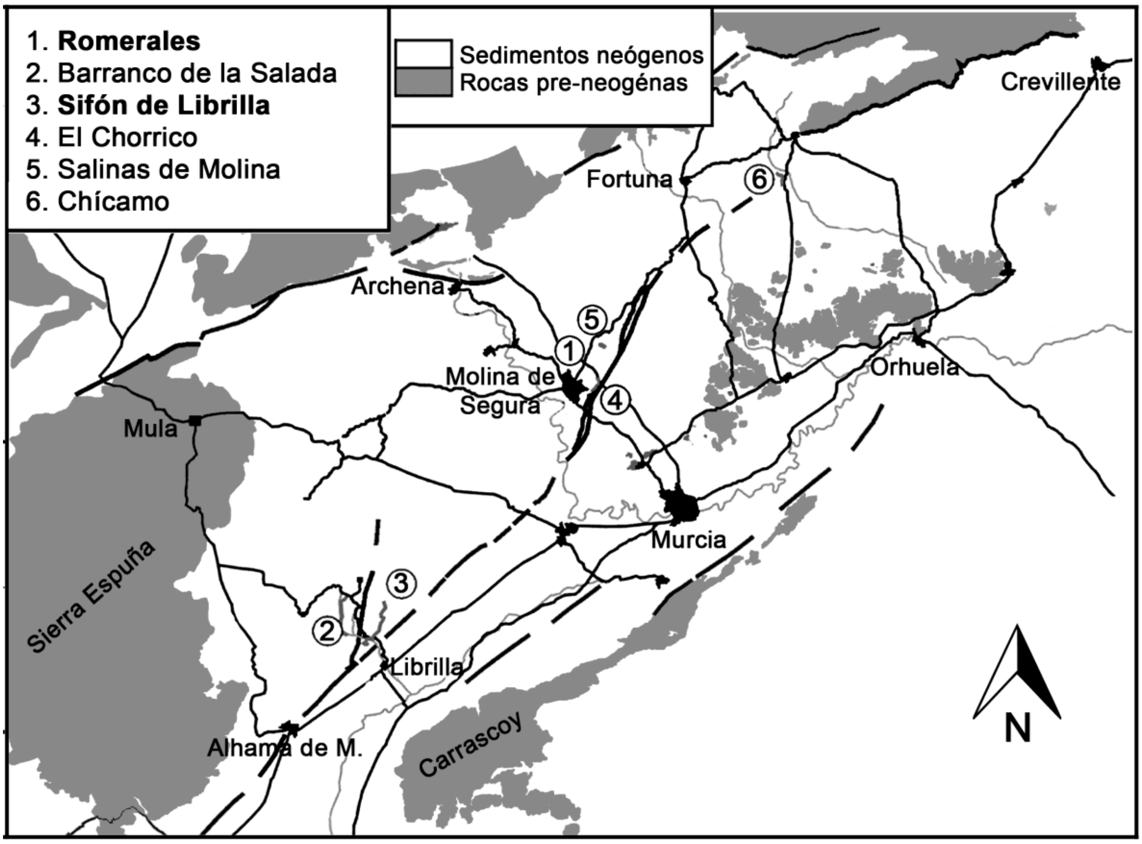

Figura III.2: Localización geográfica y geológica de la cuenca de Fortuna.

La cuenca de Fortuna sufrió una rápida subsidencia inicial y una transgresión marina durante el Tortoniense. El levantamiento de las Zonas Internas béticas que tuvo lugar durante el Tortoniense superior desencadenó el aislamiento progresivo de la cuenca de Fortuna, desconectándola de la cuenca Mediterránea. La transición marino-continental tortoniense tuvo lugar hace unos 7,6 Ma, permitiendo un registro continuo de sedimentos continentales hasta los 4,8 Ma (Garcés et al., 1998; 2001). El temprano confinamiento y la consecuente precipitación de evaporitas en la cuenca de Fortuna durante el Tortoniense superior descartan la inclusión de la cuenca en el hipotético corredor Bético durante el Messiniense superior (Müller y Hsü, 1987). A esta precipitación de evaporitas se la conoce como “Crisis de Salinidad Tortoniense” afectando únicamente a las cuencas de Fortuna y Lorca (Krijgsman et al., 2000).

La evolución sedimentaria de la cuenca de Fortuna es singular entre las cuencas neógenas de las Cordilleras Béticas, sólo guardando un paralelismo con la vecina cuenca de Lorca. A diferencia de otras cuencas como la de Guadix-Baza o Granada, la cuenca de Fortuna continuó sufriendo una fuerte subsidencia, permitiendo la acumulación de más de 600 m de sedimentos durante el Messiniense, y propiciando el registro de un pulso corto transgresivo en el Plioceno basal hacia el margen sureste de la cuenca (Mein et al., 1973). La bajada del nivel general que tuvo lugar durante la Crisis de Salinidad del Messiniense queda registrada en la cuenca de Fortuna a través de una incisión en valle seguida de una progradación repentina de gravas.

Durante el Messiniense, la cuenca de Fortuna pasó a ser una cuenca confinada pobremente drenada. En ocasiones, las áreas distales propiciaban el desarrollo de ambientes lacustres someros y palustres (Agustí et al., 2006). Los sedimentos resultantes han aportado ricas asociaciones de pequeños mamíferos del Turoliense medio (MN12) y superior (MN13) y del Rusciniense inferior (MN14), a lo largo de numerosas secciones continentales continuas: Barranco de la Salada, Río Chícamo, El Chorrico (donde se integra Romerales), Salinas de Molina y Sifón de Librilla (figura III.2).

III.2.1. Sección de Sifón de Librilla

La serie de Sifón de Librilla aflora a lo largo de la parte oriental del sinclinal que aparece al norte de la población de Librilla (figura III.3). La secuencia muestra un cierto buzamiento de unos 25-30 grados hacia el oeste. Esta sección está formada por cerca de 800 m de capas rojas de origen aluvial donde las lutitas rojas se alternan con margas grises de origen palustre, que es donde se concentra la mayor parte de los niveles con contenido en fósiles de microfauna, junto con abundantes restos de conchas de gasterópodos límnicos. La serie incluye ocho niveles fosilíferos que han aportado restos de micromamíferos con una edad que va desde la base del Turoliense superior en un estado previo a la entrada de *Paraethomys* (SIF-1, SIF-3 y SIF-52) y Turoliense superior con *Paraethomys* (SIF-61 y SIF-79), hasta la base del Rusciniense inferior (SIF-413, SIF-430 y SIF-P). La sección se puede agrupar en cuatro unidades diferentes (Garcés et al., 1998; 2001), siendo de base a techo (figura III.4):

1. Una unidad aluvial-palustre de 400 m de espesor que consta de margas palustres grises ricas en materia orgánica, sedimentos aluviales rojos cíclicos, y en menor medida de calizas lacustres. Los restos fósiles de mamíferos indican una edad MN13, e incluye los niveles de SIF-1, SIF-3, SIF-52, SIF-61 y SIF-79 (figura III.5).

2. Una unidad de conglomerados progradante de 30 m de espesor. Se trata de una prolongación de la cuenca por medio de cuñas aluviales alimentadas desde el margen occidental de la cuenca (Zonas Externas).

3. Una unidad marina somera de 30 m de espesor que consta de areniscas grises y margas con bivalvos, equinodermos y foraminíferos bentónicos. Estos últimos indican medios marinos someros y una edad pliocena basal. Esta unidad representa la transgresión marina del inicio del Plioceno tras el restablecimiento de las condiciones marinas en el Mediterráneo después de la Crisis de Salinidad del Messiniense.

4. Un miembro aluvial superior de 350 m de espesor, formado por conglomerados canalizados y limos rojos. La composición de los clastos vuelve a indicar una procedencia del margen occidental de la cuenca. Las incisiones de los canales y las curvas indican una dirección NE-SO de las paleocorrientes. La asociación de mamíferos fósiles indica una edad MN14, e incluye los niveles de SIF-413, SIF-430 y SIF-P.

III.2.2. Sección de Romerales

La sección de Romerales, con 116 m de potencia, se integra en la parte baja de la sección de El Chorrico (figura III.6). Contiene varios niveles fosilíferos ricos en restos de vertebrados. La mayoría de ellos aportan restos fragmentados de grandes mamíferos, mientras que tres contienen microvertebrados que indican una edad Turoliense superior (MN13) previa a la llegada de *Paraethomys*. Entre los niveles que contienen restos de pequeños mamíferos, ROM-2B (figura III.7) es el más bajo, situado a 36 m desde la base de la serie. Se trata de un nivel rico en gránulos de carbón, fragmentos de gasterópodos y bivalvos, y restos fragmentados de grandes mamíferos como *Hipparion*. Los fósiles de microvertebrados son abundantes y presentan un buen estado de conservación. La matriz está formada por arenas grises y ocres. Inmediatamente por encima de este nivel se encuentra ROM-2C, formado por arcillas oscuras y fragmentos de gasterópodos. Se trata del nivel más rico en microfauna. Los ejemplares presentan un estado de conservación excelente. El nivel más alto con contenido en microfauna es ROM-3A (figura III.7). Se trata del nivel más pobre en fósiles de los tres, y consta de arcillas grises y restos de huesos fragmentados de grandes mamíferos.

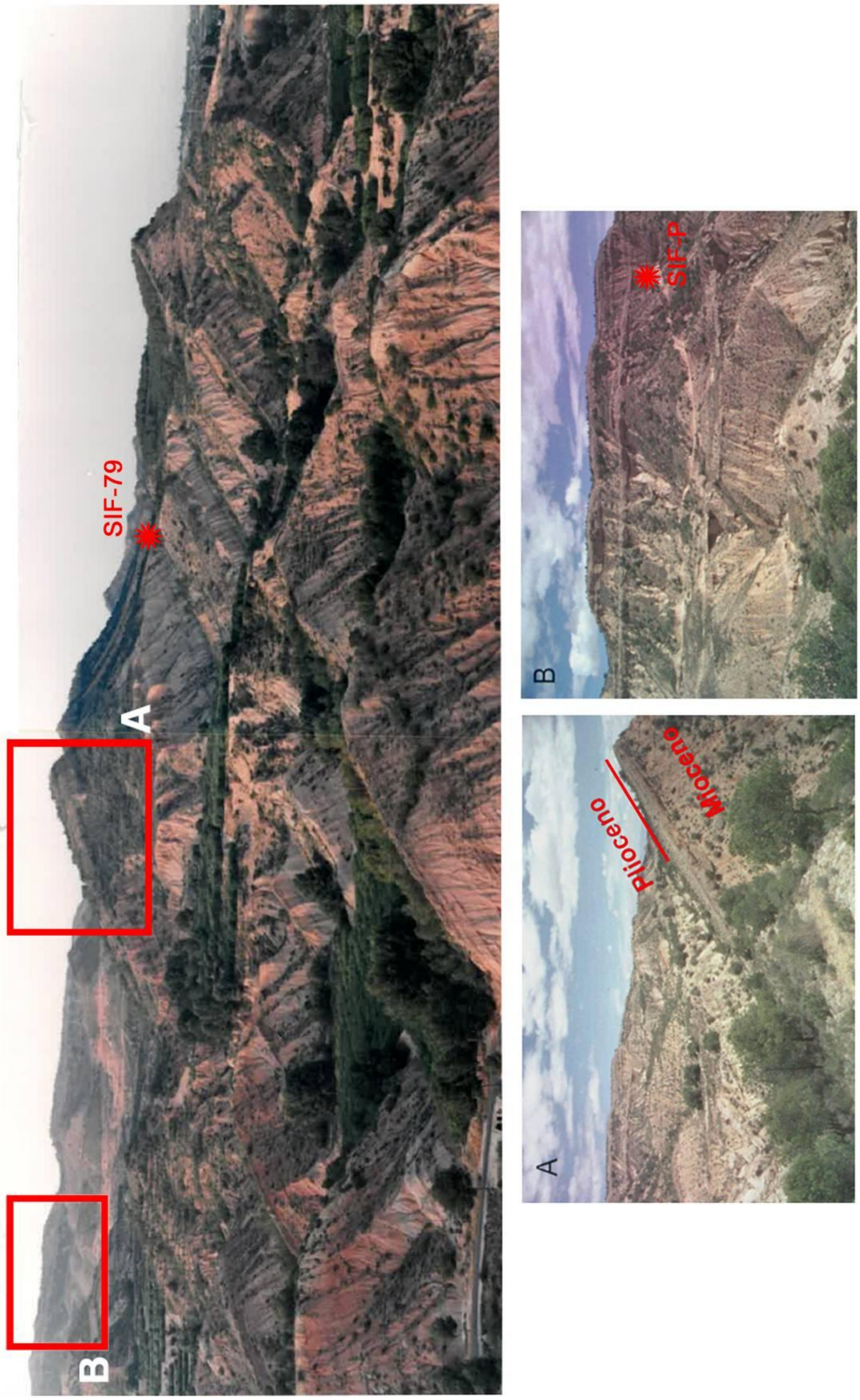

Figura III.3: Vista general de parte de la sección de Sifón de Librilla, y situación del último nivel mioceno de la serie (SIF-79). A) Límite Mioceno-Plioceno. B) Techo de la secuencia con la localización del último nivel con micromamíferos (SIF-P).

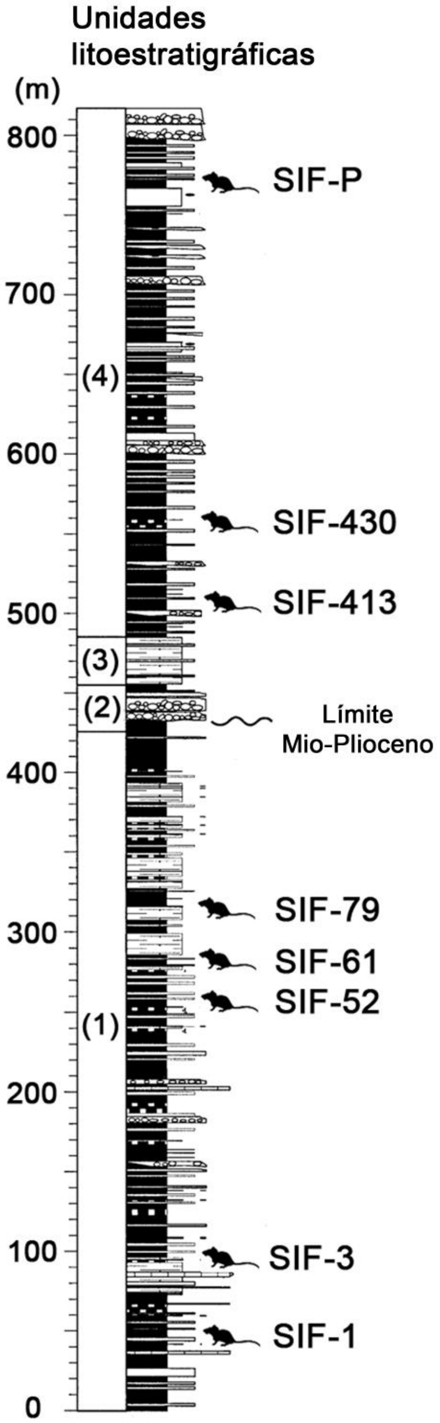

Figura III.4: Columna litoestratigráfica de la sección de Sifón de Librilla, mostrando la posición de las localidades de SIF-1, SIF-3, SIF-52, SIF-61, SIF-79, SIF-413, SIF-430 y SIF-P. Modificado de Garcés et al. (2001).

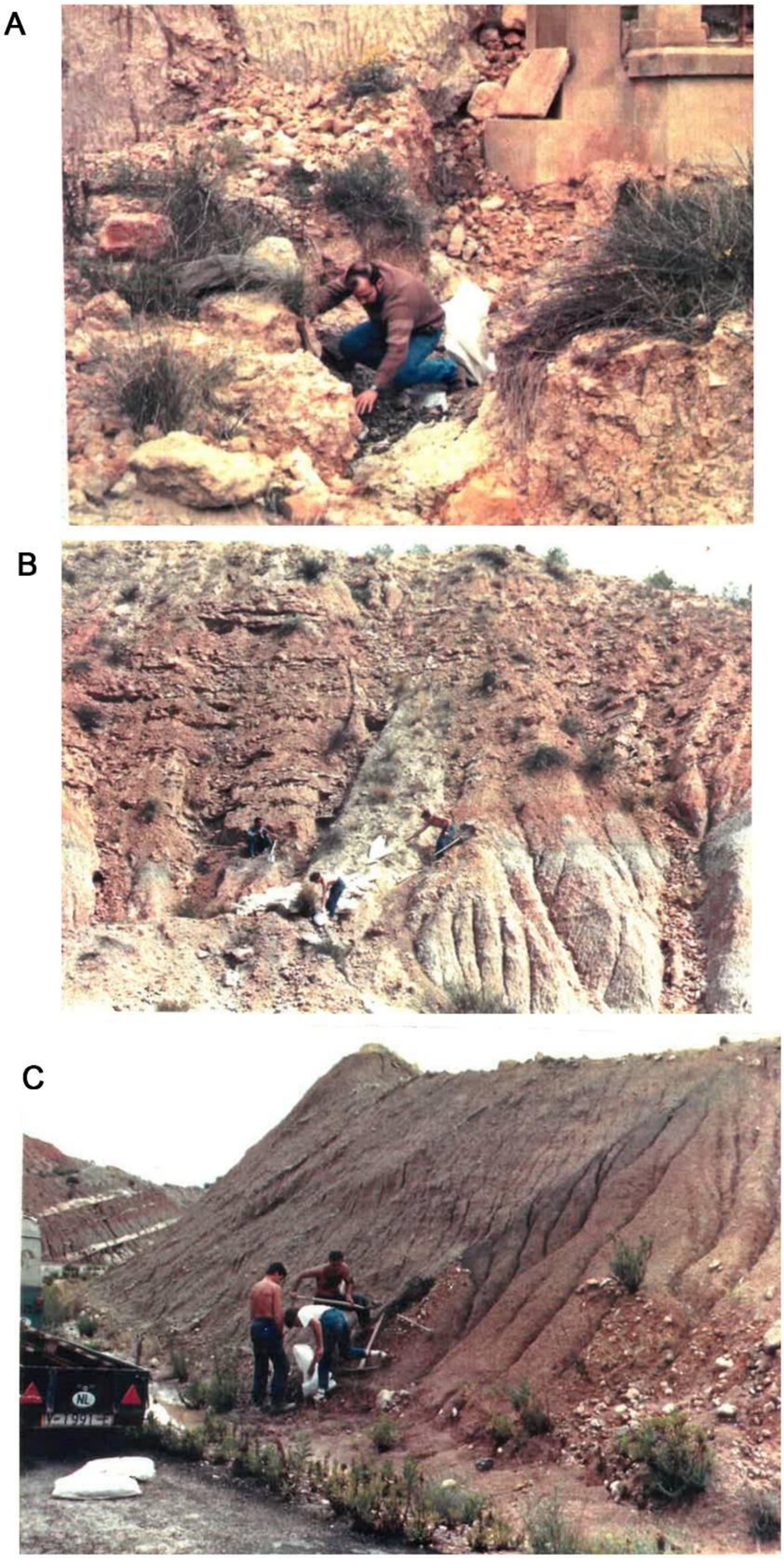

Figura III.5: Detalle de los tres primeros niveles fosilíferos de la sección de Sifón de Librilla durante su muestreo a principios del 2000. A) SIF-1. B) SIF-3. C) SIF-52.

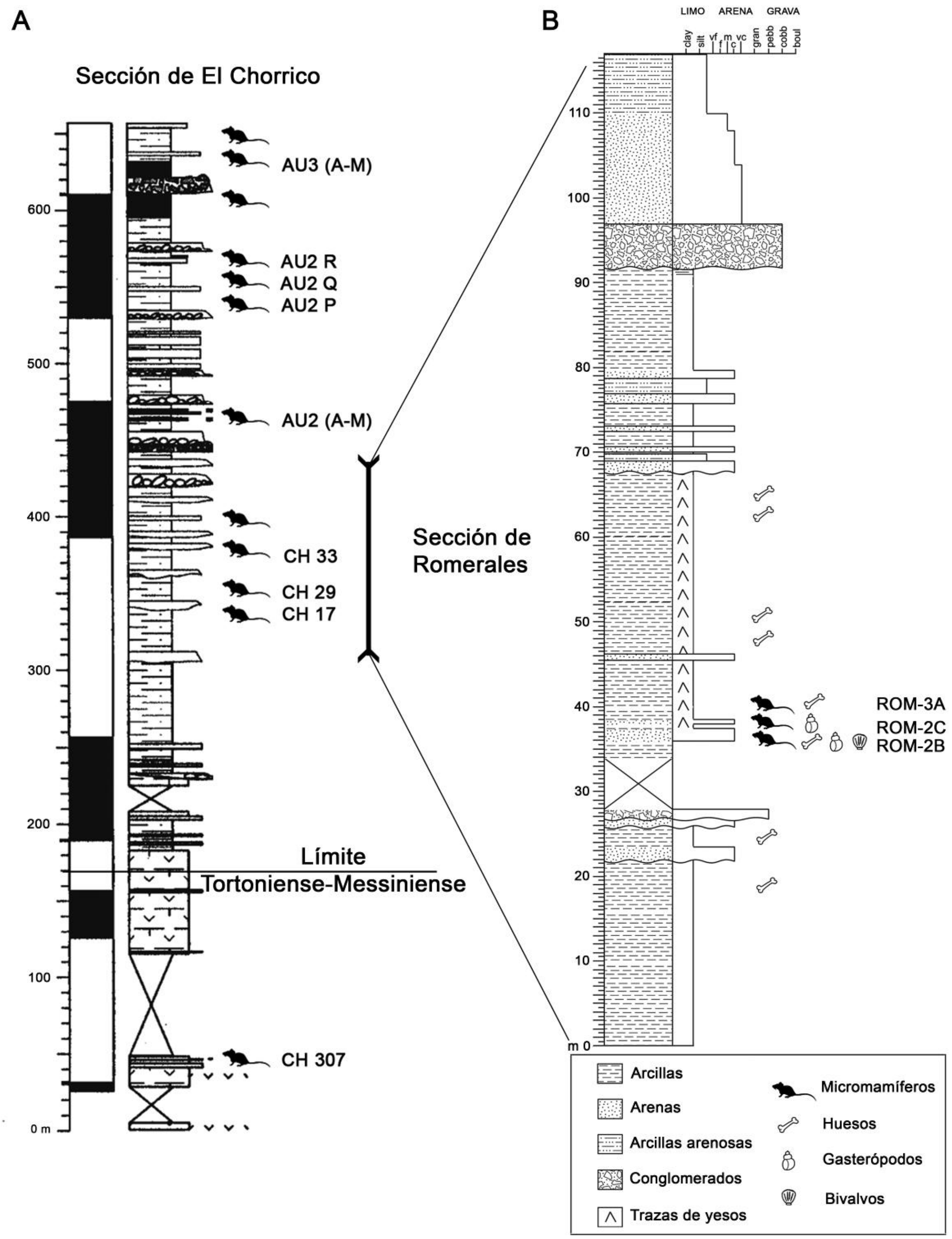

Figura III.6: A) Posición de la sección de Romerales dentro de la sección de El Chorrico (Modificado de Garcés et al., 2001). B) Columna litoestratigráfica de la sección de Romerales, apuntando la posición de las localidades de ROM-2B, ROM-2C y ROM-3A.

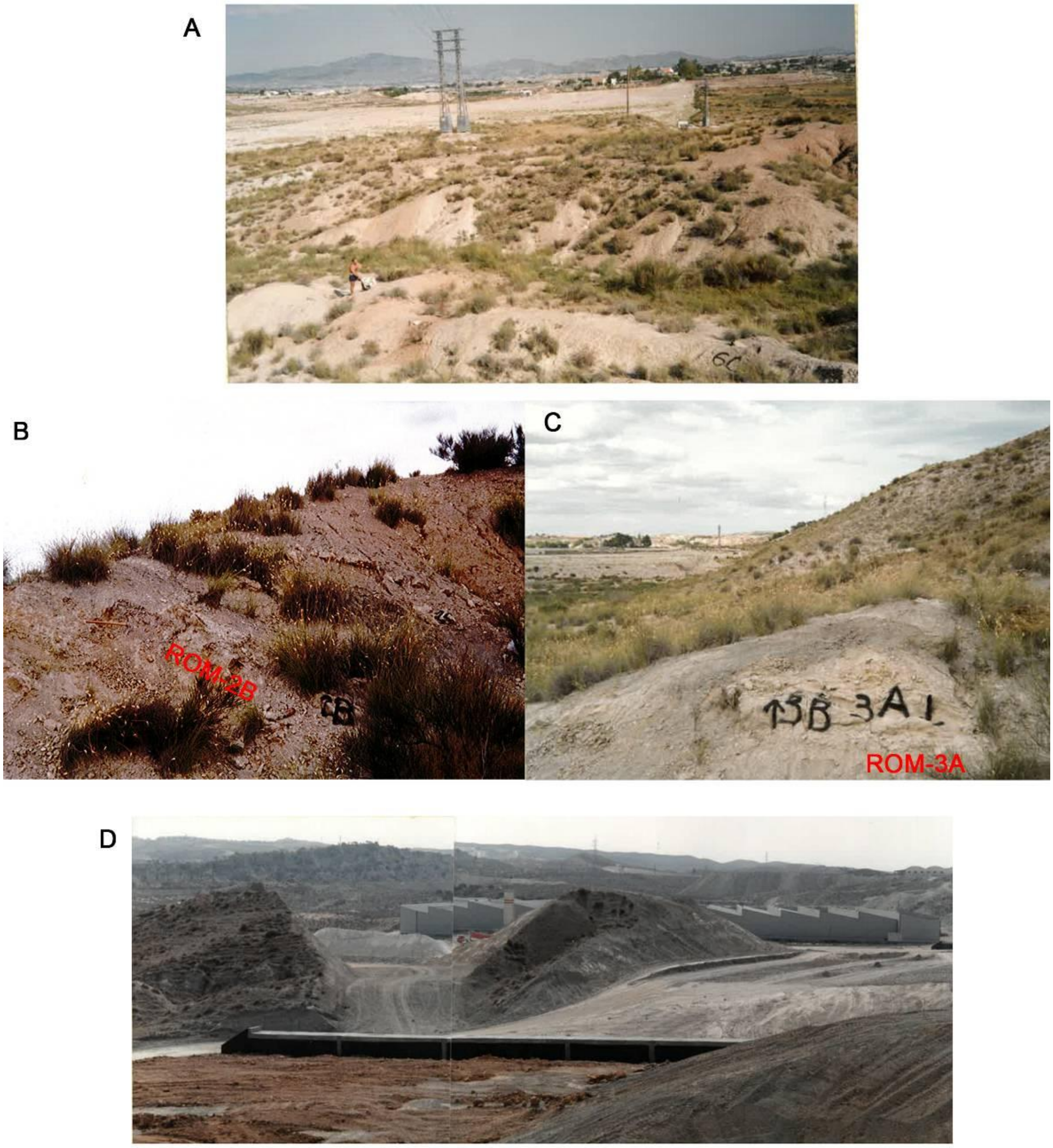

Figura III.7: A) Vista general de la sección de Romerales durante la toma de muestras en los años 90. B) Detalle del nivel ROM-2B. C) Detalle del nivel ROM-3A. D) Vista de parte de la sección de Romerales tras las obras de la autovía A30.

III.3. CUENCA DE GUADIX-BAZA

La cuenca de Guadix-Baza representa otra importante depresión intramontañosa de la Cordillera Bética que se sitúa en su sector central, en una posición intermedia entre las Zonas Externas y las Zonas Internas (figura III.8). Esta cuenca se establece en el Mioceno superior (Fernández et al., 1996a; Soria et al., 1998) tras el cese del desplazamiento del Dominio de

Alborán hacia el oeste (Sanz de Galdeano y Vera, 1992). Formó parte de los corredores que conectaban el océano Atlántico y el mar Mediterráneo durante parte del Mioceno (ver los esquemas sedimentarios generales de Fernández et al., 1996a, 1996b; Soria et al., 1998). Hacia el final del Mioceno la cuenca se elevó y quedó desconectada del mar instalándose un régimen de sedimentación endorreico, cuyos depósitos con las primeras faunas continentales tienen una edad máxima de 6,2 Ma (Minwer-Barakat et al., 2009a, 2009b, 2012a, 2012b; Hüsing et al., 2010, 2012). Ésto dio lugar a la acumulación de sedimentos continentales, proporcionando un registro continental continuo de los últimos 6 Ma. La cuenca se fue rellenando hasta su completa colmatación en el Pleistoceno medio, coincidiendo con el fin del estadio de relleno endorreico. Fue en ese momento, hace unos 205.000 años (Díaz-Hernández y Julià, 2006; Oms et al., 2011), cuando la cuenca fue capturada por la erosión remontante de un afluente del Guadalquivir, pasando a un régimen erosivo (Calvache y Viseras, 1997).

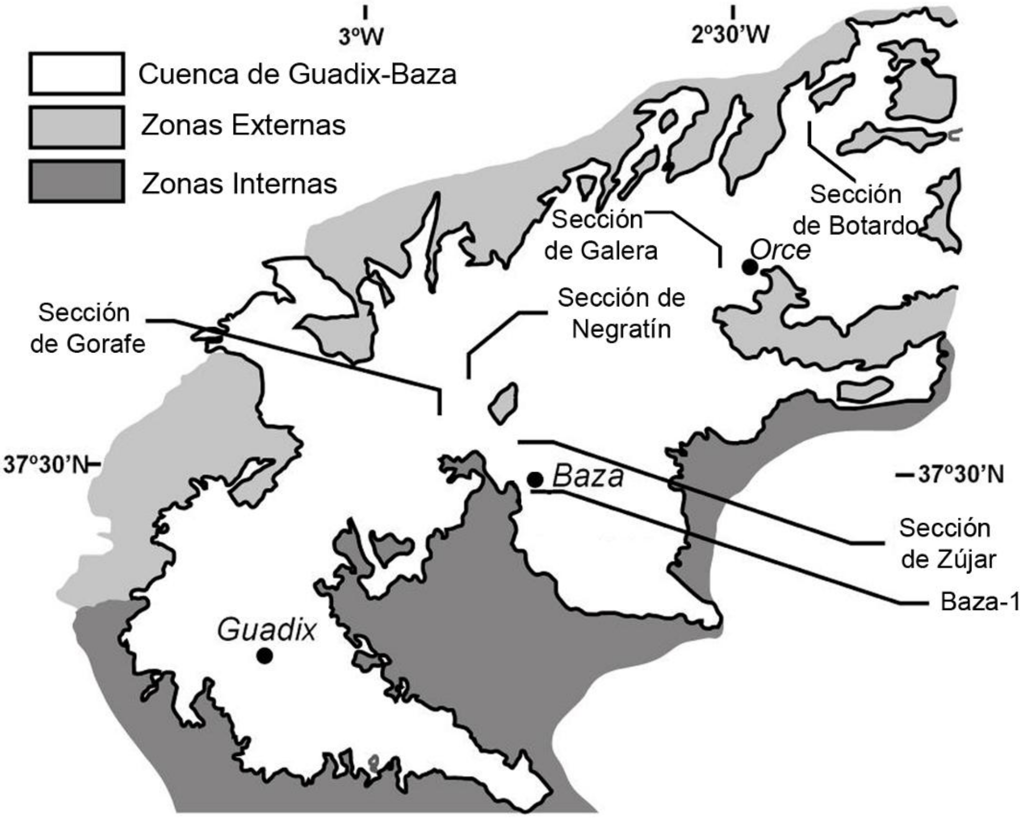

Figura III.8: Localización geográfica y geológica de la cuenca de Guadix-Baza.

La cuenca de Guadix-Baza se divide en dos sectores con características deposicionales distintas: la subcuenca de Baza al este, que en su mayor parte fue ocupada por un lago somero de grandes dimensiones que actuó como nivel de base para toda la cuenca; y la subcuenca de Guadix al oeste, donde dominan los abanicos aluviales y las llanuras fluviales, con un drenaje dirigido hacia el lago del sector oriental. Ambos sectores quedan separados por la falla de Baza (Alfaro et al., 2008), un elemento clave de la estructura de la cuenca.

La cuenca de Guadix-Baza consta de cinco grandes formaciones litoestratigráficas (Vera, 1970a):

1. Formación Guadix. Consta de sedimentos detríticos con ritmicidad y ciclo asimétrico. Principalmente se trata de conglomerados, arenas y lutitas. La base de cada ciclo es irregular con paleocanales y conglomerados, siendo los niveles detríticos más potentes y abundantes hacia el borde de la cuenca. Esta formación se encuentra en casi todo el sector occidental de la cuenca y en el margen norte del sector oriental. La acumulación de esta formación tuvo su origen en un sistema de abanicos aluviales que bordean los relieves circundantes, pasando hacia el interior a formar ríos meandriformes, trenzados y *braided*, dando lugar a lagunas de pequeña entidad (Vera, 1970a, 1970b, 1998; Viseras, 1991; Viseras y Fernández, 1992). Esta formación, escasa en fósiles de vertebrados, presenta morfologías *badlands* y tonos pardos y rojizos. Peña (1979) incluyó esta formación en el Grupo Guadix.

2. Formación Gorafe-Huélago. Está compuesta por rocas de precipitación química, calizas micríticas, dolomías y yesos, entre las que se puede encontrar intercalaciones de lignito. De forma frecuente también se encuentran margas y sedimentos intermedios entre arcillas y calizas. La heterogeneidad en las facies se liga a cambios climáticos que regulan la calidad y cantidad de los depósitos. Está situada entre las localidades que le dan el nombre, en la parte occidental de la cuenca. Esta formación está completamente rodeada por la Formación Guadix (Vera, 1970a, 1970b, 1998; Arribas et al., 1988). Se corresponde al Grupo Huélago de Peña (1979).

3. Formación Baza. Está constituida por calcilutitas de tamaño limo, aspecto terroso y color blanco amarillento, entre los que se encuentran yesos en forma de flecha de manera frecuente. También aparecen calizas compactas y arcillas, llegando a ser dominantes en lugares concretos. La mayor parte de esta formación se asienta en el sector oriental de la depresión (Vera, 1969, 1970a, 1970b, 1998). Las biofacies que

presenta son típicas de albufera (Vera, 1969). Esta formación se incluyó posteriormente en el Grupo Baza (Peña, 1979)

4. Formación Serón-Caniles. Está formada por materiales detríticos, aunque cabe mencionar el afloramiento de calizas arrecifales intercaladas con arenas y margas en algunos puntos del margen SE. En los bordes de esta formación dominan las calizas, mientras que en el interior dominan las arenas. Está situada en el área más meridional del sector oriental de la cuenca (Vera, 1970a, 1970b). Esta formación se incluyó en el Grupo Guadix (Peña, 1979).

5. Formación Solana del Zamborino. Está formada por una alternancia de materiales carbonatados y detríticos acumulados en un ambiente lacustre. Se trata de una formación de menor entidad respecto a las anteriores. Su formación está vinculada a la presencia de un lago de tamaño variable rodeado de zonas fluviales. Los roedores hallados en la base de esta formación indican que el depósito se inició al comienzo del Pleistoceno medio, mientras que el techo, donde se localiza el yacimiento de La Solana del Zamborino, está datado en el final del Pleistoceno medio. La formación está situada al SO de la Formación Gorafe-Huélago (Peña, 1975, 1979). Peña (1979) la incluyó en el Grupo Guadix.

Las dos subcuencas que conforman la cuenca de Guadix-Baza experimentaron varias conexiones y desconexiones en función de la tectónica y el desarrollo variable de la red aluvial y fluvial que forma la Formación Guadix (Viseras, 1991). Esta formación es el resultado de la acumulación de depósitos alineados con el eje principal de la cuenca, conocidos como sistemas longitudinales. Otros depósitos provienen de los márgenes norte y sur de la cuenca, denominados sistemas transversales. El desarrollo alternante de éstos dio lugar a sistemas lacustres confinados en diferentes puntos de la cuenca. Las formaciones de Baza y Gorafe-Huélago son facies distales lacustres de la Formación Guadix. Así, cuando los sistemas longitudinales eran los más activos, los sistemas lacustres se desarrollaban principalmente en la subcuenca de Baza, dando lugar a la Formación Baza. En contraste, cuando eran los sistemas transversales los más activos, la principal red fluvial se bloqueaba y se formaban sistemas lacustres menores en la subcuenca de Guadix, dando lugar a las formaciones de Gorafe-Huélago y Solana del Zamborino, quedando por tanto restringidas a la subcuenca de Guadix.

En este trabajo sólo se ha analizado la sistemática de los fósiles recuperados del yacimiento de Baza-1. Sin embargo, en los siguientes apartados se incorpora la descripción de las secciones de Negratín, Gorafe, Zújar, Galera y Botardo por su papel en el capítulo IX sobre las biozonaciones propuestas para el Mioceno superior y Plioceno de esta cuenca. También en este trabajo se publica por primera vez la magnetoestratigrafía de las secciones de Negratín, Botardo-1 y Gorafe.

III.3.1. Sección de Negratín

La sección de Negratín se sitúa en la parte central de la subcuenca de Guadix, a unos 4 km al sur de Cuevas del Campo, junto a la carretera que une esta localidad con el embalse de Negratín. Esta sección se incluye en la unidad más antigua dentro del relleno continental de la subcuenca de Guadix (Unidad IV, Viseras et al., 2004). La base de esta sección consta de margas grises sin estructura apreciable. Por encima de estas margas se localiza el yacimiento de Negratín-1 (MN13, Turoliense superior), un nivel de 50 cm de potencia de lutitas muy oscuras con abundante materia orgánica, gasterópodos y trazas de raíces rellenas de óxidos de hierro (Minwer-Barakat, 2005; Minwer-Barakat et al., 2009a). Sobre este nivel hay una alternancia de margas grises y negras, y arcillas laminadas con restos vegetales y conchas de gasterópodos, que se corresponden a depósitos de aguas estancadas del Sistema Lacustre (Fernández et al., 1996a). Sobre estos depósitos, aparece un cuerpo complejo de conglomerados y arenas con un espesor de 2 m. El hecho de que aparezcan clastos de diferente litología (desde rocas metamórficas a calizas) refleja la mezcla de aportes de distintas procedencias. Estos conglomerados y arenas proceden del Sistema Axial (Fernández et al., 1996a). La parte distal de este sistema recibe una gran cantidad de aportes del Sistema Transversal Externo. Estos sedimentos gruesos se alternan con limos y margas del Sistema Lacustre, haciéndose más abundantes hacia el techo de la sección (figura III.9; Minwer-Barakat et al., 2009a).

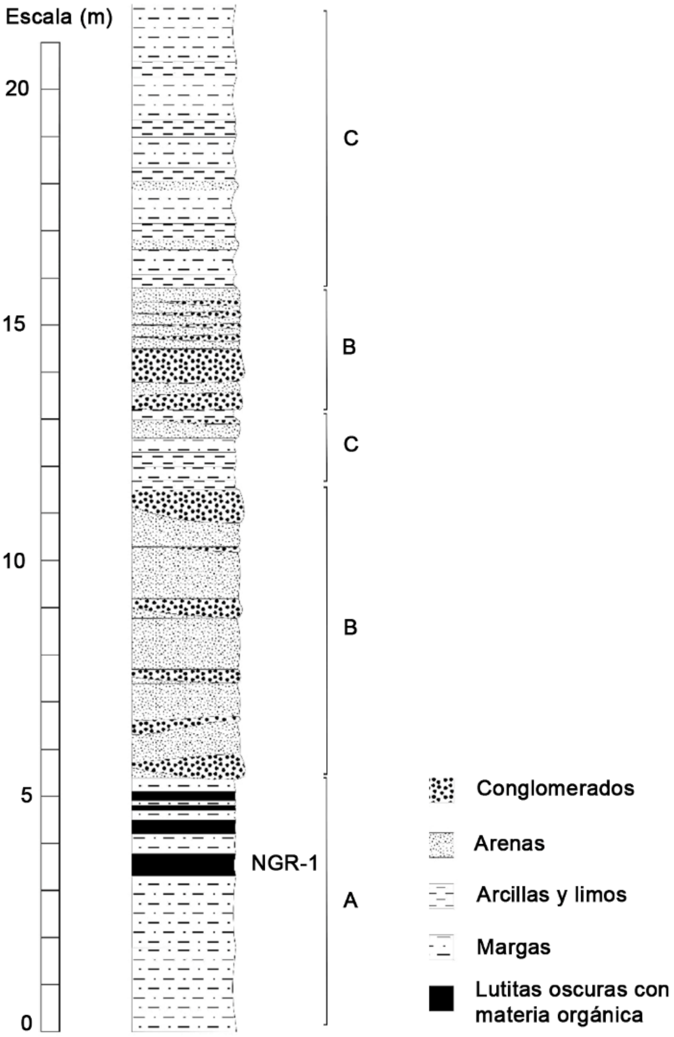

Figura III.9: Columna estratigráfica de la sección de Negratín, mostrando el nivel de Negratín-1. A) Depósitos del Sistema Lacustre. B) Depósitos del Sistema Axial. C) Intercalación de depósitos del Sistema Lacustre y Sistema Axial. Modificado de Minwer-Barakat et al. (2009a).

III.3.2. Sección de Botardo

La sección de Botardo se localiza a 10 km al ESE de la localidad de Huéscar, en un paraje conocido como Barrancos de Botardo (Martín Suárez, 1988; Soria et al., 1987). Se incluye en la Formación Baza. La secuencia aflora en una serie de barrancos excavados, en cuya base aparecen materiales conglomeráticos con episodios rojizos limo-arenosos (figura III.10). Por encima de este conjunto se encuentran margas, calizas y lutitas con lignito de colores blanquecinos a grises. En este conjunto se localizan los niveles que han proporcionado restos de microfauna: Botardo-A, B, C, D, 2 y 3. Aunque inicialmente Martín Suárez (1988) asignó estas localidades al Turoliense superior (MN13), en este trabajo se consideran localidades del Rusciniense inferior (MN14; ver capítulo IX). El siguiente tramo consta de una alternancia de calizas micríticas y margosas blanquecinas con restos de plantas, gasterópodos y nódulos de sílex. Este último incorpora de forma intercalada tramos detrítricos blancos de conglomerados y arenas gruesas. Los diferentes yacimientos aparecen debido al empuje de un diapiro (Soria et al., 1987). En esta tesis se publican los resultados paleomagnéticos de un tramo de 5 m de esta sección denominado Botardo-1. Este tramo incluye los niveles de Botardo-C y Botardo-D, localizados hacia el metro 32 de la secuencia general (figura III.10).

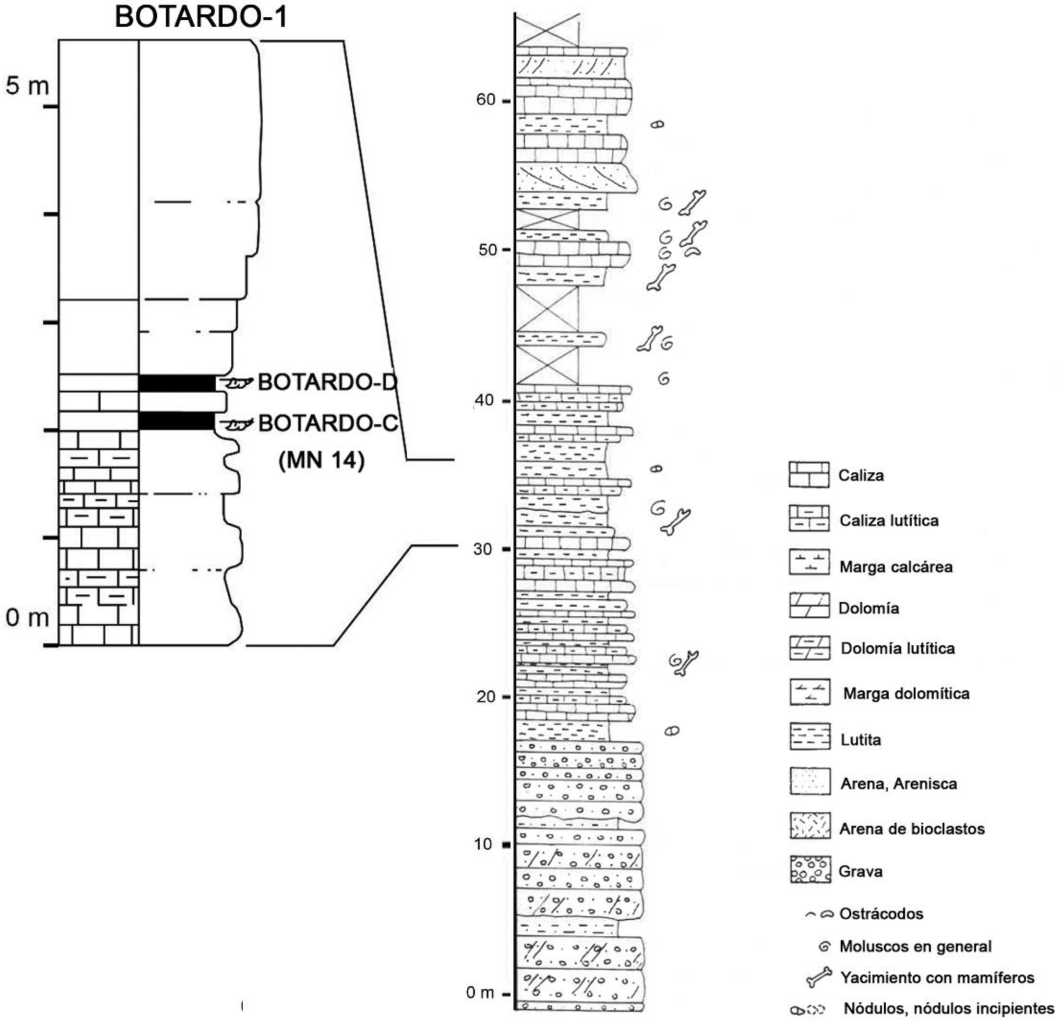

Figura III.10: Columna estratigráfica de la sección de Botardo, con detalle del tramo Botardo-1. Modificado de Soria et al. (1987) y Martín Suárez (1988)

III.3.3. Yacimiento de Baza-1

El relleno sedimentario de la cuenca de Guadix-Baza está dominado por la Formación Guadix y la Formación Baza. En las zonas marginales de la cuenca, donde la Formación Guadix evoluciona lateralmente hacia la Formación Baza, las sucesivas transgresiones y regresiones del lago resultaron en el desarrollo de ambientes palustres, que en el caso de la Formación Baza están representados generalmente por una sucesión de calizas y limos oscuros, siendo estos últimos ricos en yacimientos de micromamíferos (Oms et al., 2000b). Precisamente, este es el caso del yacimiento de Baza-1 (MN14, Rusciniense inferior; figura III.11).

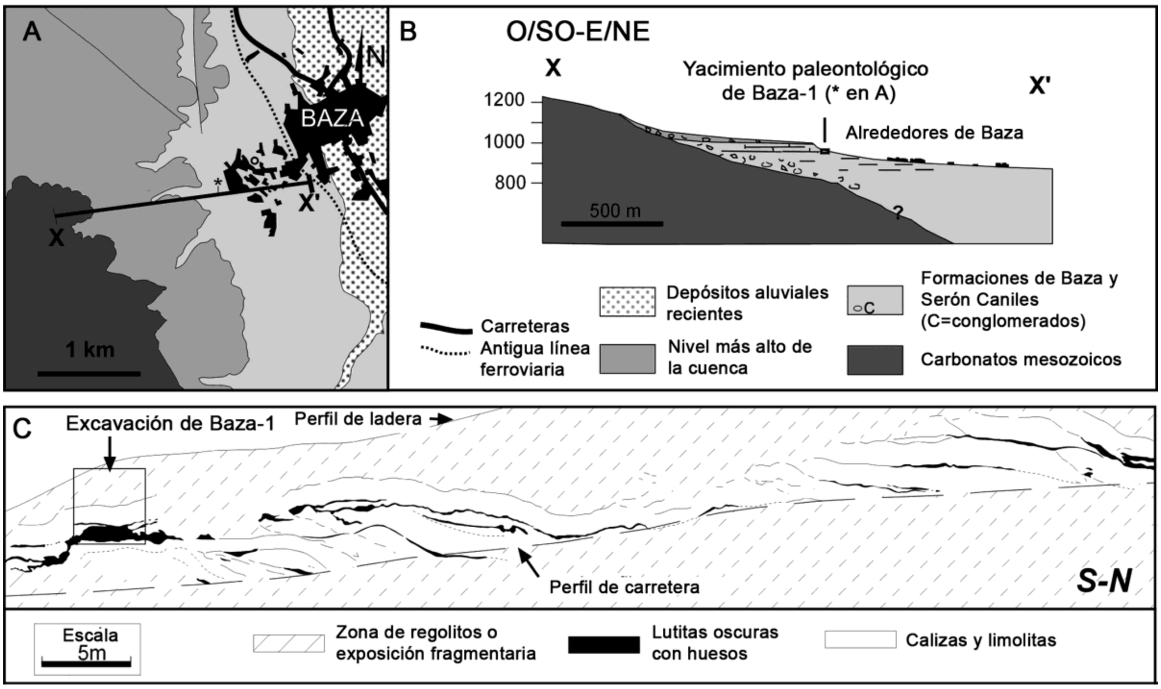

Figura III.11: A) Configuración alrededor del yacimiento y ciudad de Baza. B) Sección transversal del yacimiento de Baza-1 (ver localización en A). C) Afloramiento de Baza-1.

De manera detallada, la localidad de Baza-1 está formada por arcillas y limos de color marrón a negro, con algunos tramos finos de areniscas. Este característico nivel se encuentra en una sucesión más gruesa de calizas y calizas margosas con abundantes estructuras típicas de ambientes palustres, como nódulos calcáreos y marcas de raíz. El contraste mecánico entre las lutitas oscuras y las calizas (dúctiles y frágiles, respectivamente), junto con la dinámica geomorfológica del área, propicia el desarrollo de procesos de ladera, tal y como ocurre con el deslizamiento limitado de las rocas que forman el yacimiento de Baza-1. Es por esta razón por la que tanto el yacimiento como los estratos adyacentes aparecen muy deformados. Hacia el lado opuesto del barranco donde se encuentra Baza-1, estos procesos no se manifiestan, observándose una sucesión inalterada. El estudio minucioso de la estratigrafía de este afloramiento (figura III.11) y el hecho de que todo el material paleontológico se haya recuperado exactamente del sedimento excavado, permite concretar que todos los restos fósiles provienen de sólo 1 m de lutitas oscuras.

III.3.4. Sección de Gorafe

La sección de Gorafe se sitúa a 6 km de la localidad homónima, en la carretera que conecta este municipio con Baños de Alicún (Martín Suárez, 1988). Forma parte de la Formación Gorafe-Huélago de la subcuenca de Guadix. La descripción que aquí se expone se ha tomado de Martín Suárez (1988) según la cual la serie se describe en el margen izquierdo del Arroyo de Gor.

Esta sección (figura III.12) se asienta discordante sobre materiales plegados, cuya base está formada por un paquete de 45 m de potencia de conglomerados que gradualmente pasan a margas de diferentes colores con intercalaciones conglomeráticas (paleocanales). Estas margas pueden incluir ostrácodos y gasterópodos, y en ellas se emplaza un nivel de arcillas lignitófilas donde se sitúa el yacimiento de Gorafe-4 (MN14, Rusciniense inferior; Martín Suárez, 1988). Por encima de este paquete aparece un nivel de unos 15 m que incluye litologías variadas (calizas, microconglomerados, arenas, nódulos de limonita, limos con intercalaciones de lignitos). Por encima se sitúa un nivel de arcillas lignitófilas con abundantes gasterópodos y restos de vertebrados que se corresponde con las localidades de Gorafe-3 (MN15) y Gorafe-5 (MN15). Sobre estos yacimientos hay un nivel de 25 m con margocalizas, calizas, margas, conglomerados y limos con rizocreciones calizas. Este nivel da paso a unos materiales detríticos rojos que constituyen la Formación Guadix (Martín Suárez, 1988). El techo de esta sección está separado del glacis del Pleistoceno superior suprayacente (conglomerados rojos y costras carbonatadas) por una discordancia. Los yacimientos de Gorafe-1 (MN14) y Gorafe-2 (MN15; Bruijn, 1973, 1974) se sitúan frente a la sección descrita, al margen derecho del Arroyo de Gor. Al margen izquierdo del mismo aparece un bloque levantado originado por un complejo sistema de fracturas donde se localiza Gorafe-4, y dos bloques hundidos adyacentes donde se ubican Gorafe-3 y Gorafe-5. No obstante, en la figura III.12 se representa la serie de los bloques que permanecen *in situ*. El yacimiento de Gorafe-A (MN14; Ruiz Bustos et al., 1984) probablemente se corresponde al de Gorafe-4 (Martín Suárez, 1988; Agustí y Martín Suárez, 1984), aunque dada la incertidumbre se mantienen los dos nombres por separado.

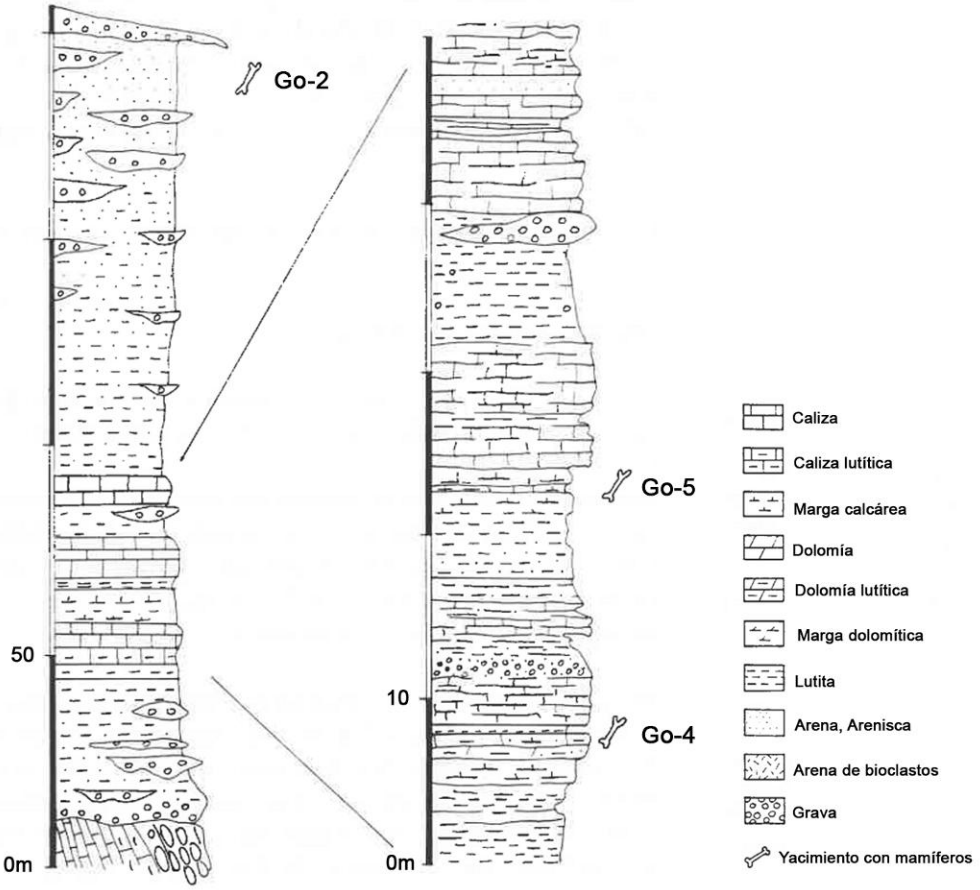

Figura III.12: Columna estratigráfica de la sección de Gorafe. Modificado de Martín Suárez (1988).

III.3.5. Sección de Zújar

Peña (1985) agrupó varias de las formaciones descritas para la cuenca de Guadix-Baza en el denominado Grupo Guadix (proximal), y otras en el Grupo Baza (distal). El grupo proximal contiene la unidad de Arcillas de Negratín, la cual aflora ampliamente en el área central de la cuenca (principalmente en la subcuenca de Guadix), donde queda reflejada en *badlands* y barrancos. La unidad de Arcillas de Negratín presenta un color característico rojizo. Ésta se depositó ampliamente en llanuras de inundación distales que estaban conectadas lateralmente a facies más proximales, las cuales se conocen como Arenas de Álamos Negros (Peña, 1985).

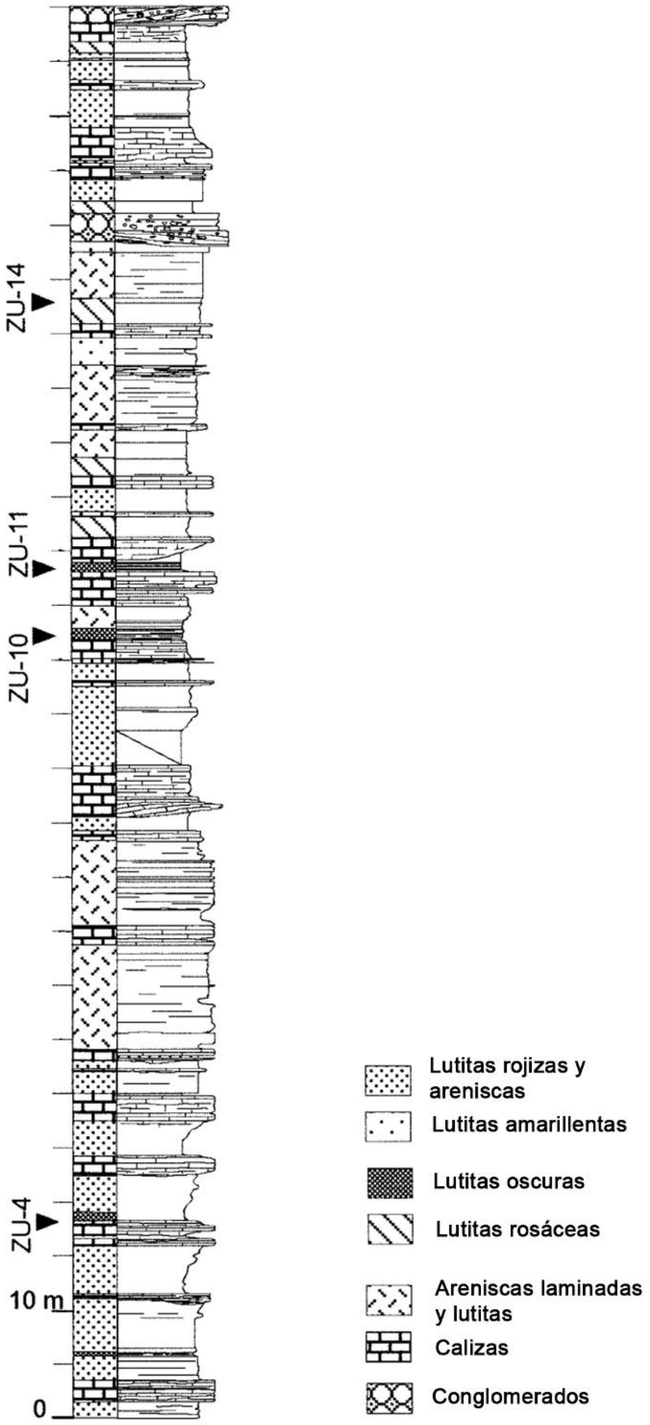

Figura III.13: Columna estratigráfica de la sección de Zújar. Modificado de Oms et al. (1999).

La sección de Zújar se sitúa a 3 km al SO de la localidad de Zújar, donde aparece un registro continuo excelente de las Arcillas de Negratín (Oms et al., 1999). Se trata de una sección de 130 m de espesor, principalmente formada por lutitas terrígenas y areniscas de colores variados y calizas blanquecinas (paleosuelos). Hacia el norte, en la zona donde se localiza el embalse de Negratín, las arcillas cubren la Formación Baza. En ambas áreas, estos sedimentos quedan cubiertos por glacis que datan del Pleistoceno superior (Peña, 1985). La sección de Zújar proporciona cuatro localidades con microfauna (figura III.13; Oms et al., 1999; Agustí et al., 2001): Zújar-4 (MN15), Zújar-10 (MN16), Zújar-11 (MN16; Agustí y Moyà-Solà, 1991) y Zújar-14 (MN17; Agustí et al., 1993).

III.3.6. Sección de Galera

La sección de Galera está situada a 2 km al SE de la localidad de Galera (Soria et al., 1987; Martín Suárez, 1988), aflorando a lo largo de la carretera que conecta Huéscar con Cúllar-Baza. Los materiales de la Formación Baza están bien representados en esta sección. Se trata de una secuencia de 100 m de espesor cuyos depósitos presentan una gran variedad de litologías (Garcés et al., 1997). Esta sección se puede dividir en tres unidades (figura III.14). La unidad inferior está formada por materiales lacustres con margas y calizas nodulares que se alternan con limos grises oscuros palustres y arcillas orgánicas negras. La unidad intermedia es aluvial y presenta arcillas (de rojizas a marrones) y areniscas. La unidad superior es lacustre y alterna areniscas carbonadas, calizas y margas. Los depósitos arenosos presentan grandes *sets* de laminación cruzada, canales erosivos y acumulaciones de clastos intraformacionales (Garcés et al., 1997). Otro tipo de litologías que aparecen en la unidad lacustre superior son yesos y arenitas laminados, depósitos de limos grises y nódulos silíceos horizontales. En la parte superior de la sección aparece una secuencia de engrosamiento ascendente con conglomerados en el techo. Los componentes detríticos son de origen metamórfico, y provienen de las Zonas Internas de la Cordillera Bética (Garcés et al., 1997). La sección de Galera presenta yacimientos con restos de mamíferos fósiles tanto en la unidad lacustre inferior como en la superior, mientras que los depósitos rojos de la unidad aluvial son estériles. La localidad de Galera-1C (MN15, Rusciniense superior) se localiza en la base de esta sección. Por encima de este yacimiento, ya en la unidad superior lacustre, se asientan las localidades de Galera-G (MN17, Villaniense superior), Galera-2 (MN17) y Galera-H (MN17).

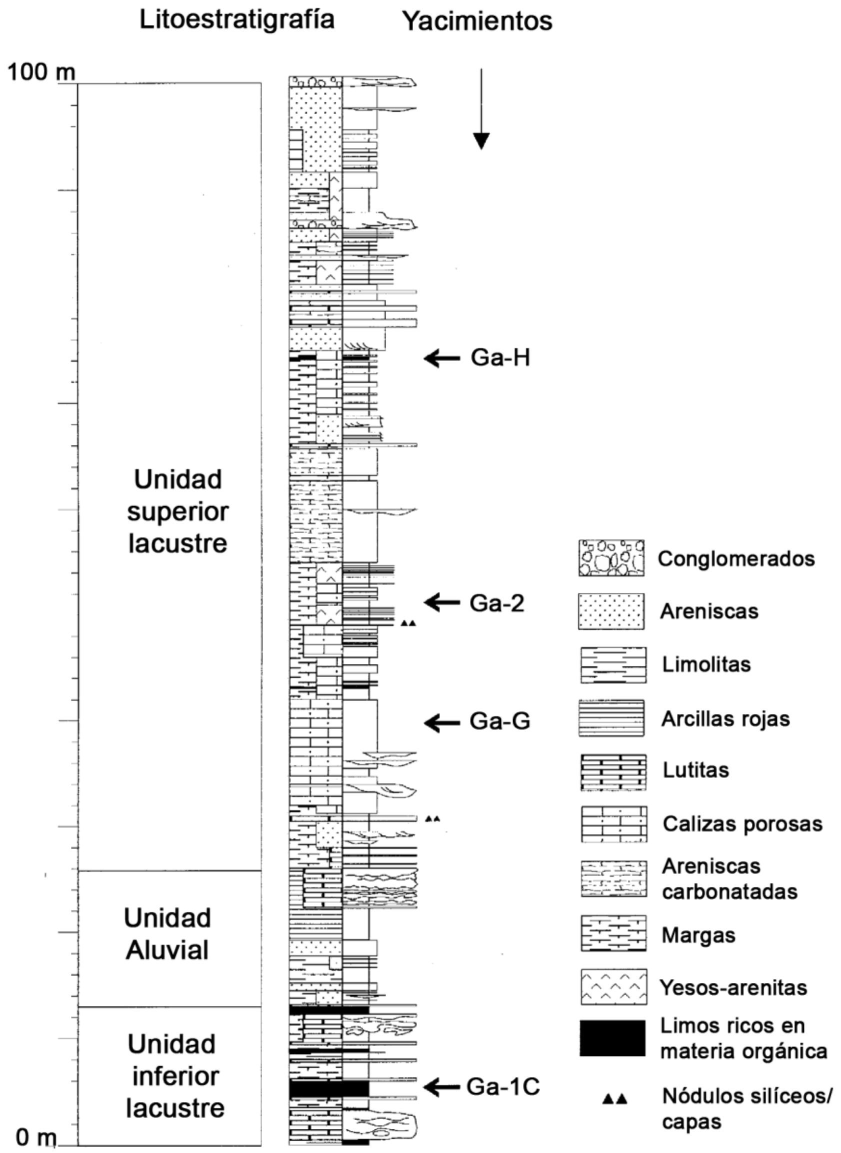

Figura III.14: Columna estratigráfica de la sección de Galera. Modificado de Garcés et al. (1997).

III.4. CUENCA DE MURCIA-CARRASCOY

La secuencia donde se localiza el yacimiento del Puerto de la Cadena forma parte del relleno neógeno de la cuenca de Murcia-Carrascoy. Esta cuenca se sitúa al norte de la Sierra de Carrascoy, y está cubierta principalmente de materiales procedentes de la erosión de las Zonas Internas de las Cordilleras Béticas, fundamentalmente de los complejos Alpujárride y Maláguide con rocas paleozoicas y triásicas, actuando como área fuente de los sedimentos que se han depositado en sus bordes durante el Neógeno (Mancheño et al., 2001). La deformación-estructuración más evidente en la cuenca es de edad post-pliocena, tal y como sugieren los antiformes de Carrascoy, los datos del mapa geológico, los cortes construidos y los resultados de las líneas sísmicas (Martínez del Olmo et al., 2006). Por otra parte, la falla sinestral de Carrascoy de dirección SO-NE y de actividad reciente, se relaciona con depósitos pre-pliocenos puesto que corta los sedimentos plio-cuaternarios (Martínez del Olmo et al., 2006).

La cuenca de Murcia-Carrascoy, similar a la cuenca del Mar Menor, está delimitada por sistemas de fallas que originariamente fueron normales de borde de cuenca, pero durante el Pleistoceno pasaron a ser de carácter inverso (Rodríguez-Estrella et al., 1999), y por fallas de salto en dirección que han tenido actividad durante diferentes etapas del Mioceno medio y superior, provocando la sedimentación en los bordes de la cuenca (Sanz de Galdeano, 1990). Las cuencas que poseen un substrato de Zonas Internas, entre las que se encuentra la de Murcia-Carrascoy, se definen como márgenes emergidos del Mar de Alborán (Martínez del Olmo et al., 2006). Núñez et al. (1974) establecen una orla sedimentaria del Mioceno superior para la vertiente norte de la Sierra de Carrascoy, sector donde se sitúa la zona de estudio. Estos depósitos se expanden de forma triangular hacia el suroeste, mientras que hacia el noreste se cubren de sedimentos cuaternarios.

Los sedimentos neógenos comienzan su serie en el Tortoniense medio con areniscas y conglomerados, que en una franja se ponen en contacto directo con los materiales triásicos del relieve de Carrascoy. En el Tortoniense superior se diferencian dos tipos de facies, destacando el marcado carácter margoso de una de ellas. En el final del Mioceno superior se registra una unidad detrítica continental atribuida al Messiniense.

Los depósitos neógenos del norte del Puerto de la Cadena presentan una dirección ENE-OSO, con un buzamiento hacia el NNO. Núñez et al. (1974) aportan una cartografía geológica que muestra importantes cambios en el buzamiento de los materiales en cortas distancias, llegando en algunos casos a los 40 grados de diferencia en tan sólo 1 km de distancia. Este hecho puede interpretarse como el efecto de la fractura frontal de la Sierra de Carrascoy. En cuanto a los sedimentos cuaternarios, se erosionan y cubren los materiales del Mioceno superior al norte de Carrascoy. Se trata de depósitos aluviales proximales, glacis y terrazas.

III.4.1. Unidad del Cigarrón

El área del Puerto de la Cadena registra varias unidades geológicas con una gran continuidad lateral, y cuya posición está influenciada por la actividad neotectónica. En el año 2008, las obras de construcción de la autovía MU-31 comenzaron a afectar a algunas de estas unidades, lo que permitió el descubrimiento y recuperación de restos de grandes y pequeños vertebrados.

El Barranco del Cigarrón (ver Mancheño et al., 2001) es uno de los mejores lugares para la descripción del registro estratigráfico del Neógeno en la ladera norte de la Sierra de Carrascoy, donde se ha documentado una sucesión estratigráfica que incluye hasta cinco unidades litoestratigráficas (figura III.15). Las tres unidades basales se pueden reconocer de forma clara y son equivalentes a las descritas en la cuenca del Bajo Segura: Formación Columbares, Formación Torremendo y Formación La Virgen (Montenat, 1990; Soria et al., 2008). Las dos unidades más altas son la Unidad del Cigarrón y Unidad La Paloma, descritas por primera vez en este trabajo.

El yacimiento del Puerto de la Cadena se asienta en la parte superior de la Unidad del Cigarrón, y podría ser el equivalente lateral de las formaciones de Rojales y Margas Jaspeadas descritas por Montenat (1977), ambas asignadas al Plioceno inferior (Soria et al., 2008). En el lado norte de la Sierra de Carrascoy, Montenat (1977) describió estas unidades, indicando que estaban compuestas de margas y arenas calcáreas grises con niveles conglomeráticos, estratificación cruzada y superficies de reactivación. También puso de manifiesto la presencia de restos de huesos fósiles en afloramientos arenosos amarillos, como son los yacimientos de La Alberca y La Paloma.

El límite estratigráfico inferior de la Unidad Cigarrón corresponde a una superficie de marcado carácter erosivo. Esta superficie afecta tanto a la Formación La Virgen como a la Formación Torremendo. Los primeros sedimentos inmediatamente por encima de esta discontinuidad estratigráfica son margas arenosas y arenas que incluyen clastos y bloques perforados por litófagos y abundantes fósiles de pequeños ostreidos afines al género *Pycnodonte*. Las margas, finamente laminadas, contienen una variada asociación de microfósiles representada por foraminíferos, ostrácodos, briozoos, lamelibranquios, espículas carbonáticas de esponjas y radiolas de erizos. Respecto a los foraminíferos, las formas bentónicas dominan (ca. 80%) sobre las planctónicas. La asociación de foraminíferos bentónicos está integrada por los géneros *Ammonia, Amphicoryna, Biasterigerina, Bigenerina, Bolivina, Bulimina, Cibicides, Elphidium, Fursenkoina, Globulina, Nonion, Pullenia, Reussella, Siphonina, Textularia* y *Trifarina*. La asociación planctónica dominante está constituida por los taxones *Globigerinoides extremus, Globigerinoides obliquus, Globigerinoides trilobus, Neogloboquadrina* spp., *Globorotalia scitula, Globigerina bulloides, Globoturborotalita* spp. y *Orbulina universa*. Todos estos datos micropaleontológicos indican que la sedimentación de la Unidad Cigarrón comienza en condiciones marinas normales, de aguas someras, marcando un evento transgresivo tras la fase erosiva reconocida a techo de la Formación La Virgen. Este evento transgresivo se registra de la misma forma en numerosos lugares de la cuenca del Bajo Segura, coincidiendo con el inicio del Plioceno (Corbí y Soria, 2016).

Los sedimentos marinos basales de la Formación Cigarrón muestran idénticas biofacies que los depósitos transgresivos de la base de la Unidad Plioceno (Soria et al., 2005) de la cuenca del Bajo Segura, lo que implica que ambos son correlacionables y que la superficie erosiva infrayacente corresponde a la discontinuidad fini-Messiniense de Soria et al. (2005). En concreto, el inicio de la Unidad Plioceno de la cuenca del Bajo Segura presenta cuatro rasgos significativos de coincidencia con la Unidad Cigarrón:

1. Abundantes ostreidos (*Pycnodonte*) y clastos perforados por litófagos (Montenat et al., 1990; Soria et al., 2005; Caracuel et al., 2011).

2. Predominio de los foraminíferos bentónicos (70 – 90%) sobre los planctónicos (Corbí, 2010).

3. Alto contenido y diversidad de foraminíferos bentónicos, mayoritariamente representados por *Ammonia, Bolivina, Bulimina, Cibicides, Elphidium, Nonion* y *Textularia* (Corbí et al., 2016).

4. Asociación de foraminíferos planctónicos de talla normal y típica de aguas cálidas-oligotróficas, que está dominada por *Globigerinoides* (principalmente *G. trilobus* y *G. obliquus/extremus*; Corbí et al., 2016).

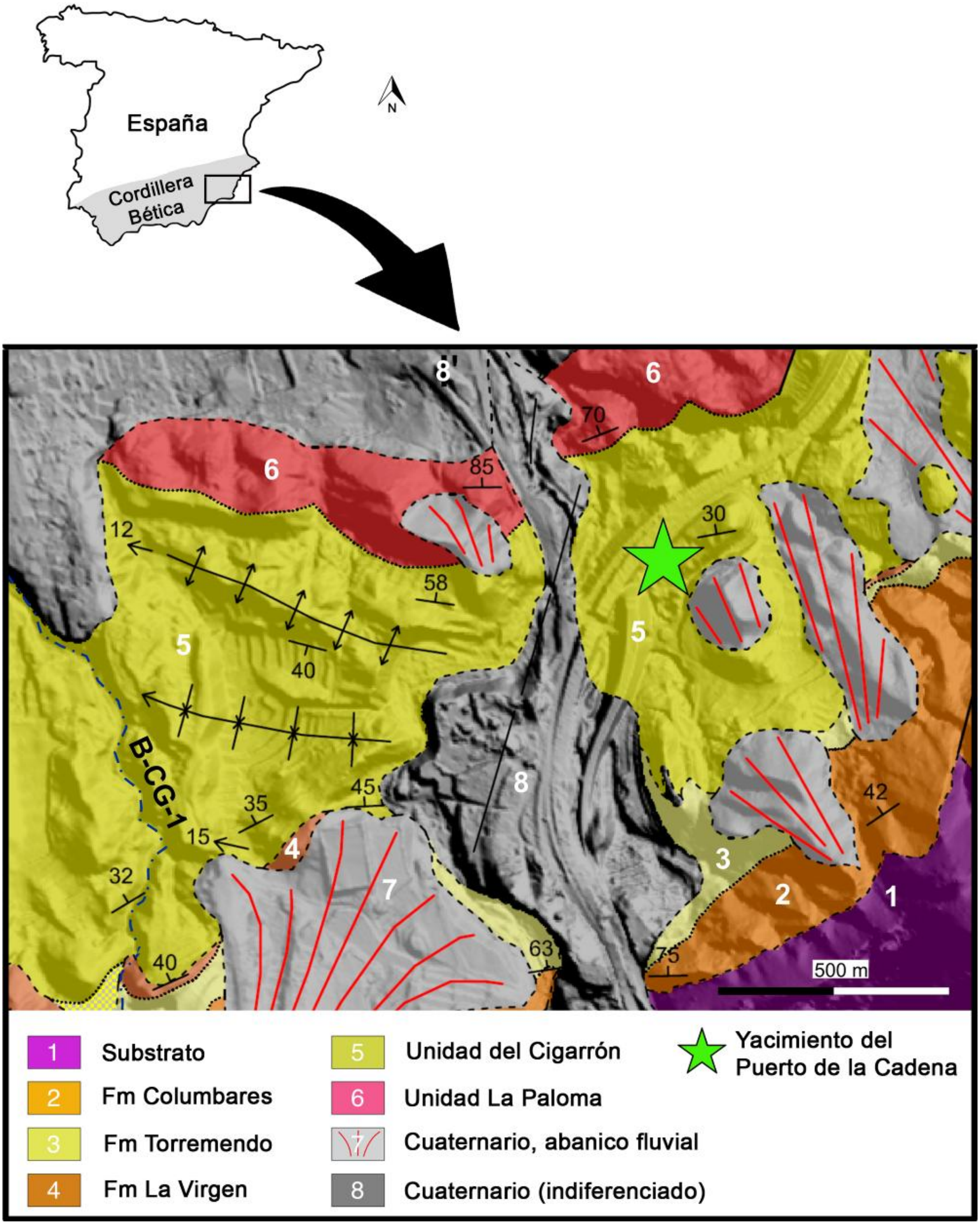

Figura III.15: Contexto geológico y geográfico del yacimiento del Puerto de la Cadena.

La asignación de la Unidad Cigarrón al Plioceno implica que su sedimentación ocurrió tras la Crisis de Salinidad del Messiniense, cuando toda la cuenca Mediterránea se reinundó a consecuencia de la entrada de aguas marinas normales desde el Atlántico. En esta cuenca pliocena, y en condiciones de nivel del mar alto, los márgenes del Mediterráneo fueron progresivamente colmatándose de sedimentos, generándose secuencias regresivas o de somerización (Caracuel et al., 2004, 2009; Soria et al., 2005). Una de estas secuencias está representada por la Unidad Cigarrón, que exhibe una evolución en el tiempo desde ambientes sedimentarios marinos someros a continentales. Estos últimos están representados por sistemas fluviales con desarrollo de canales y llanuras de inundación, contexto deposicional en el que se localiza el yacimiento del Puerto de la Cadena.

III.4.2. Sección de la Isleta

El yacimiento del Puerto de la Cadena (MN14, Rusciniense inferior; ver capítulo VII) se asienta en la sección de la Isleta, una secuencia de 20 m de potencia que es equivalente a la parte alta de la Unidad del Cigarrón (figura III.16). Los niveles con contenido en microfauna están comprendidos entre los metros 11 y 17 desde la base de la sección (figura III.17).

La Unidad del Cigarrón está representada en el yacimiento del Puerto de la Cadena por una sucesión alternante de arenas y lutitas. La asociación de facies arenosas consta de sedimentos gruesos (principalmente arenas, pero también microconglomerados y conglomerados) organizados principalmente en paquetes de estratificación cruzada planar y en surco. Estos paquetes tienen un grosor de entre unos pocos centímetros a un metro, presentando la mayoría de ellos una base erosiva. Dicha base erosiva muestra un recubrimiento basal con clastos limosos, fragmentos de huesos y restos de plantas fósiles.

Los restos de vertebrados fósiles se encuentran principalmente en las capas conglomeráticas de las arenas, o en los recubrimientos basales de los *sets* sedimentarios. Las arenas se componen de granos siliciclásticos con un tamaño que va desde mediano a grueso, y carecen de cemento. En los paquetes sedimentarios se puede observar una disposición compleja de estratificaciones cruzadas, cuya lámina interna presenta una inclinación variable, que va desde casi horizontal hasta 30º, apuntando en la mayoría de casos hacia la dirección N55ºE.

Las intercalaciones lutíticas presentan diferentes características. Así, algunas de ellas son gruesas intercalaciones (escala métrica) con una base cóncava y un techo plano. Hacia el techo de estos cuerpos se observan frecuentemente bioturbaciones de desarrollo vertical de entre 5 y 7 cm de longitud. Se trata de trazas con una característica forma en U y una sección transversal circular de unos 0,5 cm de diámetro (*Arenicolites* isp.; Simo y Olsavsky, 2007). Por otra parte, aparecen intercalaciones lutíticas delgadas (de varios centímetros a un metro) con una morfología irregular. La mayoría de restos de micromamíferos se obtuvieron de estos niveles lutíticos.

Figura III.16: Vista general del perfil de la Isleta durante la campaña de excavación del yacimiento del Puerto de la Cadena en el año 2009.

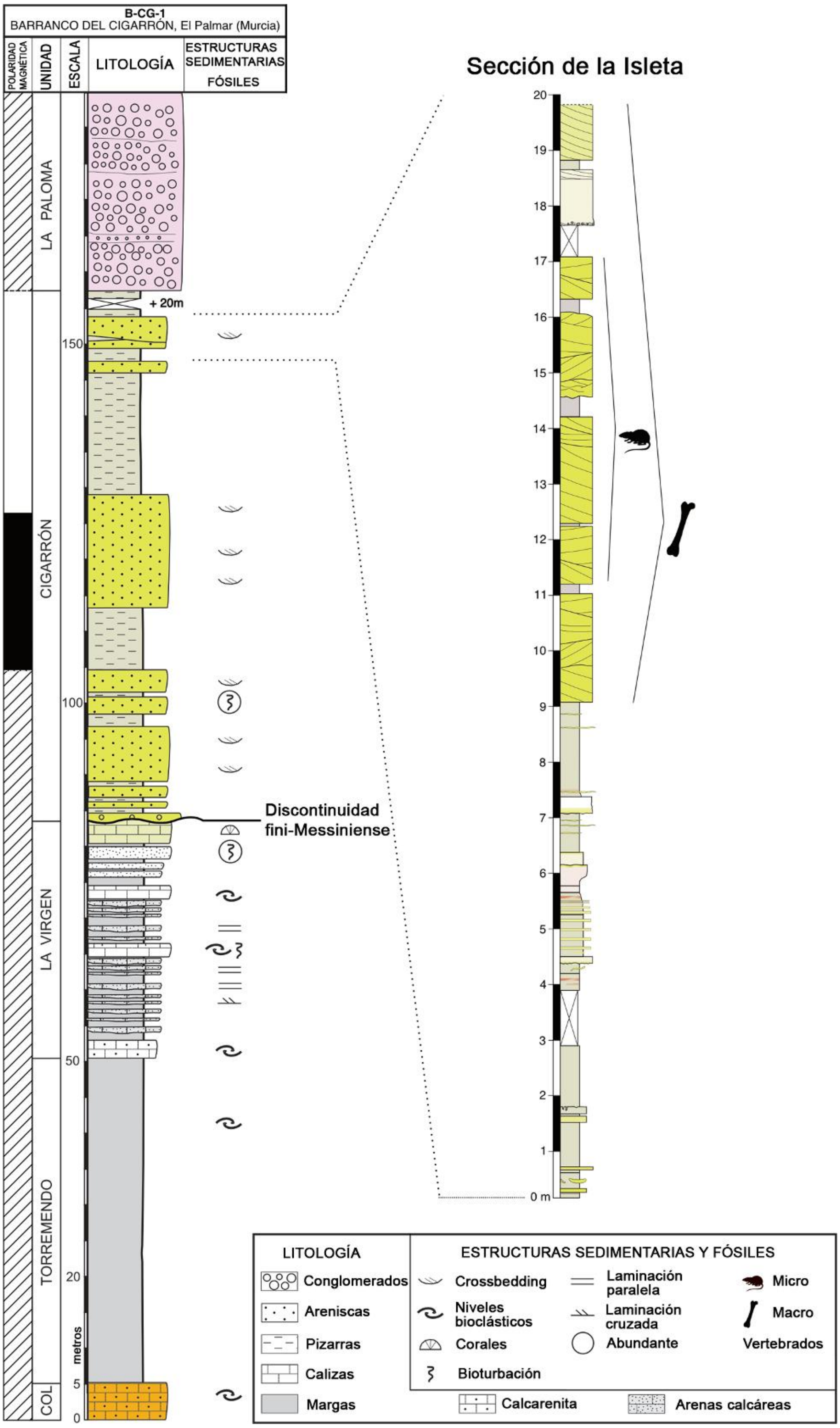

Figura III.17: Columna estratigráfica del Barranco del Cigarrón, con detalle de la sección de la Isleta donde se sitúa el yacimiento del Puerto de la Cadena.

III.5. SIERRA DE QUIBAS

La sierra de Quibas forma parte de un conjunto de relieves más o menos elevados (La Pila, Cantón, Barinas, Crevillente, etc.) que pertenecen al Dominio Subbético de las Zonas Externas de la Cordillera Bética y más concretamente a la Zona Subbética Media. Presenta en su falda meridional un relieve relativamente suave, que enlaza con la depresión de Balonga mediante un glacis. La falda septentrional, por el contrario, es más abrupta debido a la presencia de fallas normales de gran salto que provocan la existencia de conos de deyección. Representa un macizo carbonatado de dirección NE-SO, de 6 km de longitud y 2,5 km de anchura, con predominio de calizas y dolomías del Lías inferior-medio (figura III.18; Rodríguez-Estrella et al., 2004). Desde el punto de vista geomorfológico, destaca el gran desarrollo kárstico plio-cuaternario, con la presencia de formas exokársticas (lapiaces, dolinas) y endokársticas (cuevas y simas), algunas de ellas totalmente colmatadas en la actualidad por rellenos de carácter mixto detrítico y de precipitación química, en una de las cuales se localiza el yacimiento paleontológico de Quibas (Durán et al., 2004).

Se trata de un relieve mesozoico que cabalga sobre rocas principalmente cenozoicas autóctonas o parautóctonas del Prebético Meridional (Rodríguez-Estrella, 1979). El Subbético se oculta hacia el sur bajo los materiales neógenos de la cuenca de Fortuna. De esta forma, la Sierra de Quibas presenta una posición alóctona en relación con la autóctona relativa del Prebético Meridional situado bajo el mismo (Rodríguez-Estrella et al., 2004).

Desde el punto de vista estratigráfico, la Sierra de Quibas está constituida por dos tipos de materiales diferentes: los subbéticos alóctonos, que representan una serie carbonatada con predominio de materiales del Jurásico inferior; y los prebéticos autóctonos, con materiales del Eoceno al Mioceno medio con diversa litología (Rodríguez-Estrella et al., 2004). El Cuaternario queda representado por un piedemonte en los bordes norte y sur, y por rellenos en cavidades kársticas, tal como la del yacimiento paleontológico tratado.

En un contexto tectónico, la Sierra de Quibas constituye un isleo tectónico, con una estructura interna de anticlinorio, de dirección NE-SO, condicionada por la afección de numerosas fallas (normales y algunas inversas, y transversales) paralelas a la dirección principal de la estructura. La actividad neotectónica a partir del Mioceno superior ha reactivado algunas de estas fallas (Rodríguez-Estrella et al., 2004).

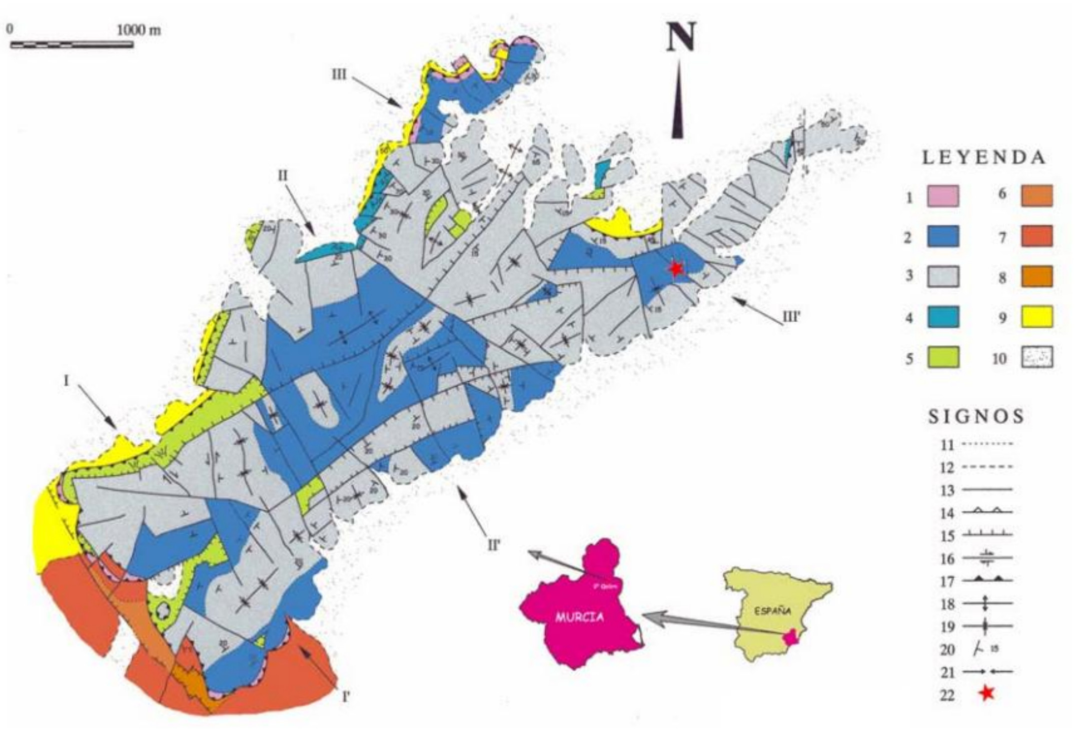

Figura III.18: Situación geográfica y contexto geológico de la Sierra de Quibas. 1) Arcillas y yesos (Triásico superior). 2) Dolomías (Lías inferior). 3) Calizas (Lías inferior-medio). 4) Calizas nodulosas (Dogger-Malm). 5) Margas y margocalizas (Cretácico inferior). 6) Margas verdosas (Eoceno inferior). 7) Calizas arrecifales (Eoceno medio). 8) Arenas, areniscas y conglomerados rojizos (Oligoceno). 9) Calizas y margas (Mioceno). 10) Conglomerados, limos, arcillas y caliches (Cuaternario). 11) Contacto concordante. 12) Contacto discordante. 13) Falla. 14) Falla inversa. 15) Falla normal. 16) Falla de desgarre. 17) Cabalgamiento. 18) Anticlinal. 19) Sinclinal. 20) Dirección y buzamiento. 21) Corte geológico. 22) Yacimiento paleontológico. Modificado de Rodríguez-Estrella et al. (2004).

III.5.1. Yacimiento de Quibas

El yacimiento paleontológico de Quibas constituye un relleno kárstico plio-cuaternario en dolomías del Lías inferior, situándose en la intersección de tres fallas con direcciones N110E, N160E y N175E (Rodríguez-Estrella et al., 2004). La karstificación plio-cuaternaria dio paso al origen de un entramado de cuevas y galerías que posteriormente se rellenaron de material detrítico rojizo rico en fósiles, o de espeleotema calcítico (las fallas de dirección N160E y N175E se vieron afectadas por esta precipitación carbonática). La explotación del espeleotema calcítico (falsa ágata), cuya cota de extracción fue condicionada por la falla de dirección N110E, expuso los rellenos fosilíferos, pudiéndose observar una importante sección de oquedades, así como las características del relleno.

Fumanal y Blázquez (en Montoya et al., 1999) indican que el yacimiento está formado por distintas galerías kársticas, unas de desarrollo vertical (chimeneas), y otras que corresponden a antiguas salas individualizadas por desplomes parietales o cenitales (cuevas). Estos conductos se muestran colmatados por depósitos sedimentarios, caracterizándose a grandes rasgos por la alternancia cíclica de niveles de bloques y cantos, con potentes aportes arcillosos. La procedencia del relleno detrítico es variable, con varios puntos de acceso, lo que condiciona una variación de su geometría así como del sentido de inclinación, según la progresión de la colmatación (Montoya et al., 1999). Trabajos posteriores (Rodríguez-Estrella et al., 2004; Durán et al., 2004) han precisado las características de estos rellenos/dolina/cueva.

El yacimiento está formado principalmente por dos rellenos detríticos que se formaron en las sucesivas fases cuaternarias: una sima de 20 m de profundidad y 2 m de anchura (1, figura III.19), y una galería de 5 m de ancho, 9 m de altura y longitud desconocida (2, figura III.19; Rodríguez-Estrella et al., 2004; Durán et al., 2004). No obstante, las prospecciones geofísicas realizadas indican que la galería y su relleno avanzan al menos 30 m longitudinalmente hacia el interior de la sierra. Ambas estructuras kársticas, aunque externamente se muestran separadas por un espeleotema calcítico de 3 m de espesor, probablemente estén conectadas interiormente (Rodríguez-Estrella et al., 2004). La muestra estudiada en este trabajo fue tomada de la Gruta-1 (3, figura III.19; el área de extracción se señala con un círculo rojo).

Fumanal y Blázquez en Montoya et al. (1999) estudian además la estratigrafía de la parte basal del relleno kárstico, amplia secuencia expuesta en el yacimiento, por su interés paleontológico, centrándose en unidades sedimentarias generales debido a la complejidad del relleno. De esta forma, en un perfil de 5 m distinguen seis niveles de sedimentos detríticos rojizos, principalmente compuestos por arcillas, limos y brechas (figura III.20).

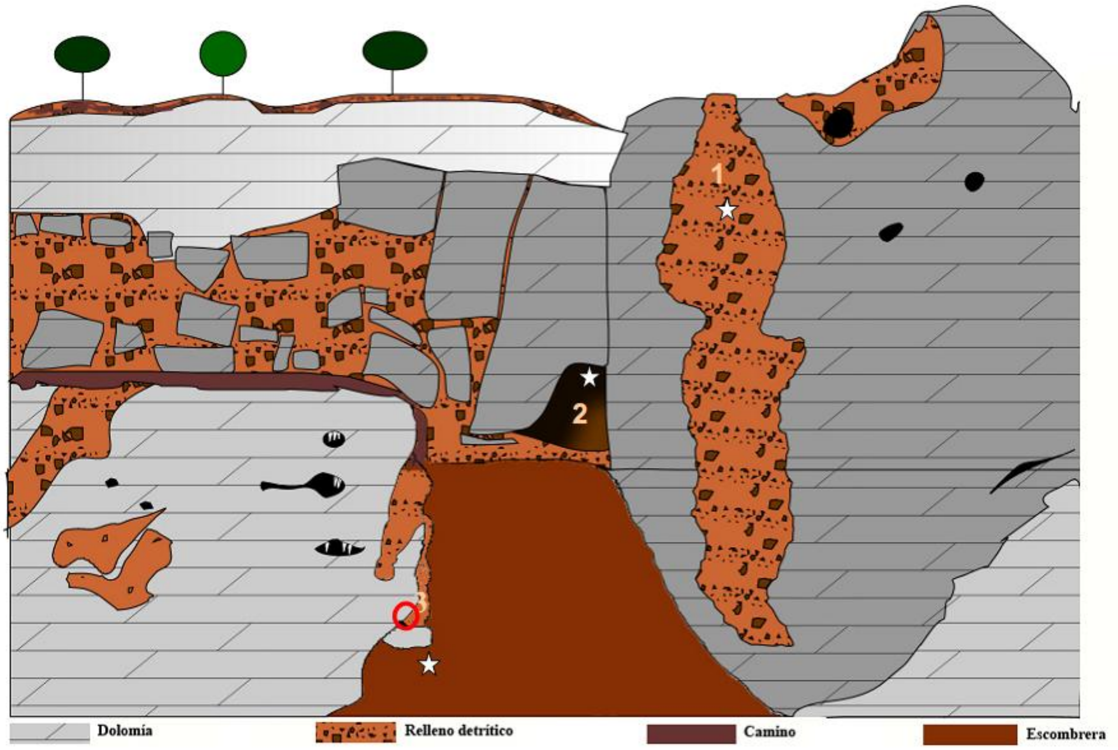

Figura III.19: Esquema del yacimiento paleontológico de Quibas en gran angular. 1) Sima. 2) Galería. 3) Gruta-1. Círculo: área de extracción de la muestra. Modificado de Cuadros (2010).

El citado tramo basal está formado por un “fondo de saco”, cuyos depósitos sedimentarios se han ido deslizando oblicuamente hacia la derecha del perfil desde un punto superior del mismo. Se cierra por una primera bóveda, la cual ofrece un gran desarrollo estalactítico que se une a gruesos revestimientos parietales. La base de la columna que describen (figura III.20) se apoya contra el ángulo formado por una potente pared estalagmítica y un conjunto caótico de grandes bloques cementados por calcita (Montoya et al., 1999):

1. Nivel Ia-Ib. El *subnivel Ia* contiene una serie de cantos muy angulosos y fragmentos de estalactitas o restos pavimentarios, con una matriz escasa de textura arcillo-arenosa. Es en este subnivel donde se ha hallado la asociación de macrovertebrados más importante, incluso a veces en forma de brechas óseas. El *subnivel Ib* está formado por una serie de cantos y bloques muy aristados, y un gran número de plaquetas de gelifracción con muy poca matriz, cuya proporción de microfauna es mayor que la del

subnivel anterior. La matriz, probablemente, ha contribuido en el desplazamiento de los materiales gruesos.

2. Nivel II. Presenta un depósito muy homogéneo de arenas limo-arcillosas con un gran contenido en $CaCO_3$, y registro de bioturbación por raíces. Su estructura consiste en agregados poliédricos de varios centímetros. El contenido en fósiles disminuye respecto al nivel anterior. En este caso, fueron determinadas arroyadas como responsables del transporte del material.

3. Nivel III. Hay un completo predominio de bloques, cantos y plaquetas de gelifracción, a los que se unen una gran cantidad de fragmentos de costra carbonatada laminar. La escasa matriz que contiene el nivel en sus intersticios, probablemente procedente del nivel suprayacente, es arcillo-limosa con minúsculos fragmentos de huesos. Se apoya contra la pared del fondo de la cámara, adoptando una estructura masiva, caótica. El transporte se debe a la fuerza gravitatoria, un desplazamiento en masa donde los materiales se deslizaron sobre el material fino del nivel inferior.

4. Nivel IV. Está formado por un sedimento fino con predominio de arcilla. Su estructura es en agregados y poliédrica. Probablemente, el material fue desplazado a través de coladas de barro. Este nivel es el que contiene mayor cantidad de restos de microvertebrados, pudiéndose observar a veces grandes concentraciones con un grado de cementación variable.

El sedimento con la muestra de microfauna fue recogido de un relleno localizado en la pequeña cavidad kárstica denominada Gruta-1 (A, figura III.21), situada muy próxima al relleno principal (Galería). Su altura topográfica es aproximadamente la misma que la del nivel III de la columna estratigráfica descrita en Montoya et al. (1999) (figura III.20). El relleno está formado por un nivel detrítico de clastos de caliza con un tamaño que oscila entre 10 y 30 cm, y una matriz limo-arcillosa de color rojizo con costras de carbonatos (B, figura III.21).

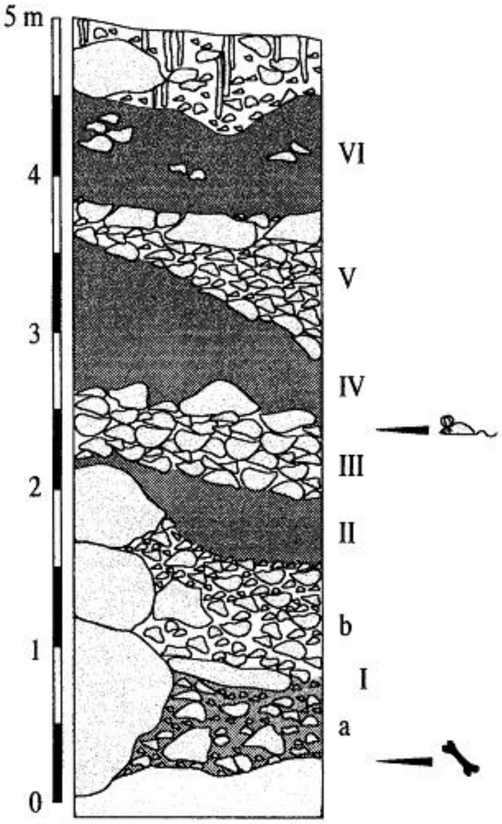

Figura III.20: Columna estratigráfica del tramo inferior del relleno kárstico, donde se señalan los dos niveles de mayor concentración de micro y macrovertebrados. La muestra se ha extraído a una altura topográfica muy próxima al nivel III. Tomado de Montoya et al. (1999).

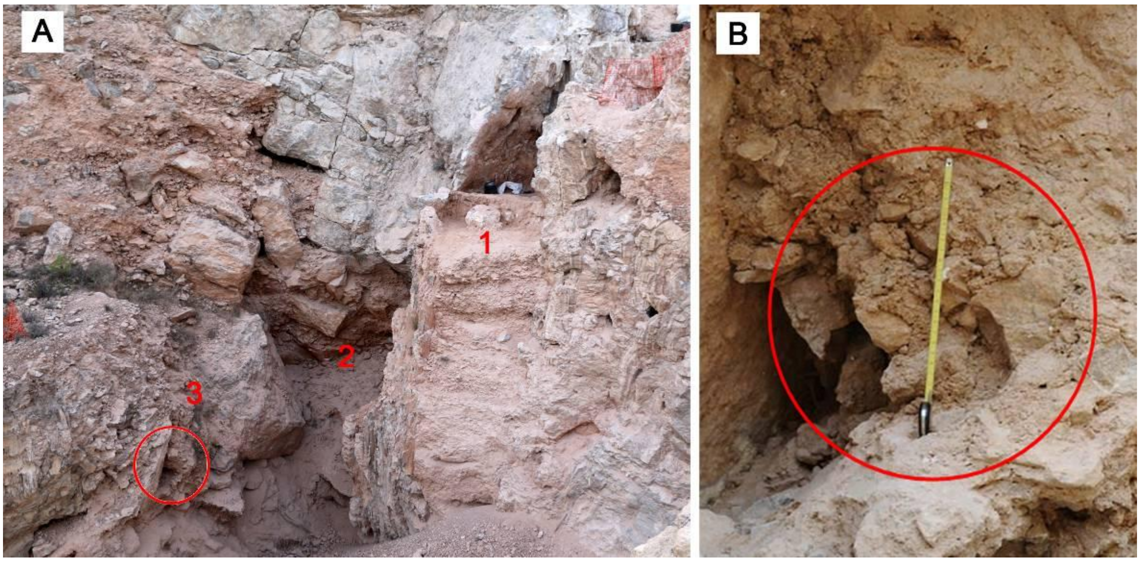

Figura III.21: A) Vista general del yacimiento de Quibas: 1, Sima; 2, Galería; 3, Gruta-1. B) Relleno detrítico de Gruta-1. El círculo rojo señala el área de recogida de la muestra.

IV. METODOLOGIA

IV.1. INTRODUCCIÓN

Las técnicas de recuperación de los fósiles de microvertebrados son diferentes de aquellas usadas para otros grupos de mayor tamaño. Esto se debe principalmente al pequeño tamaño de los restos y a su baja densidad en los yacimientos de origen fluvio-lacustre. De esta forma, se hace uso de métodos de lavado-tamizado. Aunque esta técnica comenzó a ser utilizada en el siglo XIX por Lartet, no fue hasta los años 60 cuando se desarrollaron nuevas metodologías que permitieron su perfeccionamiento y generalización en su uso (Freudenthal et al., 1976; Daams y Freudenthal, 1988). Esto permitió el procesado rápido y efectivo de grandes cantidades de sedimento.

En este capítulo se describen las técnicas usadas para la recuperación, procesado y estudio de los restos analizados en este trabajo.

IV.2. TRABAJO DE CAMPO

El objetivo del trabajo de campo es la recuperación de la microfauna en general, llevándose a cabo normalmente durante la propia campaña de muestreo y/o excavación. Para ello se extrae el sedimento de los distintos niveles en cuestión y se concentra a través de su lavado y tamizado, lo que elimina las fracciones de sedimento que no contienen el material paleontológico de interés (figura IV.1). Con esto es posible recolectar cientos o miles de fósiles.

Aunque en ocasiones los yacimientos de origen kárstico permiten la observación directa de los fósiles de microvertebrados, los paleontólogos especializados en este campo normalmente hacen uso de evidencias indirectas para elegir los niveles que presumiblemente contendrán restos. Esto es así por la dificultad de reconocerlos directamente en el campo dado su pequeño tamaño y baja densidad, especialmente en los yacimientos de origen fluvio-lacustre. En este último caso, los yacimientos más prometedores son aquellos de color oscuro debido a su contenido en materia orgánica, y los que muestran restos de gasterópodos fósiles. No obstante, estas señales no siempre son certeras, por lo que conviene antes de procesar grandes cantidades de sedimento tomar pequeñas muestras y analizar su contenido paleontológico. Así, en una primera fase de prueba se recoge una muestra mínima por nivel de 50 kg de sedimento, mientras que en una segunda fase se procede al muestreo intensivo de aquellos niveles que han ofrecido resultados positivos.

Figura IV.1: A) Realización de anotaciones tras la localización del nivel de interés, y recogida de sedimento. B) Tras la acumulación del sedimento en sacos, se procede a su traslado. C) Una vez se llega al espacio habilitado para el lavado/tamizado, el sedimento se humedece colocándolo en cubos y llenándolos de agua. D) Después de un tiempo de reposo, se procede al lavado/tamizado de las muestras. E) Detalle del lavado de la fracción fina. F) Una vez procesado, el sedimento se deja secar al aire libre.

IV.2.1. Extracción del sedimento

Una vez se localizan los niveles objeto de estudio, tiene lugar la recogida del sedimento (A, B, figura IV.1). Lo primero será hacer un cálculo del volumen necesario de sedimento para poder conseguir una cantidad útil de fósiles y desarrollar un estudio fiable. La cantidad de sedimento necesario para conseguir una muestra significativa varía desde varios kilogramos hasta varias toneladas. Esto depende de la concentración de restos en el estrato pertinente. Normalmente, los yacimientos de origen kárstico contienen una mayor riqueza de microvertebrados que aquellos de origen fluvio-lacustre. Además, los primeros cuentan con una importante ventaja respecto a los segundos, y es su mejor estado de conservación dado su escaso o nulo transporte (Bennàsar, 2010).

Para la recogida de sedimento procedente de excavaciones sistemáticas, el equipo de expertos que se ocupa de las labores de excavación, en vez de eliminar el sedimento generado durante la recuperación de grandes piezas y que a simple vista podría parecer estéril, lo acumulan en sacos apropiadamente etiquetados (por yacimiento, nivel, cuadrícula y fecha) y los ceden al equipo que se ocupa del lavado y tamizado.

Es muy importante mantener un control de la procedencia del sedimento. En todo momento se debe conocer el nivel de origen. Para cada una de las localidades estudiadas en este trabajo se ha considerado indiferente la posición horizontal de la muestra, ya que al tratarse en su mayoría de localidades de origen fluvio-lacustre, no parece haber una distribución preferente en la acumulación de restos. Tampoco así en el caso de la localidad de kárstica de Quibas. El sedimento de este yacimiento se recuperó en el año 2009.

En el caso de la extracción del sedimento procedente de los yacimientos de la cuenca de Fortuna, tuvo lugar a finales de los años 90 y principios de este siglo en una serie de campañas dirigidas por el Dr. Jordi Agustí (figura III.5). Los restos recuperados de los niveles de la sección de Romerales se extrajeron a partir de una cantidad aproximada de 300 kg de sedimento poco antes de la desafortunada desaparición de gran parte de la sección bajo obras públicas (D, figura III.7). Los fósiles de la sección de Sifón de Librilla se tomaron a partir de grandes cantidades de sedimento, en paralelo a un muestreo paleomagnético. Los trabajos preliminares desarrollados durante 1999 y 2000 proporcionaron evidencias de la existencia de una secuencia muy completa de microvertebrados. Para la campaña de 2001 los esfuerzos se centraron en el muestreo extensivo de la parte alta de esta sección, especialmente en los niveles que afloraban por encima de la transgresión marina (indicativa del inicio del Plioceno; SIF-413, SIF-430 y SIF-P), dada su ubicación estratégica para poder llevar a cabo correlaciones marino-continentales.

Para la obtención de los fósiles del yacimiento del Puerto de la Cadena se hizo necesario el procesado de importantes cantidades de sedimento, ya que éste se mostró muy pobre en restos de pequeños mamíferos. La recogida del mismo tuvo lugar durante las excavaciones sistemáticas de los años 2009, 2010 y 2011. El sedimento del yacimiento de Baza-1 se recogió durante la campaña de excavación del año 2001, aunque la recuperación de los fósiles que contenía no tuvo lugar hasta que se inició el presente trabajo.

IV.2.2. Procesado de la muestra

Una vez recogido el sedimento, se traslada a un espacio habilitado para proceder al lavado/tamizado de la muestra. Dicho espacio fue diferente según las localidades estudiadas. En el caso del sedimento procedente de las secciones de Romerales y Sifón de Librilla, el lavado/tamizado tuvo lugar a orillas del Embalse de Santomera (Murcia). El sedimento del yacimiento del Puerto de la Cadena y de Quibas se procesó en la depuradora de aguas del Campus de Espinardo (Universidad de Murcia). Las muestras procedentes de Baza-1 se lavaron en un pequeño curso de agua del municipio de Orce (Granada).

Una vez se dispone de tal espacio, los sacos se clasifican según su etiqueta para así evitar contaminación, esto es, mezcla de fósiles originarios de diferentes niveles. Posteriormente, el sedimento se reparte en cubos llenándolos hasta la mitad, y el resto con agua, lo cual permite la floculación de las arcillas facilitando el proceso de lavado (C, figura IV.1). Tras un tiempo de reposo, se pasa al lavado/tamizado con agua a presión que se consigue por medio del uso de una bomba de succión colocada junto a la fuente de agua (D, E, figura IV.1). Para el lavado se utilizan tres tamices de aluminio superpuestos, con luz de malla de 4 mm, 1 mm y 0,5 mm formando una columna en orden decreciente de tamaño de luz de malla. Esto permite la fracción de la muestra por tamaños facilitando su posterior tratamiento en el laboratorio. La fracción de 0,5 mm es el límite de luz de malla más pequeño que normalmente se emplea para recuperar la mayoría de restos de microvertebrados (López Martínez, 1992). Así, la fracción arcillosa que no contiene elementos útiles se elimina. El contenido de los cubos se vacía sobre el primer tamiz y se rocía con agua. Una vez lavado, el sedimento del primer tamiz (el de mayor tamaño) se supervisa y los restos fósiles se incorporan al segundo tamiz, desechando los residuos restantes. El sedimento del segundo y tercer tamiz se pone a secar por separado (F, figura IV.1), evitando la exposición a altas temperaturas para no dañar la muestra fósil por la aparición de grietas. Cuando se seca completamente, se recoge en bolsas por separado según el tamaño del concentrado, quedando por una parte el concentrado grueso (procedente del tamiz de 2 mm) y por otra el concentrado fino (procedente del tamiz de 0,5 mm).

IV.3. TRABAJO DE LABORATORIO

IV.3.1. Relavado

En ocasiones, y especialmente cuando la muestra no se encuentra completamente seca en el momento de su lavado en el campo, el sedimento concentrado obtenido puede contener restos de arcilla. Para reducir al máximo el volumen de estos residuos, se vuelve a lavar tras un secado en la estufa. Para ello se usan tamices con una luz de malla similar a la usada en el campo.

IV.3.2. Triado

Tras el lavado y tamizado del sedimento, el siguiente paso es el triado en el laboratorio (A, figura IV.2). Éste consiste en la separación de los restos de microfauna, del concentrado. Se hace a simple vista en el caso del material grueso, mientras que para el material fino se requiere una lupa que mejore la visibilidad. Para ello se extiende en pequeñas porciones sobre un folio en blanco (con lo que se mejora el contraste) en una superficie plana, y con la ayuda de unas pinzas se recuperan los fósiles, desechando el material estéril (B, figura IV.2). Los restos post-craneales se van acumulando en cajas transparentes de metacrilato, mientras que los elementos craneales (maxilares, mandíbulas y dientes) se van separando según el grupo taxonómico al que pertenezcan. Las cajas son sigladas por medio de etiquetas.

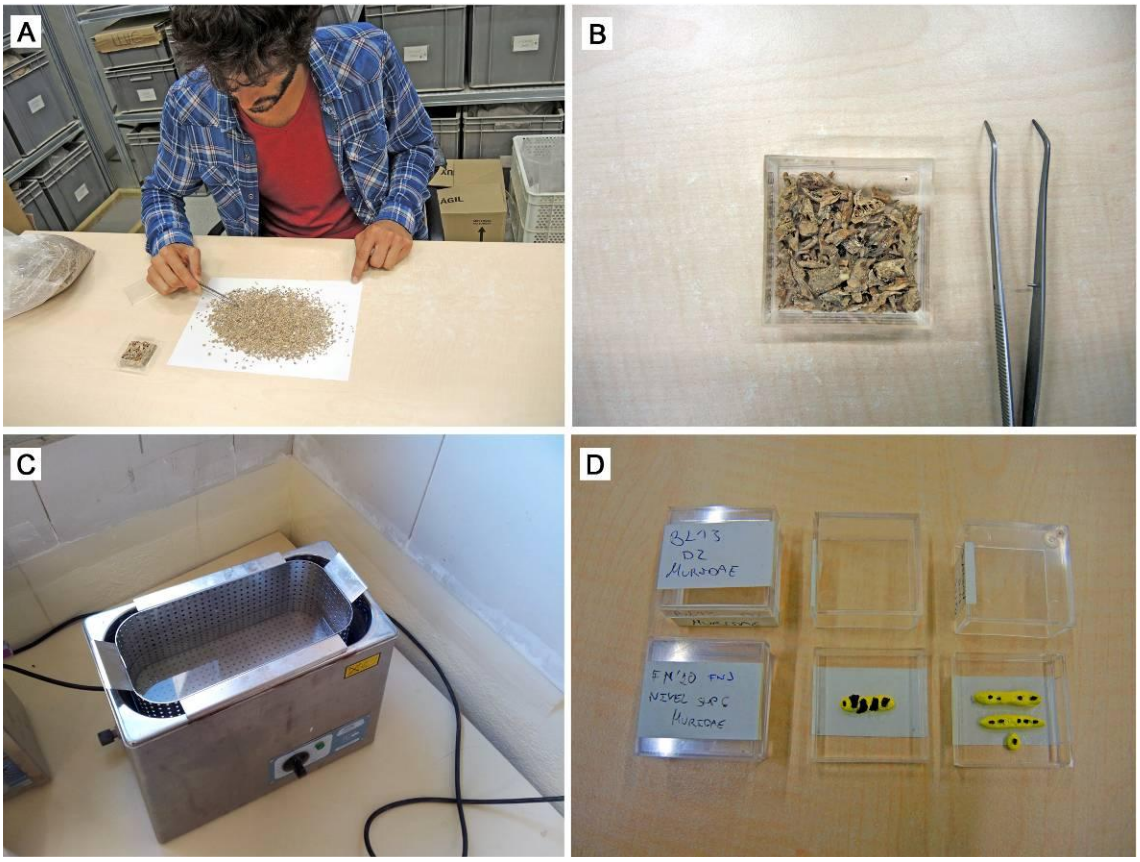

Figura IV.2: A) Triado a simple vista de la fracción gruesa del sedimento lavado y tamizado. B) Acumulación de restos de microfauna en una caja de metacrilato transparente. C) Cubeta de ultrasonidos. D) Elementos craneales montados en cajas de metacrilato debidamente etiquetadas.

IV.3.3. Preparación y conservación

La preparación consiste en la limpieza de los restos, en este caso de los craneales. La gran mayoría de los fósiles procedentes de la Gruta-1 del yacimiento de Quibas aparecieron con costras de carbonato adheridas a su superficie oclusal, lo que impedía su estudio taxonómico. Para eliminarlas, se introdujeron las muestras en una solución de ácido acético al 10% durante 10 minutos, puesto que éste reacciona con el carbonato produciendo CO_2 (que se evapora) y acetato (soluble en agua). Posteriormente, las muestras se lavaron con agua y se dejaron reposar durante 30 minutos para eliminar todo el ácido, evitando futuros daños en los fósiles.

Los dientes procedentes de las secciones de Sifón de Librilla y Romerales presentaban en su superficie oclusal restos de arcillas. Así, la muestra fue sometida durante 30 segundos a ligeras vibraciones haciendo uso de una cubeta de ultrasonidos (C, figura IV.2), consiguiendo así una limpieza absoluta de los dientes.

Cuando los restos craneales se secaron completamente se montaron en cajas transparentes de metacrilato previamente sigladas. Esto consiste en colocarlos sobre hilos de masilla adhesiva (Blue-Tack®) adherida en la tapa de las cajas (D, figura IV.2). Se ordenaron según el grupo taxonómico al que pertenecían, el tipo de molar separando los dientes superiores de los inferiores, y su posición en la serie dentaria (M1-M2-M3).

IV.4. NOMENCLATURA Y BIOMETRÍA

Para la descripción de los molares de los múridos se ha utilizado la nomenclatura propuesta por van de Weerd (1976), la cual se puede consultar en la figura IV.3. Para la toma de medidas se han seguido los criterios utilizados por Martín Suárez y Freudenthal (1993). Todas las medidas están expresadas en milímetros. Se ha establecido una serie de líneas de referencia con la finalidad de situar los elementos dentarios para tomar las medidas, distintas según el tipo de molar, pero en todo caso marcadas según la orientación de los elementos. En el M_1 y M_2, dicha línea de referencia no es necesariamente idéntica o paralela a la cresta longitudinal. Tanto la anchura como la longitud se miden según el rectángulo más pequeño circunscrito a los lados paralelo y perpendicular respecto a la línea de referencia (figura IV.4).

M_1. La línea de referencia recorre el centro del diente por la unión del anterocónido con el protocónido-metacónido, y atraviesa el centro de la pared posterior.

M_2. La línea de referencia es la base del borde anterior del molar.

M_3. La línea de referencia es el borde anterior del protocónido-metacónido al nivel de la superficie de desgaste.

M^1. La línea de referencia es la tangente al borde del t3 y t9. En la práctica, esta línea es casi paralela a la línea que conecta los centros del t2, t5 y t8.

M^2. La línea de referencia es la tangente a la base de la pared anterior del diente, o, cuando este borde es convexo, la tangente de la parte labial de dicho borde.

M^3. La línea de referencia es el borde anterior del molar al nivel de la superficie de desgaste.

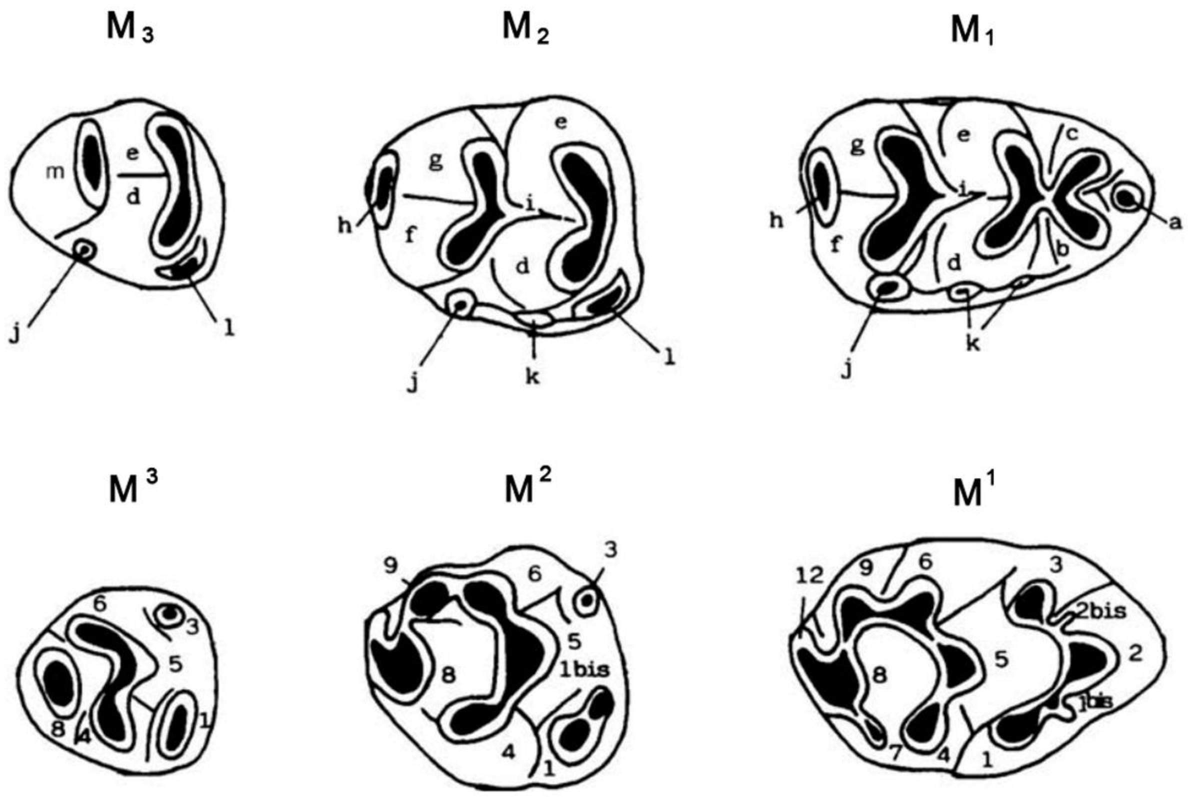

Figura IV.3: Terminología empleada para la descripción de los molares de Muridae. Molares inferiores: a) tubérculo medio anterior (tma), b) lóbulo labial del anterocónido, c) lóbulo lingual del anterocónido, d) protocónido, e) metacónido, f) hipocónido, g) entocónido, h) cíngulo posterolingual o tubérculo posterior, i) cresta longitudinal, j) cúspide accesoria posterior (c1), k) cúspides accesorias en el cíngulo labial, l) cúspide anterolabial, m) complejo posterior. Molares superiores: las cúspides se han numerado según Miller (1912), indicándose en la figura y en el texto con el prefijo t (tubérculo). Modificado de van de Weerd (1976).

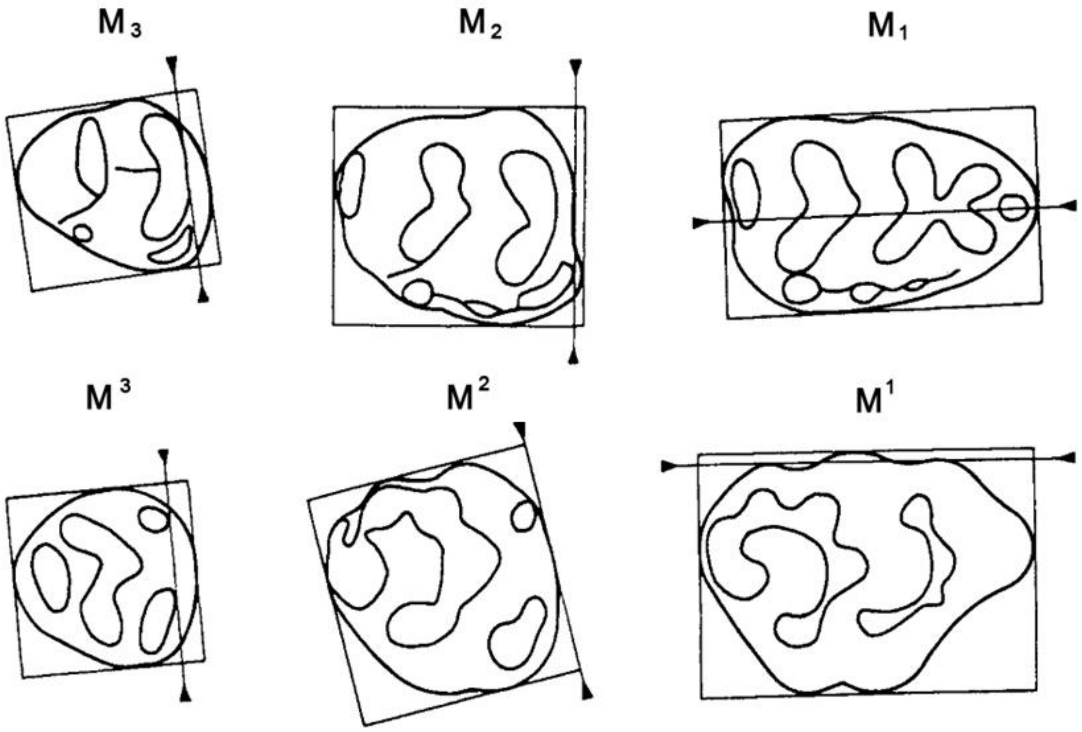

Figura IV.4: Método empleado para la toma de medidas de los molares de Muridae. Las líneas de referencia se indican mediante triángulos. Tomado de Martín Suárez y Freudenthal (1993).

IV.5. ANÁLISIS NUMÉRICOS

IV.5.1. Cálculo de la composición cuantitativa

Hay varias formas de calcular la composición cuantitativa de las asociaciones de micromamíferos. En algunos estudios se hace uso del Número Mínimo de Individuos (NMI), que se obtiene según el elemento dentario más abundante en la muestra de cada taxón, teniendo en cuenta la lateralidad. Sin embargo, este método no es usual en el análisis de las abundancias relativas dirigidas a estudios paleoecológicos, ya que generalmente se debe aplicar a muestras que no han sido transportadas (Avery, 2003; Chaline et al., 1995; Minwer-Barakat, 2005).

La composición cuantitativa de las asociaciones de micromamíferos de los yacimientos a los que se les ha aplicado un análisis paleoecológico (capítulos V, VIII y XI) se ha calculado en base a la abundancia relativa de cada taxón (siguiendo a Martín Suárez, 1988; Castillo Ruiz, 1990; Martín-Suárez et al., 2001; Minwer-Barakat, 2005; García-Alix et al., 2009; entre otros). Para evitar la sobrerrepresentación de un grupo, se ha usado el número total de dientes de cada taxón, dividido por su número de elementos diagnósticos (Muridae, Cricetidae, Gerbillidae y Trilophomyidae: 12 molares; Gliridae y Sciuridae: 16 dientes; Soricidae: 20 dientes; Erinaceidae: 44 dientes). De esta forma se obtienen índices de representación ponderada con los que se calculan los porcentajes de representación de cada taxón.

IV.5.2. Diversidad específica (Índice de Shannon-Weaver)

El índice de Shannon-Weaver (Shannon y Weaver, 1949) se ha utilizado para el análisis de la evolución de la diversidad específica en la sección de Romerales (capítulo V).

El cálculo de la diversidad específica permite establecer una estimación cuantitativa de la heterogeneidad de una comunidad expresando la relación entre el número de especies existentes y la distribución de individuos entre las distintas especies. Un alto valor puede indicar una buena organización del ecosistema y de unas condiciones ecológicas favorables (Margalef, 1974). El índice de Shannon (H´) es uno de los más extendidos, habiendo sido usado en muchos estudios micropaleontológicos (Martín Suárez, 1988; Castillo Ruiz, 1990; Sesé, 1991; Chaline et al., 1995; Ruiz Sánchez, 1999; López Antoñanzas y Cuenca-Bescós, 2002; Pazonyi, 2004; entre otros). Esta índice responde a la siguiente fórmula:

$$H' = \sum_{i=1}^{S} p_i \ln p_i$$

S: número de especies.

p_i: abundancia relativa de la especie i expresada en decimal.

El valor de este índice será nulo cuando la muestra contenga una sola especie, y será máximo cuando todas las especies estén representadas por el mismo número de individuos. De esta forma aumenta con el número de especies y con la uniformidad en la distribución de los individuos entre ellas, lo que se traduce en un aumento cuando no hay dominancia de una especie sobre otra.

IV.5.3. Variabilidad de la muestra (coeficiente de variación)

En ocasiones, las muestras de dientes estudiadas presentan una amplia heterogeneidad en el tamaño, ofreciéndonos dudas acerca de su pertenencia a una o más especies. Esta amplia heterogeneidad efectivamente puede ser debida a la mezcla de dos especies, aunque también a la mezcla de material de varios biotopos, o a que la muestra procede de un rango temporal amplio. Freudenthal y Cuenca Bescós (1984) propusieron un coeficiente de variación (V') basándose en el análisis del rango de tamaño de 140 muestras de cricétidos del "Terciario" de Europa, para estimar el grado de variabilidad de las mismas. Estos autores llegaron a la conclusión de que el coeficiente de variación de Pearson no es una buena herramienta en paleontología. El resultado del nuevo coeficiente propuesto ayuda a discernir si la muestra es homogénea o no, y así a decidir si pertenece a una o más especies. Posteriormente Freudenthal y Martín Suárez (1990) aplicaron este método para calcular el coeficiente de variación de 200 muestras de dientes de múridos fósiles y actuales. En el capítulo VI se aplica este coeficiente para determinar la variabilidad en el tamaño de los dientes de *Paraethomys* del nivel SIF-413. La fórmula de este coeficiente responde a:

$$V' = \frac{100R}{M}$$

R: rango de la muestra, es decir la diferencia entre el valor máximo y el mínimo.

M: punto medio entre el máximo y el mínimo.

El número mínimo de molares de la muestra que se quiere analizar debe ser de cinco.

IV.6. INSTRUMENTOS DE OBSERVACIÓN, FOTOGRAFÍA Y TOMA DE MEDIDAS

Para la identificación de los restos de Muridae se ha hecho uso de una lupa binocular OLYMPUS SZ-40, con un sistema de zoom que permite conseguir entre 18 y 110 aumentos. Todas las medidas se han tomado sobre el plano oclusal de los dientes con el software DinoCapture 2.0, utilizando fotografías tomadas de un microscopio digital modelo AM4115TL Dino-Lite Edge (A, figura IV.5). En el caso concreto de los fósiles procedentes de la Gruta-1 de Quibas (capítulo X) se ha usado el software Adobe Photoshop CS5 usando fotografías de una cámara Infinity X acoplada a un microscopio binocular Olympus SZ-40. Las imágenes de los molares que se muestran en las láminas de los diferentes capítulos han sido realizadas con el microscopio electrónico de barrido ambiental (ESEM) del “Servei de Recursos Científics i Tècnics de la Universitat Rovira i Virgili” de Tarragona (B, C, figura IV.5).

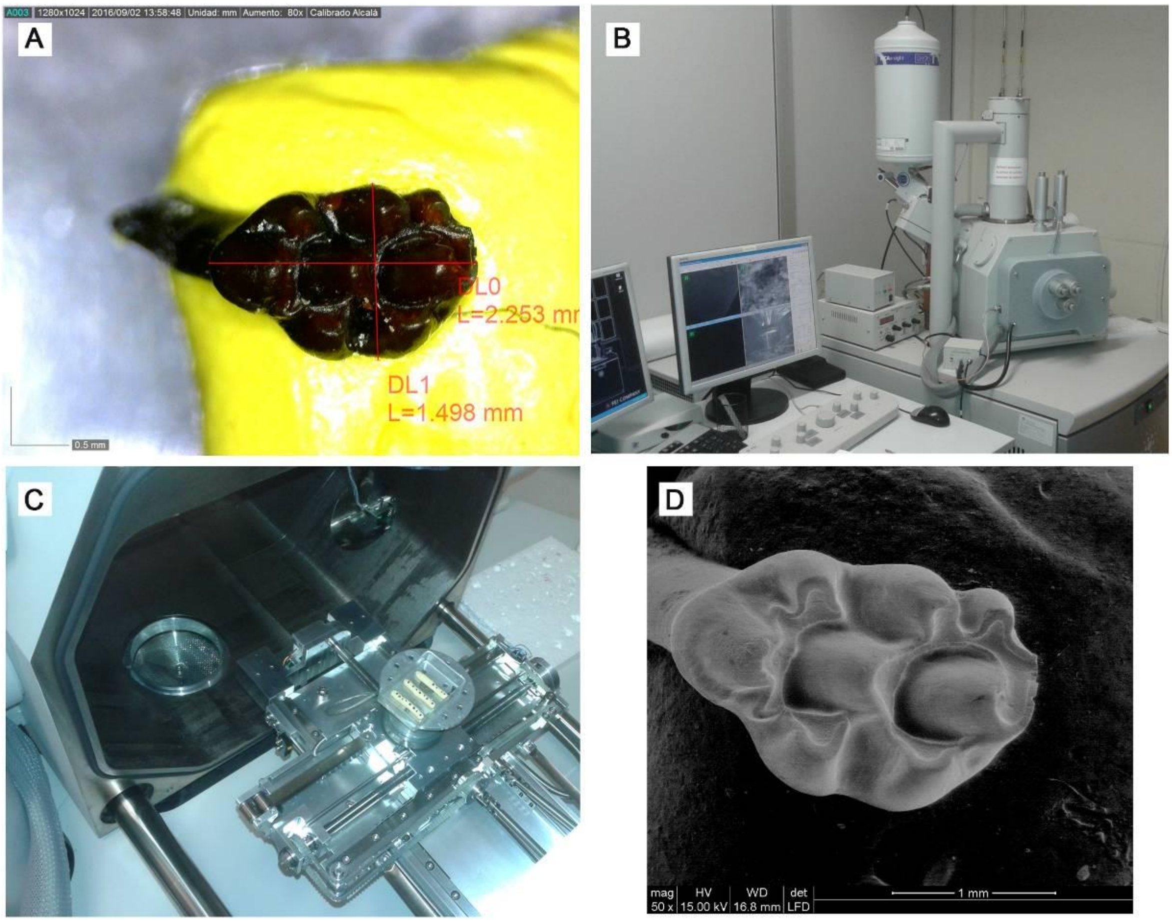

Figura IV.5: A) Toma de medidas de un M^1 de *Occitanomys brailloni* de SIF-413 mediante el uso del software DinoCapture 2.0. B) Microscopio electrónico de barrido ambiental (ESEM) del “Servei de Recursos Científics i Tècnics de la Universitat Rovira i Virgili”. C) Introducción de las muestras en el ESEM para la obtención de imágenes. D) Imagen del M^1 de *O. brailloni* obtenida a través del ESEM.

IV.7. DEPÓSITO DEL MATERIAL ESTUDIADO

El material que se ha estudiado forma parte de diferentes colecciones depositadas en diferentes instituciones. El material procedente de la Gruta-1 del yacimiento de Quibas se encuentra actualmente custodiado en instalaciones del Institut de Paleoecologia Humana y Evolució Social (Tarragona), a la espera de ser depositado en el Museo de Arqueología de Murcia (Murcia). La colección del yacimiento del Puerto de la Cadena se encuentra depositada en esta última institución. El material procedente de las secciones de Sifón de Librilla y de Romerales está depositado en el Institut Català de Paleontologia Miquel Crusafont (Sabadell, Barcelona), a la espera también de ser devueltos al Museo de Arqueología de Murcia. Los fósiles del yacimiento de Baza-1 son propiedad de la Junta de Andalucía, aunque actualmente una parte de la colección permanece en el Institut de Paleoecologia Humana y Evolució Social, y la otra parte en el Institut Català de Paleontologia Miquel Crusafont.

IV.8. ABREVIACIONES

A continuación se muestran las abreviaciones que se han usado en los diferentes capítulos para hacer referencia a localidades, centros de investigación, museos, elementos dentales, parámetros y medidas, y otros:

ACB, Almenara-Casablanca; **ABS**, Alcoi Barranc Sud; **AC**, Alcoi Cristian; **AD**, duración de la aridez; **AF**, Alcoi Forn; **AG**, Alhaurín el Grande; **AL**, Alcoy; **ALD**, Aldehuela; **ALJ**, Aljézar; **ARQ**, Arquillo; **ATNTS**, Astronomical Tuned Neogene Time Scale ; **AU**, Autovía; **Be**, Belmez; **Bo**, Botardo; **BS**, Barranco de la Salada; **Bz**, Baza; **BUN**, Bunker de Valdecebro; **c1**, cúspide accesoria posterior; **CAC**, Cacín; **CC**, Concud Cerro de la Garita; **CDA**, Casa del Acero; **CEL**, Celadas; **CH**, Chorrico; **CLC**, Calicasas; **CR**, Crevillente; **DHS**, Dehesa; **ES**, error estándar; **FAD**, First Appearance Datum; **FO**, First Occurrence; **FV**, Fuente del Viso; **G1**, Gruta-1; **Go**, Gorafe; **ICP**, Institut Català de Paleontologia Miquel Crusafont; **IPHES**, Institut Català de Paleoecologia Humana i Evolució Social; **IPS**, Institut de Palentologia de Sabadell Miquel Crusafont (actualmente Institut Català de Paleontologia Miquel Crusafont); **JUN**, Canteras de Jun; **L**, longitud; **LAD**, Last Appearance Datum; **LB**, La Bullana; **LF**, La Fontana; **LIB**, Librilla; **LG**, La Gloria; **LM**, Los Mansuetos; **M1/M^1**, primer molar superior; **m1/M$_1$**, primer molar inferior; **M2/M^2**, segundo molar superior; **m2/M$_2$**, segundo molar inferior; **M3/M^3**, tercer molar superior; **m3/M$_3$**, tercer molar inferior; **MAM**, Museo Arqueológico de Murcia; **MAP**, precipitación media anual; **MAT**, temperatura anual media;

MATA, amplitud térmica media anual; **MCC**, Moncucco Torinese; **MDV**, Masada del Valle; **MN**, European Neogene land mammal units; **MNA**, Mina; **Mo**, Moreda; **MS**, Molina de Segura; **MSC**, Messinian Salinity Crisis; **MTC**, temperatura media del mes más frío; **MTW**, temperatura media del mes más cálido; **NGR**, Negratín; **ORR**, Orrios; **OTU**, Otura; **PC**, Puerto de la Cadena; **PER**, Peralejos; **PUR**, Purcal; **QB**, Quibas; **r^2**, coeficiente de determinación; **RCH**, Rambla de Chimeneas; **ROM**, Romerales; **SIF**, Sifón de Librilla; **t1-t12**, tubérculos numerados del 1 al 12; **TCH**, Tollo de Chiclana; **tma**, cúspide anterocentral; **TO**, Tortajada; **VAR**, Villalba Alta Río; **VDC**, Valdecebro; **VER**, Verduno; **VIL**, Villastar; **VIZ**, Viznar; **VVm**, Venta del Moro; **W**, anchura; **YEG**, Yeguas; **ZOR**, Zorreras.

V. ROEDORES E INSECTÍVOROS DEL MIOCENO SUPERIOR DE ROMERALES (CUENCA DE FORTUNA, SE ESPAÑA)

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Rodents and insectivores from the late Miocene of Romerales (Fortuna Basin, Southern Spain)

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ABSTRACT

The Neogene Fortuna Basin (Murcia Region, SE Spain) is rich in microvertebrate sites. Its continental sections include localities extended from the middle Turolian (MN12) to the early Ruscinian (MN14). However, there are few works dealing with the taxonomy of these fossil assemblages. In this paper we provide a complete taxonomic study of the rodents and insectivores from three levels (ROM-2B, ROM-2C and ROM-3A) within the Romerales section. We infer a late Turolian age (late Messinian) for these levels, among which the richest and most diverse level is ROM-C, including at least 11 different taxa. In addition, the paleoecological analysis of these fossil assemblages suggests the dominance of open herbaceous meadows under temperate climate during the formation of these sites, with a slight decrease in temperature and humidity from ROM-2B to ROM-2C.

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Late Miocene; micromammal; biostratigraphy; palaeoecology; Fortuna Basin

Introduction

The Fortuna Basin is a Neogene filling located in the Murcia Region (SE Spain). It is situated at the contact between the Internal and the External Betic Zones. The Romerales section is placed shortly after leaving the town of Molina de Segura (Figure 1). Unfortunatley, after the extraction of the studied material during the nineties, most of the outcrop disappeared under civil works. The coordinates correspond to 38° 4′ 21″ N, 1° 12′ 10″ W.

The first studies of the continental records in the Fortuna Basin were carried out by Montenat and Crusafont (1970) showing up the late Turolian locality of Librilla. After the site came to light, some works on the vertebrate remains were published (Montenat 1973; de Bruijn et al. 1975; Montenat et al. 1975; Alberdi et al. 1981). Another classic site of the Fortuna Basin is Casa del Acero, close to the Chícamo section (Agustí et al. 2001, 2006; Garcés et al. 2001). This middle Turolian locality (late Tortonian, MN12) was studied by Agustí et al. (1981), followed by Agustí (1986), Agustí et al. (1983) and Pons-Moyà (1987). Agustí et al. (1983) was the first geological and bioestratigraphical synthesis of the continental deposits placed in the Fortuna basin, including also the late Turolian sequence of Molina de Segura (= Salinas de Molina in Agustí et al. 2006).

The Fortuna Basin records evaporite sediments over a regressive marine sequence below the continental packets. The dating of these deposits has been the target of a wide discussion (Santisteban 1981; Santisteban and Taberner 1983; Muller and Hsu 1987; Muller and Schrader 1989; Ortí et al. 1993; Mankiewicz 1995; Playà et al. 1995; Dinarès-Turell et al. 1999; Krijgsman et al. 2000; Tent-Manclús et al. 2008).

Garcés et al. (1998, 2001) established a reliable time frame for the sedimentary infilling of the Fortuna Basin through detailed magnetostratigraphic studies, in which the continental sequences from middle Turolian (MN12) to lower Ruscinian (MN14) were included (Barranco de la Salada, Río Chicamo, El Chorrico, Salinas de Molina and Sifón de Librilla). Based on the fossil vertebrate record and the magnetostratigraphic information, Agustí et al. (1999, 2006) established an accurate chronology for the main mammalian events occurred in the Western Mediterranean between 7.6 and 4.5 Ma. These authors published small-mammal lists from several sites, though the taxonomic information is very limited.

As stated above, the continental sequences of the Fortuna Basin provide a reliable and detailed biostratigraphic record, being exceptionally suitable for the study of small mammal evolution fossil during the late Miocene and early Pliocene. This paper presents a complete taxonomic study of the rodents and insectivores obtained in the Romerales section, as well as their biostratigraphical and palaeoecological implications.

Material, methods and abbreviations

The microfaunal remains were extracted from about 300 kg of sediment from the levels ROM-2B, ROM-2C and ROM-3A. All the sediment was water-screened using superimposed 4, 1 and 0.5 mm mesh screens. The specimens described are currently kept at the *Institut Català de Paleontologia Miquel Crusafont* (ICP; Sabadell, Barcelona, Spain).

The material from the level ROM-2B comprises 131 teeth of rodents and insectivores, while ROM-2C is the richest with

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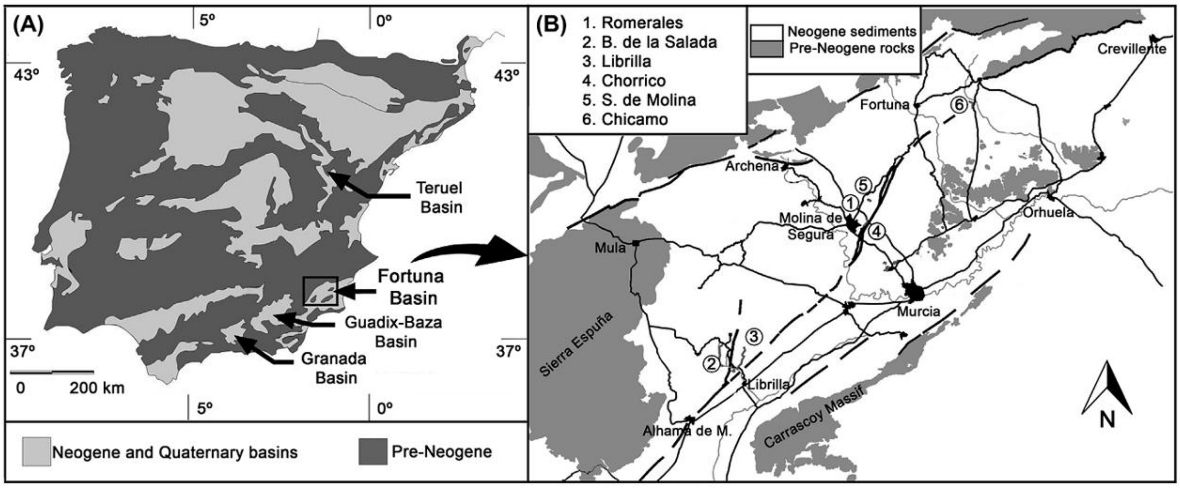


Figure 1. Geological setting of the Romerales section.
Notes: (A) Simplified map of the Iberian Peninsula, with indication of main Neogene and Quaternary basins referred in text. (B) Fortuna Basin with location of Romerales and other related sections.

414 specimens and ROM-3A represents the poorest locality with only 4 elements. The assemblage represents at least 11 taxa. All the measurements ($L \times W$) are expressed in millimeters and were taken on the occlusal plane of the molars with the software DinoCapture 2.0, using photographs from the Digital Microscope AM4115TL Dino-Lite Edge. The images shown in the plates were made with the Environmental Scanning Electron Microscopy (ESEM) of the 'Servei de Recursos Científics i Tècnics de la Universitat Rovira i Virgili' (Tarragona). The upper teeth are designates as I1, P3, P4, M1, M2 and M3 and the lower teeth as p2, p3, p4, m1, m2 and m3.

The nomenclature and measuring methods used in the descriptions of the Muridae teeth are those defined by van de Weerd (1976) and Martín Suárez and Freudenthal (1993), respectively. Mein and Freudenthal (1971) have been followed in describing and measuring the Cricetidae teeth. Van de Weerd (1976) and Qiu (1996) have been followed for the measurement and nomenclature of the Sciuridae respectively. We use the terminology and methods of Reumer (1984) for the Soricidae family and Mein and Martín Suárez (1993) for the Erinaceidae family. The terminology used for the description of the teeth of Gliridae is that of Daams (1981), and length and width have been measured as defined by Freudenthal (2004).

The quantitative composition of the micromammal assemblage has been calculated on the basis of the relative abundance of each taxon (following Martín Suárez 1988; Castillo Ruiz 1990; Martín-Suárez et al. 2001; Minwer-Barakat 2005; García-Alix et al. 2008a; García-Alix et al. 2009). To avoid the over-representation of a taxon, we used the total number of teeth of each taxon, divided by its number of diagnostic elements (Murinae and Cricetidae: 12 molars; Gliridae and Sciuridae: 16 teeth; Soricidae: 20 teeth; Erinaceidae: 44 teeth).

The specific diversity (distribution of the number of individuals in relation to the number of species) has been measured using the Shannon-Wiener index (Shannon and Weaver 1949) since it is the most widely used to measure ecological diversity (Matín Suárez 1988; Castillo Ruiz 1990; López Antoñanzas and Cuenca Bescós 2002; Minwer-Barakat, 2005, among others). The Shannon-Wiener index is usually indicated by the symbol H' and is designated by the next mathematical formula:

$$H' = \sum_{i=1}^{S} p_i \ln p_i$$

where S is the number of species and p_i is the relative abundance of the species i expressed as a decimal. The value of this index is lower when there is clear dominance of one species over others, i.e. when the specific variability is low.

Abbreviations: ALJ, Aljézar; ARQ, Arquillo; AU, Autovía; BS, Barranco de la Salada; CAC, Cacín; CEL, Celadas; CH, Chorrico; CR, Crevillente; PUR, Purcal; DHS, Dehesa; JUN, Canteras de Jun; LIB, Librilla; LG, La Gloria; LM, Los Mansuetos; MDV, Masada del Valle; MNA, Mina; MS, Molina de Segura; NGR, Negratín; OTU, Otura; RCH, Rambla Chimeneas; ROM, Romerales; SIF, Sifón de Librilla; VDC, Valdecebro; VIL, Villastar; VIZ, Víznar; ZOR, Zorreras.

IPHES, Institut Català de Paleoecologia Humana i Evolució Social; ICP, Institut Català de Paleontologia Miquel Crusafont.

AW, anterior width; BL, buccal length; c1, posterior accessory cusp; FAD, First Appearance Datum; H, height; L, length; LL, lingual length; LT, length talon; MN, European Neogene land mammal units; PE, posterior emargination; PW, posterior width; t1-t12, numbered tubercules from 1 to 12; TAW, talonid width; tma, anterocentral cusp; TRW, trigonid width; W, width.

Geological setting

The Fortuna Basin was formed as a result of the Late Tortonian to Present NE-SW strike-slip tectonics in the Eastern Betics, in the context of the convergence between the African and Iberian plates (De Larouzière et al. 1988; Montenat et al. 1990; Sanz de Galdeano 1990; Sanz de Galdeano and Vera 1992; Garcés et al. 2001; Agustí et al. 2006). Garcés et al. (1998, 2001) distinguished three main units in the sedimentary infill of the Fortuna Basin:

(1) a Tortonian transgressive marine unit;
(2) a latest Tortonian regressive marine to transitional evaporitic unit;
(3) a Messinian to Pliocene thick continental alluvial and lacustrine unit.

In the Tortonian, a rapid initial subsidence and marine transgression started in the Fortuna Basin. Then, the uplift of the Internal Zones of the Betic chain occurred during the Late Tortonian lead to a progressive isolation of the Fortuna Basin from the open Mediterranean Basin. This marine-continental transition took place between 7.8 and 7.6 Ma, and those continental beds are continuously recorded along the time interval between 7.6 and 4.8 Ma (Garcés et al. 1998, 2001). The confinement and the following precipitation of evaporites in the Fortuna Basin in the latest Tortonian rejects the inclusion of the Fortuna basin in a hypothetical Betic marine corridor during the Late Messinian (Muller and Hsu 1987). In any case, what we can find are Messinian marine sediments interfingered with late Turolian continental units due to a marine connection towards the southeastern margin (Mein et al. 1973). The Fortuna Basin records the sea level drop occurred during the Messinian Salinity Crisis at 5.96 Ma in the Librilla area by a valley incision followed by sudden gravel progradation. The normal marine conditions in the Mediterranean at the beginning of the Pliocene are represented in the Fortuna Basin by a short pulse of a very restricted transgression (Agustí et al. 2006).

The Fortuna Basin was a poorly drained, confined continental basin during the Messinian. Occasionally the distal areas developed shallow lacustrine and palustrine environments (Agustí et al. 2006). The resulting palustrine-lacustrine sediments embedded over the confined shallow basin of Fortuna have yielded rich small mammal assemblages from latest Tortonian (middle Turolian) to Messinian (late Turolian) and early Pliocene (early Ruscinian) along a number of continuous continental sections. In the studied case, the Romerales section is integrated in the lower part of the Chorrico section (Garcés et al. 1998, 2001) (Figure 2(A)), in a state prior to the arrival of *Paraethomys*.

The Romerales section (Figure 2(B)) contains various fossiliferous levels rich in vertebrate remains. Most of them present fragmented bones of large mammals, and three have yielded microvertebrates. The level named ROM-2B is the lowest among those containing microfauna, and is situated at the metre 36 of the section. It is a grainstone level rich in coal granules and gastropod and bivalves fragments as well as fragmented remains of large mammals (such as *Hipparion*). The microvertebrate fossils are abundant and well-preserved. The matrix consists of ocher and gray sands. Immediately thereabove is bedded the level named ROM-2C, formed by dark clays and gastropods fragments. It is the richest level in microfauna whose specimens are very well-preserved. The uppermost level is known as ROM-3A and is very poor in small mammals compared to the previous two. This level is formed by grey clays and contains fragmented bones of large mammals.

Systematic palaeontology

Order Rodentia Bowdich, 1821
Family Muridae Illiger, 1811
Subfamily Murinae Illiger, 1811
Genus *Stephanomys* Schaub, 1938
Stephanomys ramblensis van de Weerd, 1976 (Figure 3(A)–(M))

Material and localities

ROM-2B: 14 M1 (IPS-90194–IPS-90203, IPS-90210–IPS-90212, IPS-90218), 11 M2 (IPS-90204–IPS-90209, IPS-90213–IPS-90217), 5 M3 (IPS-90220–IPS-90224), 21 m1 (IPS-90219, IPS-90225–IPS-90244), 6 m2 (IPS-90245–IPS-90250), 7 m3 (IPS-90251–IPS-90257).

ROM-2C: 63 M1 (IPS-90296–IPS-90358), 45 M2 (IPS-90359–IPS-90403), 21 M3 (IPS-90404–IPS-90424), 66 m1 (IPS-90425–IPS-90490), 51 m2 (IPS-90491–IPS-90541), 20 m3 (IPS-90542–IPS-90561).

ROM-3A: 1 m2 (IPS-90193).

Measurements: Table 1.

Description of the material from ROM-2C

m1: Nine out of 53 molars show a small and low tma. The longitudinal crest is medium-sized in most specimens but weak in three of them. It is usually connected to the metaconid-protoconid junction. The anteroconid is symmetrical in almost all molars. The protoconid and hypoconid are slightly displaced backward with respect to the metaconid and entoconid, respectively. The posterior heel is long and narrow in most individuals but oval in five of them. It may extend behind the entoconid. The labial cingulum is generally weak or moderate. The c1 is subtriangular or oval and connected to the hypoconid by a crest. One to two accesory labial cusps are distinguished in 14 out of 53 elements. There are two roots.

m2: The anterolabial cusp is large, oval and it is in contact with the anterior side of the protoconid and with a low labial cingulum. A small c1 is present in most specimens. There are seven individuals with one or two accessory labial cusps. The longitudinal ridge is strong and connected to the center of the metaconid-protoconid center in most specimens. The terminal heel is narrow and elongated or oval. There are two roots.

m3: The anterolabial cusp is low and reduced. A small c1 attached to the hypoconid-entoconid complex is present in seven individuals. There is no t3. The longitudinal crest is developed in 16 out of 20 specimens. There are two roots.

M1: The t1 is situated backwards. The t1-t5 connection is basal in 48 specimens, high in 6 and absent in 7. The t3 contacts the t5 through a high crest in 14 molars and moderate or weak in 27. The others 20 individuals have a small spur directed to t5 but there is no contact. The t1bis is present in all specimens but four. The t2bis is developed in 41% of the specimens. One specimen (IPS-90343) develops an extra-cusp in the anterolabial face of the t2 connected to an elongated t2bis. The connection between

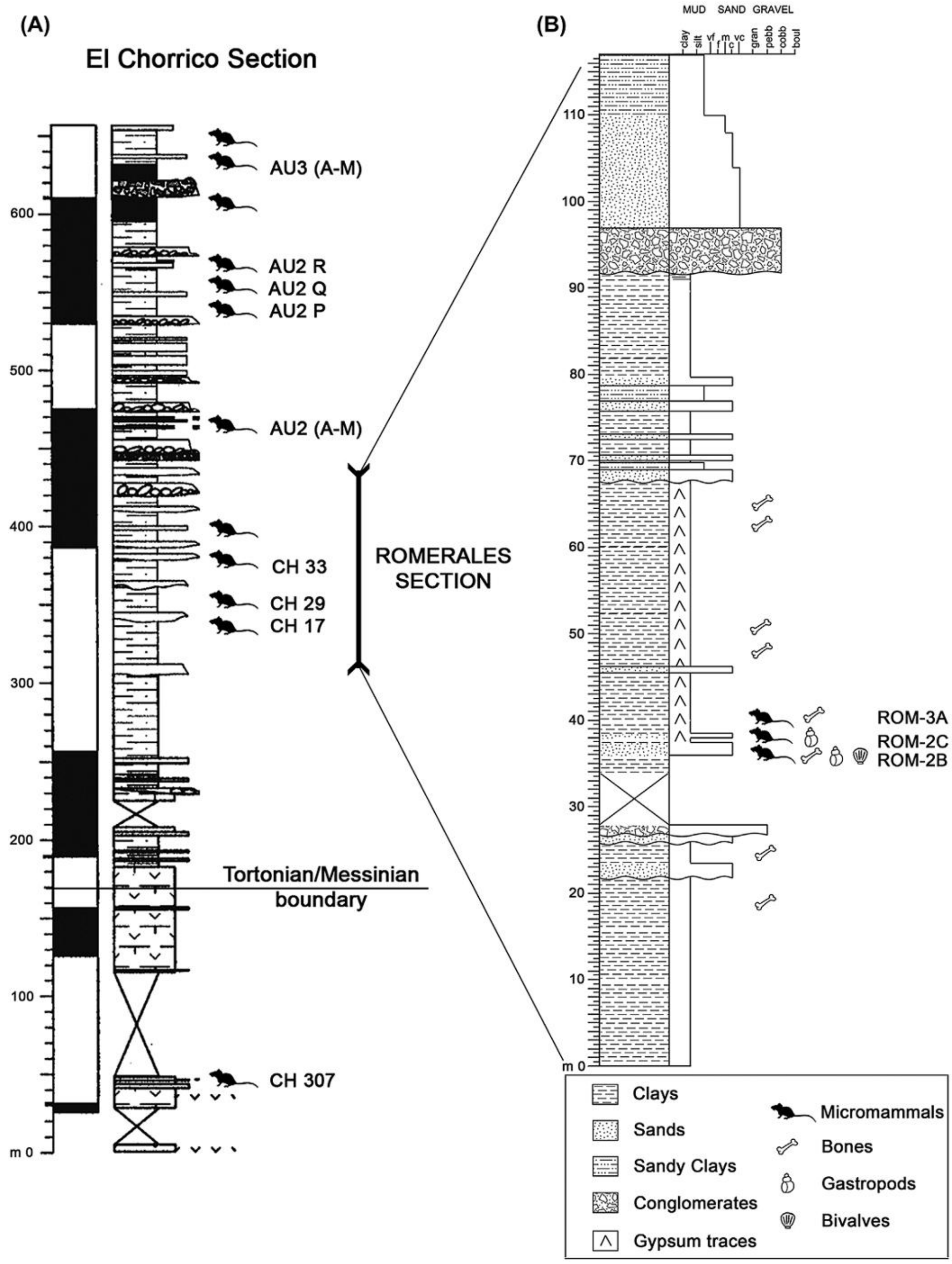


Figure 2. (A) Position of the section of Romerales within the section of El Chorrico (Fortuna Basin).
Note: Modified from Garcés et al. (2001). (B) Lithostratigraphic column of the Romerales section (Fortuna Basin), pointing out the position of the localities ROM-2B, ROM-2C and ROM-3A. Note: Scale in metres.

t1 and t2 is strong in most individuals but weak in two of them. The t12 appears as a salient angle of the t8 whose size is variable. It is absent in only one molar. There are three roots.

M2: The t1 is large and comma-shaped in most specimens and some of them reach the anterolingual side of t5. Many individuals have the t1 connected to the posterolingual face of t5 by a low crest. Nine out of 42 specimens develop an oval t1bis. The small and round t3 is connected to t5 by a weak ridge in only four pieces. The t12 is present in 11 specimens as a salient angle of t8, and absent in the others. There are three roots.

M3: The t3 is absent except in one molar in which is extremely reduced (IPS-90413). The t9 is individualised in two specimens

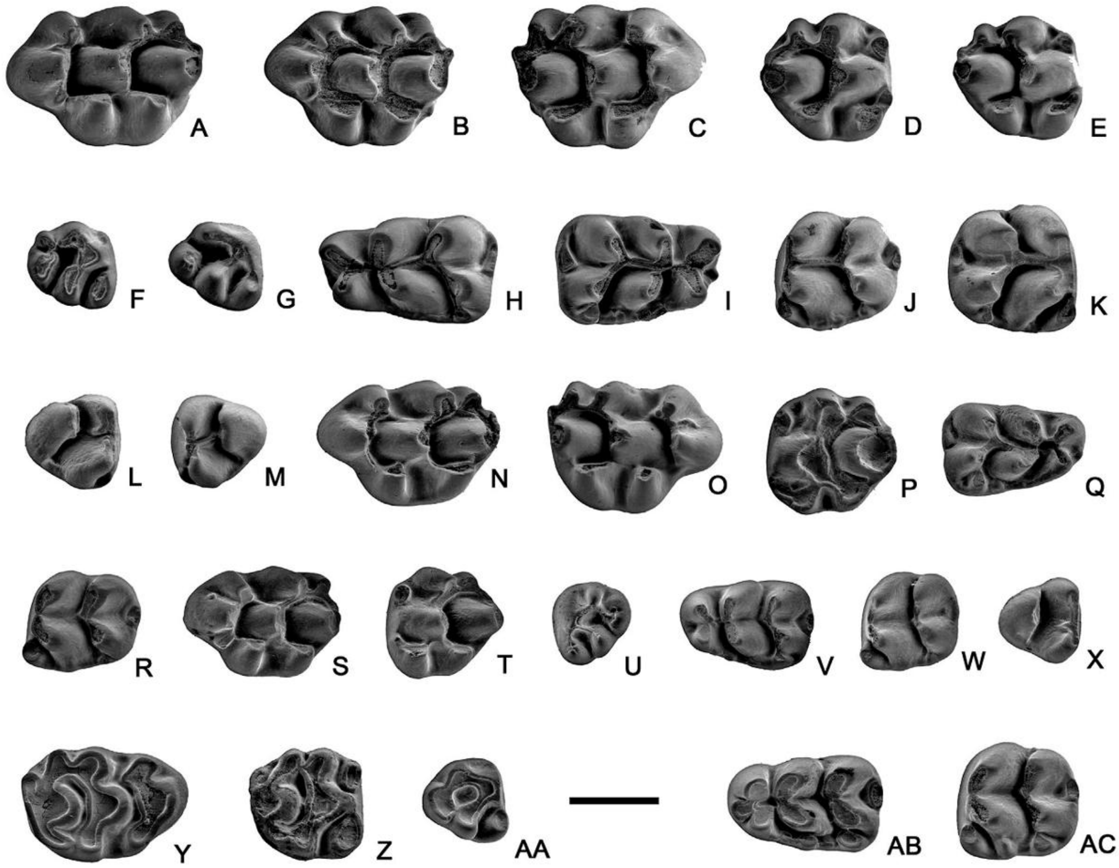


Figure 3. ESEM photographs of murids from Romerales. *Stephanomys ramblensis*: (A) left M1, IPS-90296 (ROM-2C); (B) left M1, IPS-90316 (ROM-2C); (C) right M1, IPS-90352 (ROM-2C); (D) right M2, IPS-90354 (ROM-2C); (E) right M2, IPS-90400 (ROM-2C); (F) right M3, IPS-90413 (ROM-2C); (G) right M3, IPS-90414 (ROM-2C); (H) left m1, IPS-90428 (ROM-2C); (I) right m1, IPS-90463 (ROM-2C); (J) left m2, IPS-90493 (ROM-2C); (K) right m2, IPS-90539 (ROM-2C); (L) right m3, IPS-90551 (ROM-2C); (M) left m3, IPS-90552 (ROM-2C). *Occitanomys* aff. *adroveri*: (N) left M1, IPS-90597 (ROM-2C); (O) right M1, IPS-90599 (ROM-2C); (P) left M2, IPS-90600 (ROM-2C); (Q) right m1, IPS-90602 (ROM-2C); (R) left m2, IPS-90607 (ROM-2C). *Occitanomys alcalai*: (S) left M1, IPS-90562 (ROM-2C); (T) left M2, IPS-90566 (ROM-2C); (U) left M3, IPS-90567 (ROM-2C); (V) left m1, IPS-90261 (ROM-2B; (W) left m2, IPS-90578 (ROM-2C); (X) right m3, IPS-90580 (ROM-2C). *Apodemus gudrunae*: (Y) right M1, IPS-90271 (ROM-2B); (Z) right M2, IPS-90273 (ROM-2B); (AA) right M3, IPS-90582 (ROM-2C); (AB) left m1, IPS-90585 (ROM-2C); (AC) left m2, IPS-90590 (ROM-2C).

Note: Scale bar equals 1 mm.

and fused to t8 in the rest. The t8–t9 complex is isolated in most teeth, but connected to t6 in two molars. There are two roots.

Discussion

The populations from ROM-2B and ROM-3A share the same features of the specimens from ROM-2C. Only one m1 (IPS-90240) has no longitudinal spur, but the size and morphology of this specimen are consistent with the molars ascribed to *Stephanomys* from the same locality. The crown-height, the development of longitudinal crests in the lower teeth and the presence of posterior crests and spurs on t1 and t3 in the upper teeth of the studied specimens are consistent with the genus *Stephanomys*.

The *Stephanomys* species from the Pliocene have a higher crown, larger size and greater development of the stephanodonty than the studied populations. The measurements of the latest Miocene or early Pliocene *Stephanomys numidicus* Coiffait, Coiffait and Jaeger, 1985, *Stephanomys dubari* Aguilar, Michaux, Bachelet, Calvet and Faillat, 1991, and *Stephanomys debruijni* de Giuli, 1989, always exceed the mean values of the studied molars. The size is similar to that of the most primitive member of the genus, *Stephanomys stadii* from the French locality of Cucuron (Mein and Michaux 1979). However, the specimens studied in this paper have a more developed connection between the cusps in the upper molars (such as the t3–t5 union), higher longitudinal crests in the lower teeth, and a greater asymmetry between labial and lingual tubercles in m1. The studied teeth are larger, and have more developed longitudinal connections than those of *Occitanomys adroveri* (Thaler, 1966), the probably ancestor of *Stephanomys* (Agustí et al. 2006; García-Alix et al. 2008b).

The size of the studied specimens agrees very well with that of *S. ramblensis* from its type locality VDC-3 (van de Weerd 1976). Their size is also close to that of the populations from MDV-7 (van de Weerd 1976), PUR-23, PUR-24A, PUR-25A (García-Alix et al. 2008b), VIL and VDC-6 (Adrover et al. 1993a). In addition, the moderate size, stephanodonty and hypsodonty

Table 1. Measurements (mm) of the teeth of *Stephanomys ramblensis* from ROM-2C, ROM-2B and ROM-3A.

		Length				Width			
Element	Locality	*N*	Min	Mean	Max	*N*	Min	Mean	Max
M1	ROM-2C	50	2.07	2.25	2.46	58	1.51	1.63	1.74
	ROM-2B	9	2.09	2.27	1.47	9	1.51	1.61	1.71
M2	ROM-2C	39	1.48	1.64	1.77	42	1.56	1.55	1.74
	ROM-2B	8	1.46	1.61	1.70	7	1.48	1.56	1.67
M3	ROM-2C	20	1.03	1.14	1.25	21	0.95	1.08	1.16
	ROM-2B	4	1.03	1.11	1.18	5	0.98	1.06	1.16
m1	ROM-2C	53	1.90	2.04	2.25	53	1.18	1.29	1.44
	ROM-2B	12	1.88	2.04	2.22	14	1.16	1.26	1.37
m2	ROM-3A	1		1.40		1		1.40	
	ROM-2C	47	1.39	1.52	1.65	47	1.31	1.42	1.58
	ROM-2B	6	1.36	1.53	1.65	5	1.38	1.42	1.48
m3	ROM-2C	19	1.10	1.21	1.29	19	1.07	1.14	1.23
	ROM-2B	6	1.14	1.23	1.29	4	1.00	1.12	1.21

agree with this species. However the studied specimens include certain archaic features that differ slightly from the type population: greater development of t12 in M1, lower longitudinal spur in m1 (even there are three specimens in which this ridge is very weak), and greater amount of lower molars with a moderate labial cingulum and development of accessory labial cusps, and presence of a well-differentiated t1bis in some M2 (closer to *Occitanomys*) and lower t6-t9 connection. Examples of morphological traits close to *O. adroveri* are also presented by somewhat younger representatives of the genus *Stephanomys* such as the very large population of *S. dubari* from Venta del Moro (Mansino et al. 2016a).

According to our data, the populations of *S. ramblensis* from Romerales might be one of the oldest in the Iberian Península. Freudenthal and Martín Suárez (1999) reported that the evolutionary trends of *Stephanomys* genus are increasing crown height, development of longitudinal crests in both upper and lower molars, and increasing stephanodonty. Minwer-Barakat (2005) proposed a single evolutionary line in which there is a continued increase in size, crown height and stephanodonty: *S. ramblensis* – *S. dubari* – *S. cordii* – *S. margaritae* – *S. vandeweerdi.*

Genus *Occitanomys* Michaux, 1969
Occitanomys* aff. *adroveri (Thaler, 1966) (Figure 3(N)–(R))

Material and localities

ROM-2B: 1 M3 (IPS-90266), 1 m1 (IPS-90267), 2 m2 (IPS-90268, IPS-90269).

ROM-2C: 6 M1 (IPS-90595–IPS-90600), 1 M2 (IPS-90601), 4 m1 (IPS-90602–IPS-90605), 3 m2 (IPS-90606–IPS-90608).

Measurements: Table 2.

Description of the material from ROM-2C

m1: The tma may be absent or low, small and weak. The anteroconid is asymmetrical. Three out of four specimens have a complete longitudinal crest connecting the entoconid-metaconid union with the lingual face of the protoconid. The labial cingulum is usually well developed with up to two accessory cusps. The c1 can be large or medium-sized and oval or subtriangular, but it is always in contact with the hypoconid by a spur. The terminal heel is elongated and reaches the posterior side of the entoconid. There are two roots.

m2: The longitudinal spur is weak or absent. The labial cingulum is well developed. There are medium-sized or small c1 and c2. The posterior heel is oval or laminar. There is a high and oval or round anterolabial cusp. There are two roots.

M1: The t1 is displaced backwards and isolated in two molars (IPS-90599, IPS-90601). Three out of five specimens have t1bis. Only one specimen has t2bis. The connection between t1 and t5 is basal or absent. The posterior spur of t3 is poorly developed (except in IPS-90596). The union t1–2 and t4–t5 are lower than those of t2–t3 and t5–t6 respectively. There is t12 as a salient angle of t8. There are three roots.

M2: There is an oval or laminar t1bis connected to the lingual side of t5. The posterior spur of t1 is in contact with t5. The t3 is isolated, small and round. The t6 and t9 are close but the union is very weak. There is a shallow valley between t5 and t1. The t12 is much reduced. No roots preserved.

Description of the material from ROM-2B

M3: The t1 connects basally to the t5. The t3 is not present. The t4, t5 and t6 are connected. The t8 is joined to t6 by a low ridge. There are no roots.

Discussion

The longitudinal spur in the m2s from ROM-2C is weak or absent but it is well developed in those from ROM-2B. This difference is probably as a result of the scarcity of specimens. The remaining features of *Occitanomys* aff. *adroveri* from ROM-2C and ROM-2B are similar.

The material from the studied localities differs from the oldest species of *Occitanomys* as are *Occitanomys hispanicus* (Michaux, 1971) and *Occitanomys sondaari* van de Weerd, 1976, by its larger size, greater development of t1bis and higher t6–t9 connection. Although the single M2 of *O.* aff. *adroveri* of our collection has a weak t6–t9 union, all the M1s present a strong connection between these cusps. Our specimens are smaller than *Occitanomys brailloni* Michaux, 1969, and both lower and upper molars have less developed longitudinal connections, the t12 is less reduced and the tubercles are less swollen (Martín Suárez 1988).

The size of these teeth is larger than *Occitanomys alcalai* Adrover, Mein and Moissenet, 1988 but smaller than *S. ramblensis*. The crown-height is among both species. The shape

Table 2. Measurements (mm) of the molars of *Occitanomys* aff. *adroveri* from ROM-2C and ROM-2B.

		Length				Width			
Element	Locality	*N*	Min	Mean	Max	*N*	Min	Mean	Max
M1	ROM-2C	5	2.01	2.08	2.14	6	1.38	1.44	1.52
M2	ROM-2C	1		1.48		1		1.43	
M3	ROM-2B	1		1.04		1		0.92	
m1	ROM-2C	4	1.68	1.81	1.94	4	1.10	1.17	1.25
	ROM-2B	1		1.78		1		1.08	
m2	ROM-2C	3	1.33	1.37	1.45	3	1.15	1.21	1.25
	ROM-2B	2	1.31	1.35	1.38	2	1.20	1.21	1.21

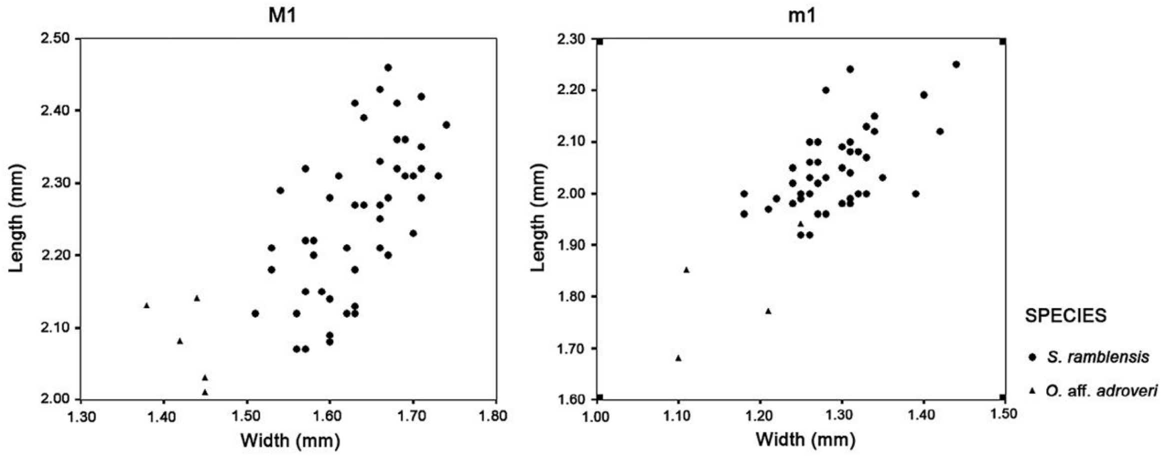


Figure 4. Scatter plots comparing the measurements of the first upper molars of *Stephanomys ramblensis* and *Occitanomys* aff. *adroveri* from ROM-2C.

and size of our specimens agrees with *O. adroveri* from its type locality, LM (van de Weerd 1976). In addition, both populations share some similarities, such as most m1s and m2s develop a longitudinal spur (three out of four m1s in ROM-2C), the terminal heel is elongated and it even reaches the posterior side of the entoconid, presence of t1bis in most M1s, t1 separated from t2 or connected to it by a low crest, low t4-t5 connection, t12 as a small salient angle of t8, shallow valley between t5 and t1 in M2, and postero-labial spur on t1 directed towards t5. The dimensions of the teeth also fit within the range size and have similar average values to those of *O. adroveri* from localities like OTU-1, OTU-3 (García-Alix et al. 2008b), CR-17, CR-7 (Martín Suárez and Freudenthal 1993), ALJ-B and Tortajada (Adrover 1986). According to Martín Suárez and Freudenthal (1993) there is an increase in longitudinal spurs and crests from the oldest Crevillente populations of *O. adroveri* to the youngest one. In this case the population shows typical features of younger levels such as CR-17. Nevertheless, the frequency of complete ridges in m1s in this latter locality is 16.2%, while in ROM-2C it is 75%, making them near to 'archaic' population of *Stephanomys*. Other differences with respect to the population from CR-17 lie in the M1s: the studied specimens have the t12 more developed, closer to *S. ramblensis*.

The analysed population has a combination of morphological characters from *O. adroveri* and *S. ramblensis* as said above. However, this population differs from *S. ramblensis* since this latter species has usually larger size (Figure 4), higher crown height, greater degree of stephanodonty with stronger and higher spurs and the longitudinal ridge in m1 connected to the protoconid-metaconid junction. Both morphology and size of the studied molars are closer to *Occitanomys*, and therefore they are ascribed to *Occitanomys* aff. *adroveri*. It is a population related to *O. adroveri*, with certain derived features as the relatively high crown-height and a good development of longitudinal crests in lower molars combined with archaic characters as the low t6–t9 connection in M2.

Althought *O. adroveri* is usually larger than *O. alcalai*, sometimes the size of both species overlaps. This fact complicates the distinction between them in those levels where both appear together. We ascribed to *O.* aff. *adroveri* the largest specimens with asymmetrical anteroconid, well-developed or complete longitudinal crest in the lower teeth, and low development of the spur in t3 and more backwards t1 in first upper molars (Minwer-Barakat et al. 2009a; Minwer-Barakat et al. 2009b; García-Alix et al. 2008b).

The presence of *O.* aff. *adroveri* together with *S. ramblensis* at the same level suggest an independent evolution of the latter species from *O. adroveri* throughout an increase in size and stephanodonty. Maybe *S. ramblensis* is an inmigrant in the Fortuna Basin joining the local offshoot of *O. adroveri*. Alike García-Alix et al. (2008b) considered *S. stadii* an alternative descendant of *S. ramblensis* but not the ancestor. Adrover (1986) noted some Mediterranean climatic conditions could induce the development of stephanodonty several times.

Table 3. Measurements (mm) of the teeth of *Occitanomys alcalai* from ROM-2C, ROM-2B and ROM-3A.

		Length				Width			
Element	Locality	*N*	Min	Mean	Max	*N*	Min	Mean	Max
M1	ROM-3A	1		1.83		1		1.31	
	ROM-2C	2	1.85	1.86	1.86	2	1.28	1.28	1.28
	ROM-2B	1		1.85					
M2	ROM-2C	3	1.30	1.34	1.36	3	1.26	1.29	1.31
	ROM-2B	1		1.28		1		1.30	
M3	ROM-3A	1		0.86		1		0.82	
	ROM-2C	3	0.95	0.96	0.96	3	0.93	0.95	0.97
	ROM-2B	1		0.92		1		0.88	
m1	ROM-3A	1		1.58		1		1.08	
	ROM-2C	5	1.60	1.64	1.68	6	1.03	1.10	1.17
	ROM-2B	2	1.55	1.56	1.57	2	1.05	1.06	1.07
m2	ROM-2C	4	1.15	1.25	1.34	4	1.03	1.12	1.15
	ROM-2B					2	1.15	1.17	1.18
m3	ROM-2C	1		1.00		1		1.00	

Occitanomys alcalai Adrover, Mein and Moissenet, 1988 (Figure 3(S)–(X))

Material and localities

ROM-2B: 1 M1 (IPS-90258), 1 M2 (IPS-90259), 1 M3 (IPS-90260), 3 m1 (IPS-90261–IPS-90263), 2 m2 (IPS-90264–IPS-90265).

ROM-2C: 2 M1 (IPS-90562, IPS-90563), 3 M2 (IPS-90564–IPS-90566), 3 M3 (IPS-90567–IPS-90569), 6 m1 (IPS-90570–IPS-90575), 4 m2 (IPS-90576–IPS-90579), 1 m3 (IPS-90580).

ROM-3A: 1 M1 (IPS-90190), 1 M3 (IPS-90191), 1 m1 (IPS-90192).

Measurements: Table 3.

Description of the material from ROM-2C

m1: The tma is absent. The anteroconid is symmetrical. Only in one specimen (IPS-90573) there is a hint of longitudinal crest, absent in other specimens. The labial cingulum is well developed. The c1 may be large or medium sized, low and subtriangular, joined basally to the hypoconid. Another accessory cusp is present in one molar (IPS-90571). The posterior heel is low and oval, of a similar size to the c1. There are two roots.

m2: The longitudinal crest is absent or very weak. The anterolabial cusp is medium-sized or large, round and low. The posterior heel is very low, weak and elongated. The labial cingulum is poorly developed. There is a medium-sized c1, attached to the hypoconid when it is present. There may be other small accessory labial cusps attached to the protoconid. There are two roots.

m3: The protoconid and metaconid are symmetrical. The longitudinal spur, anterolabial cuspid and c1 are absent. There are two roots.

M1: The t1 is displaced backward and connected to t2 by a lower ridge than that of t2–t3. The t1bis is well developed. There is no t2bis. The t3 has a small posterior spur directed towards t5 but does not reach it. The small spur of t1 reaches the t5. There is a small thickening of the enamel at t4–t5 union. The t4 and t8 are separated. There is a weak t12. There are three roots.

M2: One specimen (IPS-90566) has a t1bis connected to t5. The t1 is in contact with the anterolingual side of t5 by a spur. The posterior spur is low and reaches the t5. The t3 is reduced, round and separated from the t5. Only one specimen has a small t12 (IPS-90565) connecting t8 and t9. The t4 and t8 are separated. There are three roots.

M3: The t1 is connected to the t5. The t3 is not present. The t5 is in contact with the t4 and t6. The t8 may be joined to t6 or isolated. There are two roots.

Discussion

The M1 from ROM-2B is quite similar to that of ROM-2C except for the small t2bis and the connection of t4 and t8. In the M2 from ROM-2B the union t4-t5 and the anterior connection of t1 with t5 are very low. One out of three m1s (IPS-90263) has a hint of longitudinal spur.

The dimension of the teeth from ROM-2B, 2C and 3A fall within the variation range of *O. alcalai* from its type locality, Peralejos E (Adrover et al. 1988), being the mean values quite similar. The size of the studied molars is also close to that of *O. alcalai* from other Spanish populations such as VIL (Adrover et al. 1988), LG-5, VDC-6, VDC-3 (Adrover et al. 1993a), OTU-1, PUR-23, PUR-24A, PUR-25, PUR-25A, MNA-2 and MNA-4 (García-Alix et al. 2008b), but slightly smaller than those from RCH-3, NGR-1, Botardo-C in Guadix Basin (Martín Suárez 1988; Minwer-Barakat et al. 2009a, 2009b), Alcoi Forn (Mansino et al. 2015a) and CR-5 (Bruijn et al. 1975). The morphology of the analysed specimens is consistent with the diagnostic characters of *O. alcalai*: relatively high tubercles, well-developed t1bis, absence of isolated tubercles, and lack of complete longitudinal spurs in the lower teeth (Adrover et al. 1988).

Occitanomys hispanicus is smaller than the studied populations; in addition all of our specimens have the t6–t9 connection. The size of *O. sondaari* is quite similar to that of the studied teeth. The main difference lies in the morphology: the lower molars of *O. sondaari* have more developed longitudinal crests and more reduced labial cingulum than the pieces. The upper molars of this latter species have lower connections, weak or absent t6–t9 union, reduced or absent t1bis, and occasionally single t4 and t9, contrary to the specimens from our levels. *Occitanomys alcalai* from ROM-2B, ROM-2C and ROM-3A can be distinguished from *O. adroveri* by its relatively smaller size and some morphological features: the M1 have a less posterior t1, and the t1bis and the spur from t3 are better developed. The lower molars have weak or absent longitudinal connections, the posterior heel in

Table 4. Measurements (mm) of the teeth of *Apodemus gudrunae* from ROM-2C and ROM-2B.

		Length				Width			
Element	Locality	*N*	Min	Mean	Max	*N*	Min	Mean	Max
M1	ROM-2C	1		1.96		1		1.26	
	ROM-2B	1		2.03		2	1.34	1.35	1.36
M2	ROM-2B	1		1.38		1		1.34	
M3	ROM-2C	2	1.04	1.06	1.08	2	1.03	1.05	1.08
	ROM-2B	1		0.89		1		0.91	
m1	ROM-2C	3	1.88	1.93	2.01	3	1.14	1.18	1.25
m2	ROM-2C	5	1.28	1.43	1.52	5	1.18	1.26	1.39
	ROM-2B	4	1.26	1.29	1.30	4	1.10	1.15	1.18
m3	ROM-2C	3	1.12	1.13	1.14	3	1.06	1.08	1.09
	ROM-2B	1		1.11		1		1.06	

m1 is oval and lacks of a crest directed towards the entoconid as it occurs in *O. adroveri* from LM and ALJ-B (van de Weerd 1976; Adrover 1986). In m2 the posterior heel and the accessory labial cuspid are less developed than those of *O. adroveri*.

Genus *Apodemus* Kaup, 1826
Apodemus gudrunae van de Weerd, 1976 (Figure 3(Y)–(AC))

Material and localities

ROM-2B: 2 M1 (IPS-90271, IPS-90272), 1 M2 (IPS-90273), 1 M3 (IPS-90274), 1 m1 (IPS-90275), 4 m2 (IPS-90276–IPS-90279), 1 m3 (IPS-90280).

ROM-2C: 1 M1 (IPS-90581), 2 M3 (IPS-90582, IPS-90583), 3 m1 (IPS-90584–IPS-90586), 5 m2 (IPS-90587–IPS-90591), 3 m3 (IPS-90592–IPS-90594).

Measurements: Table 4.

Description of the material from ROM-2C

m1: The tma is well developed. The anteroconid is symmetrical and separated from the protoconid-metaconid complex (except in much worn specimens). The labial cingulum is well developed. The c1 is large, oval and separated from the hypoconid. There is up to three accessory labial cusps. The posterior heel is oval and as large as the c1. There is no evidence of longitudinal ridge. There are two roots.

m2: The anterolabial cuspid and the c1 are round and large. There is another small accessory labial cusp in contact with the protoconid. The posterior heel may be large or medium-sized and oval. There are two roots.

m3: There is a small and low anterolabial cusp and c1. There are two roots.

M1: The t1 is connected to t2 but separated from t5. There is a weak and low posterior spur in t3. The t7 is elongated and separated from t4 by a narrow and shallow valley, but connected to t8 by a crest. The t12 is well developed, connected to t8 but disconnected from t9. The t8 and t9 are joined by a ridge. There are three roots.

M3: The t1 is large and oval. The t3 is absent. The t4 and t8 are in contact. The t8 and t9 are joined. The roots are not preserved.

Description of the material from ROM-2B

M2: The round t1 is twice as large as the oval t3. The t7 is elongated and connected to t4 and t8. The t6 is weakly joined to t9 by a spur. The t12 is large and connected to t8 but separated from t9. There are no preserved roots.

Discussion

Unlike the M1 from ROM-2C, the two specimens from ROM-2B have the t7 connected to t4. The dimensions of *A. gudrunae* from the studied levels fall within the biometrical variability of *A. gudrunae* from its type locality, VDC-3 (van de Weerd 1976). The measurements are also quite similar to that of *A. gudrunae* from LG-5, VIL and VDC-6 (Adrover et al. 1993a) except for the width of the m1. Regarding morphology, our teeth coincide in many features with the population from VDC-3 such as the symmetrical anteroconid complex, well-developed tma and c1 in m1, t1 connected to t2 but disconnected from t5 in M1, elongated t7 in M1 and M2, the presence of a narrow and shallow valley separating the t7 from the t4 in some cases or a weak connection between t6 and t9 in M2 in some specimens.

The upper molars of *A. gudrunae* from ROM-2C and 2B are in general smaller than those of *Apodemus barbarae* (van de Weerd 1976), but they overlap with the size range of the latter species from LM (type population), MDV-2 and MDV-5, Concud 3 (van de Weerd 1976), CR-5A and CR-15 (Martín Suárez and Freudenthal 1993) and ALJ-B (Adrover 1986). However the studied specimens differ from *A. barbarae* by the presence of a well-developed t7 in M1 and M2 and a complete t6-t9 union. The measurements of *Apodemus atavus* Heller, 1936 and *Apodemus lugdunensis* (Schaub, 1936) are notably smaller than those of our population. On the contrary, *Apodemus gorafensis* Ruiz Bustos, Sesé, Dabrio, Peña and Padial, 1984, *Apodemus meini* Martín Suárez and Freudenthal, 1993 and *Apodemus jeanteti* Michaux, 1969 are all of them larger than our specimens. In addition, the studied specimens differ from *A. jeanteti* by the presence of a large tma in the m1, and from *A. meini* by the presence of a well-developed t7 in M1 and M2.

According to Martín Suárez and Mein (1998) *Apodemus barbarae* from the middle Turolian (MN12) is the most probable ancestor of *A. gudrunae* from the late Miocene (MN13). In turn, *A. gudrunae* gave rise to the late Miocene-early Pliocene *A. gorafensis*. This lineage experienced a size increase overtime and a reduction of the stephanodonty (Martín Suárez and Mein 1998).

Family Gliridae Muirhead, 1819
Subfamily Dryomyinae de Bruijn, 1967
Genus *Eliomys* Wagner, 1840

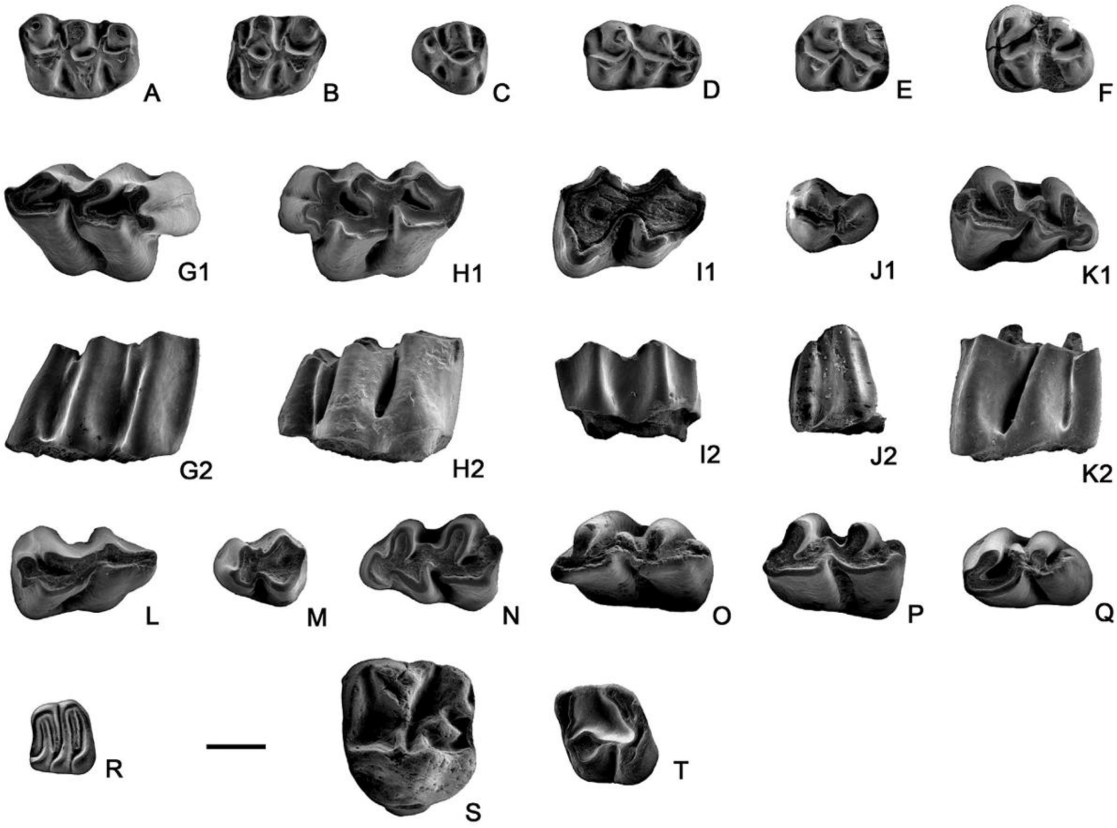


Figure 5. Fossil rodents from ROM-2C. *Apocricetus* aff. *plinii*: (A) right M1, IPS-90610 (ROM-2C); (B) left M2, IPS-90611 (ROM-2C); (C) right M3, IPS-90613 (ROM-2C); (D) right m1, IPS-90614 (ROM-2C); (E) right m2, IPS-90615 (ROM-2C); (F) left m3 IPS-90616A (ROM-2C). *Ruscinomys* aff. *gilvosi*: (G) right M1, occlusal (1) and labial (2) views, IPS-91840; (H) left M1, occlusal (1) and lingual (2) views, IPS-91841; (I) left M2, occlusal (1) and labial (2) views, IPS-90625; (J) left M3, occlusal (1) and labial (2) views, IPS-90617; (K) right m1, occlusal (1) and labial (2) views, IPS-91862; (L) left M2, IPS-91853; (M) left M3, IPS-91857; (N) left m1, IPS-91863; (O) left m2, IPS-91884; (P) left m2, IPS-91885; (Q) left m3, IPS-91896. *Eliomys* cf. *truci*: (R) left m12, IPS-90630 (ROM-2C). *Pliopetaurista* sp.: (S) left M1-2, IPS-90628. *Heteroxerus* sp.: (T) left m1-2, IPS-90629.
Note: Scale bar equals 1 mm.

Eliomys* cf. *truci Mein and Michaux, 1970 (Figure 5(R))

Material, localities and measurements

ROM-2B: 1 M1-2 fragmented (IPS-90295) (*W*: 1.32).
ROM-2C: 1 m2 (IPS-90630) (*L*: 1.21; *W*: 1.31).

Description of the material from ROM-2C

m2: Well-developed anterolophid, not fused to the protoconid. The anterotropid is absent. Very long centrolophid, which does not reach the labial wall of the tooth. The labial ends of the mesolophid and posterolophid are anteriorly directed. Very long posterotropid. There are no preserved roots.

Discussion

The species *Eliomys truci* was originally described in the early Pliocene site of Hautimagne (Southern France, Mein and Michaux 1970). Later this species has been recognised in the late Miocene and early Pliocene of a number of Neogene basins in Spain: Teruel (van de Weerd 1976; Adrover 1986; Adrover et al. 1993a), Guadix (Minwer-Barakat 2005) and Granada (García-Alix et al. 2008c). It has been considered either as a separate lineage from the Pliocene species *Eliomys intermedius* (Mein and Michaux 1970; Adrover 1986) or as an ancestor of the latter species (García-Alix et al. 2008c; Mansino et al. 2015b), being part of the lineage comprising *E. truci*–*E. yevesi*–*E. intermedius*–*E. quercinus* (Mansino et al. 2015b). Although older in age, the sample from Romerales coincides both in size and morphology with the original sample from Hautimagne. Prior to Romerales, *Eliomys* cf. *truci* was recognised in the Fortuna Basin at the middle Turolian (MN12) site of Casa del Acero (Agustí et al. 1981).

Family Cricetidae Fischer, 1817
Subfamily Cricetodontinae Stehlin and Schaub, 1951
Genus *Ruscinomys* Depéret, 1890
Ruscinomys* aff. *gilvosi Adrover, Mein and Moissenet, 1988 (Figure 5(G)–(Q))

Material and localities

ROM-2B: 1 M3 (IPS-90289), 1 M1 (IPS-90290), 12 fragments (IPS-90281–IPS-90288, IPS-90291–IPS-90294).

Table 5. Measurements (mm) of the molars of *Ruscinomys* aff. *gilvosi* from ROM-2C and ROM-2B.

		Length				Width			
Element	Locality	*N*	Min	Mean	Max	*N*	Min	Mean	Max
M1	ROM-2C	11	3.37	3.62	3.87	14	2.11	2.26	2.47
	ROM-2B	1		2.74					
M2	ROM-2C	6	2.62	2.70	2.83	6	1.77	1.81	1.90
M3	ROM-2C	6	1.72	1.81	1.87	6	1.35	1.43	1.53
	ROM-2B	1		1.62		1		1.38	
m1	ROM-2C	15	2.56	2.79	2.98	17	1.55	1.80	2.00
m2	ROM-2C	12	2.61	2.80	3.00	12	1.72	1.79	1.90
m3	ROM-2C	9	2.30	2.42	2.52	8	1.41	1.49	1.56

ROM-2C: 17 M1 (IPS-90618, IPS-90619, IPS-90621, IPS-91839–IPS-91852), 6 M2 (IPS-90624, IPS-90625, IPS-91853–IPS-91856), 6 M3 (IPS-90617, IPS-91857–IPS-91861), 19 m1 (IPS-90620, IPS-90622, IPS-90623, IPS-90627, IPS-91862–IPS-91876), 12 m2 (IPS-91877–IPS-91888), 10 m3 (IPS-90626, IPS-91889–IPS-91897).

Measurements: Table 5.

Description of the material from ROM-2C

m1: Small, round anteroconid. A very small and tiny anterolophid is present in four specimens, while in another specimen a small labial and a small lingual anterolophid is present. Transverse metaconid, which connects directly to the anteroconid. Well-developed mesolophid which only reaches the posterior wall of the metaconid in highly worn specimens. Small, round posterolophid which only in one case develops an ectolophid connected to the posterior wall of the entoconid.

m2: There is no evidence of anterolophid. Well-developed mesolophid which only in one case reaches the posterior wall of the metaconid. The posterolophid is fused to the hypoconid and can be hardly distinguished from this cusp. In the cases in which it can be distinguished, it presents a round shape.

m3: As in the m2, there is no evidence of anterolophid. Well-developed, transverse mesolophid, which only connects to the posterior wall of the metaconid at high stages of wearing.

M1: A deep groove which reaches the base of the crown is always present at the anterior wall of the anterocone. This groove separates the anterocone into two lobes, the labial one being always larger than the lingual one. In five out of 12 teeth the lingual lobe develops a lingual spur. In poorly worn specimens, the anterior ectoloph is always incomplete, reaching the paracone as abrassion progresses. The posterior ectoloph between the paracone and the metacone is always well developed. The posterior wall of the protocone is projected backward in four teeth. The hypocone is directly connected to the posterior wall of the paracone or, in a more labial position, to the posterior ectoloph. A residual posteroloph is always present, even in highly worn specimens.

M2: This is a trapezoidal tooth, the width at the protocone-paracone level being larger than at the hypocone-metacone level. In three out of four teeth there is a residual lingual anteroloph. The anterior ectoloph is incomplete, even in relatively worn teeth. The anterosinus is deep and narrow. The posterosinus is very much reduced. The hypocone and metacone are almost in contact. Their anterior walls are directly connected to the posterior ectoloph. A residual posteroloph can be observed in two teeth.

M3: Very simple design, reduced to two interconnected rhombus. The anterior rhombus includes the protocone and the paracone, although none of these cusps can be distinguished. A deep sinus separates this anterior rhombus from the posterior one. In contrast, the mesosinus is much superficial. As in the case of the anterior rhombus, neither the hypocone nor the metacone can be recognised as separated cusps. The width of this posterior rhombus is lower than that of the anterior one. A residual posteroloph is always present at the posterior wall of this rhombus.

Discussion

The hypsodont Cricetodontinae present in ROM-C fits as a species of *Ruscinomys* rather than *Hispanomys*, provided its highly hypsodont molars and simplified dental pattern. However, it differs from all the late Miocene and early Pliocene species of *Ruscinomys,* such as *Ruscinomys schaubi* Villalta and Crusafont, 1956 and *Ruscinomys lasallei* Adrover, 1969 mainly because of its smaller dimensions, but also in other features, such as the development of long mesolophids that usually reach the posterior wall of the metaconid. In this way, it clearly differs from the coeval *R. schaubi* from the late Miocene of Teruel. In size, it fits the species *Ruscinomys gilvosi,* originally described from the early Pliocene site of PER-E, in the Teruel Basin (Adrover et al. 1988). Comparison with this species is hampered by the small size of the PER-E sample: two m1 (one broken), one broken m2, four M1 (two broken), and two M2. The differential diagnosis of *R. gilvosi* is established only on the basis of its small size. As morphological traits, Adrover et al. (1988) also mentioned 'a very simplified morphology in occlusal view' and that the M2 'can' have five roots. The sample from ROM-2C fits in size the species from PER-E and differs from it in some few characters. Therefore, a very small labial anterolophid can be distinguished in four m1 from ROM-2C, which is better developed in another m1, while in PER-E it seems that the complete (not figured) m1 does not present anterolophid. However, most of the m1 from ROM-2C do not present anterolophid either. Provided the small hypodigm from PER-E, from a statistical point of view this character cannot be used to differentiate both samples. Other morphological character provided by Adrover et al. (1988) is the presence of five roots in one of the complete M2 from PER-E. This character can be hardly distinguished in the ROM-2C sample, since almost all the specimens have not yet developed roots. In the few teeth that started to develop roots from ROM-2C, it appears that the M1 could have had five while the M2 could have developed four. As in the case of the anterolophid, the small size of the hypodigm of *R. gilvosi* prevents to use this character to differentiate it from the sample from ROM-2C. However, if true, it would imply that *Ruscinomys* aff. *gilvosi* from ROM-2C presents some less derived features (retention in some molars of anterolophid, M2 with four roots) than the population from PER-E, which is consistent with the older age of ROM-2C (latest Miocene) with respect PER-E (early Pliocene).

Morphologically, *Ruscinomys* aff. *gilvosi* from Romerales differs from *R. shcaubi* in a number of characters which, in its turn, are present in the previously described *Hispanomys adroveri*, from the older site of Casa del Acero, also in the Fortuna Basin (Agustí 1986): development of long mesolophids that usually reach the posterior wall of the metaconid, and development in some molars of a small spur in the posterolophid that reaches the posterior wall of the entoconid. Therefore, *Ruscinomys gilvosi* could have evolved locally from *Hispanomys adroveri* by a reduction in size and increasing hypsodonty. In fact, Freudenthal et al. (1991) recognised a size diminution of *H. adroveri* in the Crevillente section, from the level of CR-15 to the younger levels of CR-5, CR-8, CR-14 and CR-17 (*Hispanomys* aff. *adroveri*). The confirmation of this hypothesis would imply that morphological traits of *Ruscinomys* evolved independently in two Cricetodontinae lineages and that *Ruscinomys gilvosi* should be included in a different genus, either *Hispanomys* or a new one. As in other cases, the presence of *Ruscinomys* aff. *gilvosi* in ROM-2C reinforces the need for a deep revision of the late Miocene and early Pliocene Cricetodontinae included in the genera *Hispanomys* and *Ruscinomys*.

Subfamily Cricetinae Fischer, 1817
Genus *Apocricetus* Freudenthal, Mein and Martín Suárez, 1998
Apocricetus* aff. *plinii (Freudenthal, Lacomba and Martín Suárez, 1991) (Figure 5(A)–(F))

Material and localities

ROM-2B: 1 M2 (IPS-90270).

ROM-2C: 2 M1 (IPS-90609, IPS-90610), 2 M2 (IPS-90611, IPS-90612), 1 M3 (IPS-90613), 2 m1 (IPS-90614, IPS-90616A), 1 m2 (IPS-90615), 1 m3 (IPS-90616B).

Measurements: Table 6.

Description of the material from ROM-2C

m1: Trifid anteroconid, composed of three cusps. There is one central, simple anterolophid, which reaches the central cusp of the anteroconid. At the base of the crown a small lingual one can be distinguished, directed to the lingual wall of the anteroconid. There is no developed prelophid. The protolophid is in anterior position. There is no mesolophid. Anterior metalophid. The posterolophid is low, and its lingual end attached to the entoconid and closing the posterosenid. There are no preserved roots.

m2: Well-developed labial cingulum which reaches the base of the protoconid. There is no evidence of lingual cingulum or anterosinusid. The mesolophid is absent. There is an anterior metalophid and protolophid. As in the m1, there is a low, cusp-like posterolophid, which does not reach the entoconid. The roots are not preserved.

m3: This element is close in size to the m2. Well-developed labial cingulum which reaches the base of the protoconid. A small lingual cingulum delimitates a small anterosinusid. The protolophid is in anterior position. There is a short mesolophid. The metalophid is anteriorly positionated. The lingual end of the posterolophid reaches the entoconid closing the posterosinusid. The roots are not preserved.

M1: The anterocone is composed of two round cusps which are separated by a superficial groove. The anterolophule is double but the labial branch is labially oriented and not fused to the posterior wall of the labial lobe of the anterocone. Double protolophule, the anterior branch being lower than the posterior one. The mesoloph is of medium lenght. Labial and lingual sinuses are closed by basal cingula that develops a small cuspule. There is no posterior metalophule, the posteroloph connecting directly to the metacone, therefore closing the posterosinus. The roots are not preserved

M2: Well-developed labial and lingual anterolophes, the lingual one being larger. They reach the base of the paracone and protocone, closing the anterosinus and the protosinus respectively. The sinus is closed by a cingulum. The protolophule is double. The mesoloph in of medium length in all the cases, not reaching the anterior wall of the metacone. The posterior metalophule is absent, while the posterolophe reaches the posterior wall of the metacone, therefore closing the posterosinus. The roots are not preserved.

M3: Well-developed labial anterolophe. A small lingual anterolophe is also present. Double protolophule. There is an anterior metalophule. The posterolophe connects to a vestigial metacone closing a reduced posterosinus. The roots are not preserved.

Discussion

The species *Neocricetodon plinii* was originally described from the middle Turolian (MN12) site of CR-15 (Freudenthal et al. 1991). A posterior revision led Freudenthal et al. (1998) to place this species in the new genus *Apocricetus*. The small sample of *Apocricetus* aff. *plinii* from Romerales is characterised by the presence of one central and simple anterolophid in m1, lack of mesolophids in m1 and m2, large m3 with developed mesolophid, and double protolophule in the upper molars, the posterior one being more developed than the anterior one. In this way, it differs from the previously described *Neocricetodon* (= *Kowalskia*) *meini* from the site of Casa del Acero in the same Fortuna Basin (Agustí 1986), which still presents mesolophids in the lower m1 and m2, and is characterised by m1 with a simple, lingual anterolophulid and small m3. In contrast, it fits the size and morphology of *Apocricetus plinii*. As in the case of CR-15, the sample from Romerales presents m1 with splitted anteroconid, labial anterolophulid, absence of mesolophids in m1 and m2 and large m3 which still retains a mesolophid. In the upper molars, the protolophule is double (as it happens in the majority of upper molars from CR-15; Freudental et al. 1991) and they present medium-sized mesolophs, as is also the case of the type-species from CR-15. In this way, as happened also with the original sample from CR-15, *A.* aff. *plinii* from Romerales still retains archaic features that are absent from the subsequent species of the genus, such as *Apocricetus alberti* Freudenthal, Mein and

Table 6. Measurements (mm) of the teeth of *Apocricetus* aff. *plinii* from ROM-2C and ROM-2B.

		Length				Width			
Element	Locality	*N*	Min	Mean	Max	*N*	Min	Mean	Max
M1	ROM-2C	1		2.22		1		1.52	
M2	ROM-2C	2	1.73	1.77	1.80	2	1.33	1.41	1.49
	ROM-2B	1		1.65		1		1.41	
M3	ROM-2C	1		1.41		1		1.27	
m1	ROM-2C	1		2.13		2	1.24	1.27	1.29
m2	ROM-2C	1		1.70		1		1.34	
m3	ROM-2C	1		1.90		1		1.47	

Martín-Suárez, 1991, *Apocricetus barrierei* (Mein and Michaux, 1970) and *Apocricetus angustidens* (Depéret, 1890). This is the case for the retention of double protolophules instead of posterior ones and the well developed mesolophs, which led Freudenthal et al. (1991) to the original adscription of this species to the genus *Neocricetodon*.

As pointed out by Freudenthal et al. (1998), *Neocricetodon meini* cannot be considered as a member of the same lineage than *Apocricetus plinii*, since this former shows a more simplified dental pattern, closer to the Vallesian and early Turolian genus *Cricetulodon*. Since the Romerales sites are younger (late Turolian) than Casa del Acero (middle Turolian), it means that a replacement proccess took place between the middle and late Turolian, *Apocricetus* aff. *plinii* being a new immigrant in the basin.

Family Sciuridae Fischer von Waldheim, 1817
Subfamily Pteromyinae Brandt, 1855
Genus *Pliopetaurista* Kretzoi, 1962
***Pliopetaurista* sp.** (Figure 5(S))

Material, localitiy and measurements

ROM-2C: 1 M1-2 (IPS-90628) (*L*: 2.40; *W*: 2.65).

Description of the material

M1-2: The specimen is slightly corroded by digestion or abrasion. The outline of the molar is almost square. Two main depressions can be appreciated: the widest, the anterior valley, is delimited by the anteroloph and protoloph, and the other one, the trigone basin, delimited by the metacone, metaconule and protoloph. Three other minor depressions are situated between the crests that connect metacone, metaconule and posteroloph. The different development and position of these depressions gives the molar a labyrinthine appearance. Three main cusps, protocone, paracone and metacone, can be recognised, whereas hypocone is much reduced. A well-developed metaconule is also present. A slightly undulated protoloph connects the paracone with the anterior arm of the protocone. A low crest connects the large metacone and the metaconule, each of which is connected independently to the posteroloph. The metaconule connects to the protocone too. Due to its corroded surface, it is not possible to appreciate any signs of undulation or granulation at the bottom of the depressions. The molar has three roots.

Discussion

The large size and labyrinthic design of the oclusal surface of the molar, as well as the very well-developed metaconule, are typical of *Pliopetaurista* (Mein, 1970). In Western Europe, this genus is represented by at least eight species: *P. pliocaenica* (Depéret, 1890), *P. dehneli* (Sulimnski, 1964), *P. bressana* Mein, 1970, *P. meini* Black and Kowalski, 1974, *P. rugosa* Qiu, 1991, *P. raui* Daxner-Höck, 2001 and *P. kollmanni* Daxner-Höck, 2004, and *P. speciosa* Qiu and Ni, 2006. In the Iberian Peninsula, the oldest record of the genus comes from the late early Vallesian (MN9) (*Pliopetaurista* sp. at Can Llobateres 1; Casanovas-Villar et al. 2015), but is more frequent from the late Turolian till the end of the Ruscinian (MN13 to MN15). During this time interval, *P. pliocaenica* and maybe another species slightly larger in size referred as *P.* cf. *pliocaenica* were identified in some Iberian sites (Adrover et al. 1993b; García-Alix et al. 2007; Mansino et al. 2016b). Another species, *P. bressana* was cited in two other sites (Romanyà d'Empordà – MN13 – and Galera C – MN15) but these materials remain undescribed (Furió 2007; Garcés et al. 1997, respectively). The presence of a small-sized species of the genus identified as *Pliopetaurista* sp. is signalled in the late early Ruscinian (MN14) locality of ALC-D (Mansino et al. 2013) and in the Mio-Plio-Pleistocene locality of Canal Negre I (Guillén Castejón 2010).

The tooth from ROM-2C is larger than molars of *P. bressana*, *P. meini*, *P. raui* and *P. kollmanni*, and smaller than *P. rugosa*. It is more similar in size to *P. pliocaenica* and *P. dehneli*, two species previously recorded in southwestern Europe. Compared to *P. pliocaenica*, it has smaller dimensions than most of the previously known samples attributed to this species. Only at LG-2 (Adrover et al. 1993b) there is a damaged M1-2 whose length (*L* = 2.30 mm) is smaller than the specimen of ROM-2C (*L* = 2.40 mm). When compared with the remainder record of *P. pliocaenica* (Figure 6), this specimen clearly appears as an outlier, because of its much smaller size. The sample of LG-2 has never been described nor figured, so it is difficult with the available data to evaluate the meaning of the differences in size between the specimen of this site and those from other Iberian and European sites. In summary, because of its smaller dimensions, the molar from ROM-2C falls outside the range of variation of the known samples of *P. pliocaenica*, with the exception of the undescribed specimen from LG-2.

The specimen of ROM-2C agrees in size with *P. dehneli*. Its dimensions are within the range of variation of most of the known samples of this species, as Maramena (Greece), Rebielice Królewskie and Weze 2 (Poland) and Hautimagne (France) (Figure 6). Its morphology is also similar to this species. In our opinion, this could be the first record of this species in the Iberian Peninsula, but taking into account the extremely scarce material and the lack of other diagnostic elements, and the fact that the molar is also included in the extreme range of variation

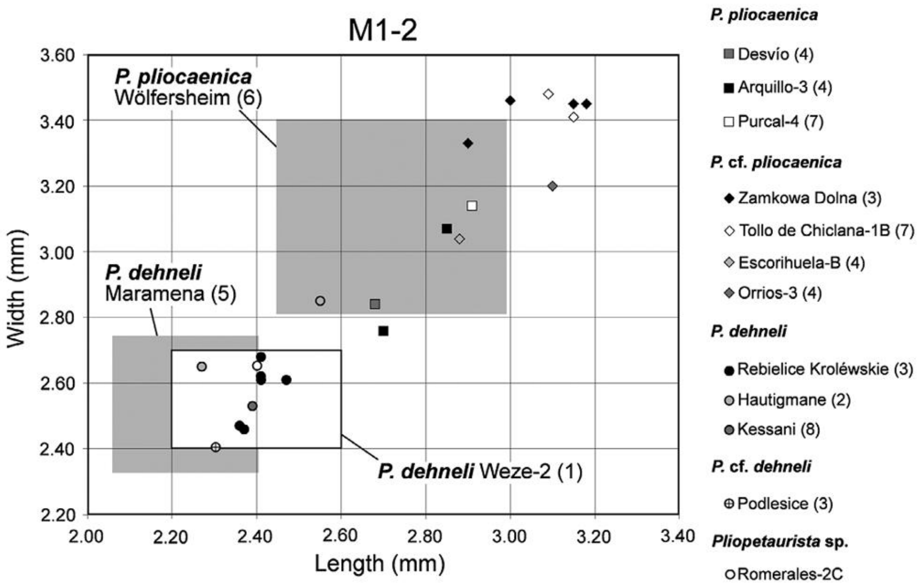


Figure 6. Scatter plot of the dimensions (length vs. width) of the first-second upper molars in different European populations of the species *P. pliocaenica*, *P.* cf. *pliocaenica*, *P. dehneli* and *P.* cf. *dehneli*, and comparison with the specimen of Romerales-2C. Rectangles represent the maximum range of variation of the samples indicated in the graph.

Notes: Data from (1) Sulimski (1964); (2) Mein (1970); (3) Black and Kowalski (1974); (4) Adrover et al. (1993b); (5) de Bruijn (1995); (6) Dahlmann (2001); (7) García-Alix et al. (2007); (8) Vasileiadou et al. (2012).

of the Iberian *P. pliocaenica* samples, we prefer to identify it as *Pliopetaurista* sp. until more material is available.

Subfamily Sciurinae Fischer de von Waldheim, 1817
Genus *Heteroxerus* Stehlin and Schaub, 1951
***Heteroxerus* sp.** (Figure 5(T))

Material, localitiy and measurements

ROM-2C: 1 m1-2 (IPS-90629) (*L*: 1.60; *W*: 2.02).

Description of the material

m1-2: The outline of the molar is rhomboidal. The molar is heavily worn, and extensive dentine fields are visible in the position of the main cusps and lophs. The four main cusps and the hypoconulid are well developed. Due to the advanced wear stage of the tooth, a small anterior cingulum is hardly visible. The mesoconid and mesostylid cannot be distinguished. The entolophid is long and connects the entoconid to the hypoconulid. The posterolophid reaches the base of the entoconid. The talonid basin lacks of any kind of ornamentation. The molar has four roots.

Discussion

The presence of an entolophid is a differencial character of the tribe Xerini Osborn, 1910 (Cuenca-Bescós 1988). Within this tribe, three genera have been identified in the Miocene and Pliocene of the Iberian Peninsula: *Aragoxerus* Cuenca Bescós, 1988, *Atlantoxerus* Forsyth Major, 1893 and *Heteroxerus* Stehlin and Schaub, 1951. The genus *Aragoxerus* (considered a *nomen dubium* by de Bruijn 1999, or a synonym of *Heteroxerus* by Krystufek et al. 2016) includes two species: *A. ignis* (Cuenca, 1988) and a yet unnamed new species from the Baixas site (MN4, France; Aguilar 2002). Both species differ from the specimen of ROM-2C by their smaller dimensions, the ellipsoidal outline in their m1-2, their simple dental patterns and their reduced entolophids. The genera *Atlantoxerus* and *Heteroxerus* are very similar based on molars morphology (Peláez-Campomanes 2001). According to de Bruijn (1995), the differences between species of both genera are often subtle, being the main morphologically difference between them the robustness of the molars. From a biometrical point of view, usually *Atlantoxerus* species are larger than those included in *Heteroxerus*, although some *Atlantoxerus* species share with *Heteroxerus* their reduced dimensions. The specimen from ROM-2C is smaller than the smaller representatives of the genus *Atlantoxerus*. From a morphological point of view, lower molars of this genus are characterised by the absence of anterior cingulum and the development of ornamentation in the talonid basin (Cuenca Bescós, 1988), whereas in *Heteroxerus* and the Romerales specimen the anterior cingulum is present and the ornamentation is lacking. The size of the molar from ROM-2C is bigger than *H. paulhiacensis*, smaller than *H. molinensis* Lacomba Andueza, 1988 and *H. mariatheresae* Adrover, Mein and Moissenet, 1993b, and it is more similar in size to *H.* cf. *huerzeleri* Stehlin and Schaub, 1951 from Los Valles de Fuentidueña (early Vallesian; Sesé and López Martínez 1981) and Molina de Aragón (Lacomba Andueza 1988) or the middle Miocene *H. grivensis* (Forsyth Major, 1893) samples described by Cuenca-Bescós (1988). Taking into account the scarcity of material, and the advanced wear stage of the only tooth available, the molar from ROM-2C cannot be identified at the species level.

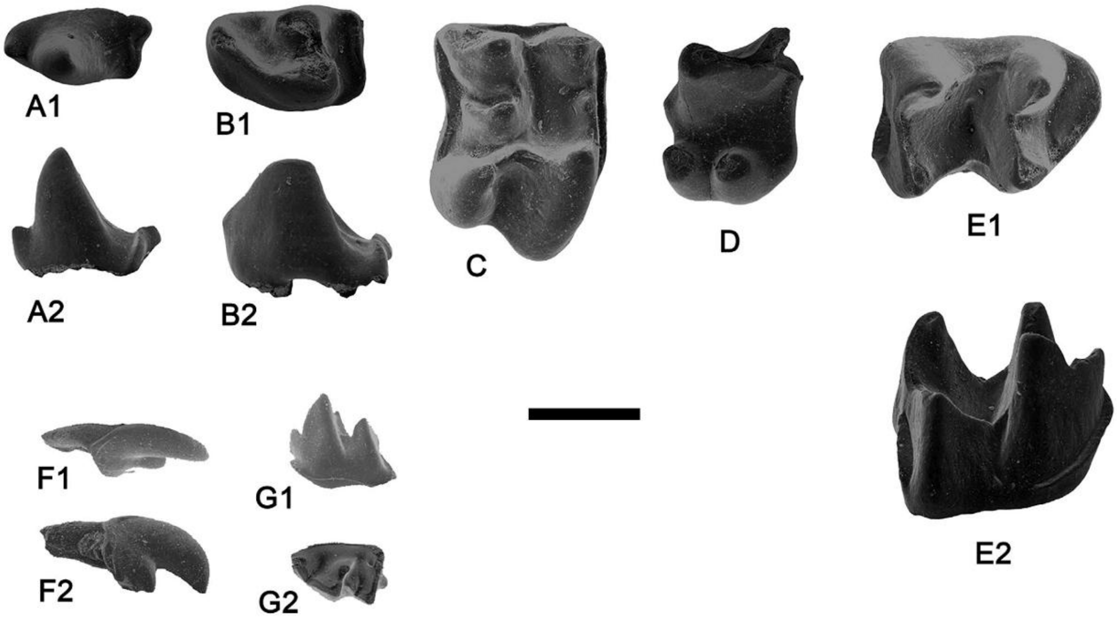


Figure 7. ESEM photographs of insectivores from Romerales. *Parasorex* sp.: (A) left p3, occlusal (1) and labial (2) views, IPS-93626 (ROM-2B); (B) left p4, occlusal (1) and labial (2) views, IPS-93625 (ROM-2B); (C) right M2, IPS-93642 (ROM-2C); (D) left P3, IPS-93645 (ROM-2C); (E) right m2, occlusal (1) and labial (2) views, IPS-93644 (ROM-2C). *Paenelimnoecus repenningi*: (F) right m2, occlusal (1) and labial (2) views, IPS-93657 (ROM-2C); (G) left m1, labial (1) and occlusal (2) views, IPS-93656 (ROM-2B).
Note: Scale bar equals 1 mm.

Table 7. Measurements (mm) of the specimens of *Parasorex* sp. from ROM-2C and ROM-2B.

		Length				Width			
Element	Locality	N	Min	Mean	Max	N	Min	Mean	Max
P3	ROM-2C	1		1.47		1		1.64	
M1	ROM-2C	1		2.30		1		2.98	
M2	ROM-2C	1		1.83		1		2.56	
M3	ROM-2C	3	1.21	1.25	1.29	3	1.79	1.90	1.95
p2	ROM-2C	1		1.06		1		0.48	
p3	ROM-2C	2	1.53	1.59	1.64	2	0.77	0.84	0.91
	ROM-2B	2	1.44	1.53	1.61	2	0.87	0.90	0.93
p4	ROM-2B	1		1.97		1		1.20	
m2	ROM-2C	1		2.07		1		1.47	

Order Erinaceomorpha Gregory, 1910
Family Erinaceidae Fischer, 1814
Subfamily Galericinae Pomel, 1848
Tribe Galericini Pomel, 1848
Genus *Parasorex* Von Meyer, 1865
***Parasorex* sp.** (Figure 7(A)–(E))

Material and localities

ROM-2B: 2 P4 fragm. (IPS-93639, IPS-97995), 2 M fragm. (IPS-93635, IPS-93636), 1 M3 fragm. (IPS-93640), 1 p fragm. (IPS-93627), 1 p2 (IPS-93624), 2 p3 (IPS-93624, IPS-93626), 1 p4 (IPS-93625), 18 m fragm. (IPS-93628, IPS-93629, IPS-93631–IPS-93633, IPS-93637, IPS-93638, IPS-93641, IPS-97996, IPS-97998, IPS-98001, IPS-98003, IPS-98004, IPS-98005, IPS-98009, IPS-98010, IPS-98011, IPS-98016), 12 fragm. indet. (IPS-97997, IPS-97999, IPS-98000, IPS-98002, IPS-98006, IPS-98007, IPS-98008, IPS-98012, IPS-98013, IPS-98014, IPS-98015, IPS-98017).

ROM-2C: 1 P3 (IPS-93645), 1 P4? fragm. (IPS-93647), 1 M1 (IPS-93643), 1 M2 (IPS-93642), 3 M fragm. (IPS-98019, IPS-98020, IPS-98023), 1 p? fragm. (IPS-93650), 2 p3 (IPS-93648; IPS-93654), 3 m fragm. (IPS-93646, IPS-98021, IPS-98022), 1 m2 (IPS-93644), 1 m3? fragm. (IPS-93649), 1 fragm. indet. (IPS-98018).

Measurements: Table 7.

Description of the material from ROM-2C

p3: The specimens are longitudinally elongated and their main cusp occupies a central position. There is a faint anterior elevation which can be tentatively identified as the paraconid, but there is no real paralophid connecting both elevations. The distal margin is covered by a low cingulid.

m2: the metaconid is more advanced than the protoconid and the labial cingulid only covers the base of the trigonid. The rest of the characters are not different than in any other species of *Parasorex*.

P3: The sole P3 has its posterolabial extreme broken. The lingual part shows a protocone and a hypocone of similar size. The parastyle is not much protruding, so the anterior emargination is not either much pronounced.

P4: Only the lingual part is preserved. The protocone and the hypocone are isolated cusps similar in size.

M1: The only specimen is missing its posterolabial quarter, but it is possible to discern that width and length are quite similar, thus acquiring an overall rather quadrate aspect in occlusal view. However, the base of the protocone is more protruding lingually than the base of the hypocone. The entoloph and the metaconule are not connected. The protoconule is separated from the base of the paracone by a small notch. There is a thin basal cingulum covering most of the anterior margin.

M2: The shape is wider than long. The base of the protocone is more protruding by the lingual margin than the base of the hypocone in occlusal view. This tooth has the posterior arm of the metaconule interrupted by the posterior cingulum, thus not connecting with the posterolabial corner. There is neither connection between the entoloph and the metaconule.

M3: The three specimens found show a rather variable morphology. They all have in common a triangular occlusal outline, with a conical paracone as the highest cusp and a cingulum covering most of the anterior base of the tooth, but not reaching the lingual side. The three specimens differ in the relative proportions of each side, the interruption of the inner crests (some notches in them) and the extent of the basal cingulum, which in one specimen finishes at the anterolabial edge, but it continues a bit further by the labial side in the other two specimens.

Description of the material from ROM-2B

p3: There are no significant differences between the p3 from ROM-2B and ROM-2C.

p4: This premolar has a well-developed trigonid and basal cingulid which is more elevated at its posterior margin.

P4: The only two specimens available show a rather short aspect, much wider than long. The parastyle is not protruding and the posterior margin is covered by a thin cingulum. Neither the protocone nor the hypocone are visible in any of these two fragmented teeth.

Discussion

Parasorex is the most likely erinaceid genus present in all these two localities according to the geographical and temporal context. Morphologically, this ascription is reinforced by the absence of connection between the protocone and the metaconule in the upper molars, and the p4 with well-developed paralophids. However, the morphology of the posterior arm of the metaconule in the specimen from ROM-2C, not reaching the posterolabial corner, is atypical in the genus *Parasorex* but frequent in *Galerix* according to the criteria of van den Hoek Ostende (2001). This character is quite peculiar, but it has been considered insufficient to ascribe all this material to *Galerix*. Whether the M2 from ROM-2C is indicating that *Galerix* is present in this basin as a lazarus genus or if it is a simple morphologic anomaly within *Parasorex*, will need further research. However, the second option is followed here because it is considered more likely and conservative.

Table 8. Measurements (mm) of the teeth of *Paenelimnoecus repenningi* from ROM-2C.

Element	LL	PE	BL	AW	PW	L	TRW	TAW	LT	H
I1						1.14			0.61	0.83
M1	0.94	0.75	0.94	1.22	1.11					
m1						1.15	0.60	0.61		
m1						1.02	0.56	0.58		

Notes: LL = lingual length; PE = posterior emargination; BL = buccal length; AW = anterior width; PW = posterior width; L = length; TRW = trigonid width; TAW = talonid width; LT = length talon; H = height.

The specific identification is problematic as well. The material from ROM-2B and ROM-2C does not completely match the characters of any species of *Parasorex* described hitherto. The rather squared M1 and the m2 with a short posterior cingulid are similar to *P. depereti* according to the diagnosis provided by Crochet (1986), but the teeth from the Pliocene French sites are significantly larger than the elements from ROM. On the other hand, the dimensions of the teeth studied in the present work are close to the range of *P. ibericus*, but the morphology of some teeth is different. To preclude adding unnecessary noise to the taxonomy, the identification is left at the genus level, pending on further material and research.

Order Soricomorpha Gregory, 1910
Family Soricidae Fischer, 1814
Subfamily Allosoricinae Fejfar, 1966
Genus *Paenelimnoecus* Baudelot, 1972
Paenelimnoecus repenningi (Bachmayer and Wilson, 1970) (Figure 7(F)–(G)).

Material and localities

ROM-2B: 1 m1 (IPS-93656).

ROM-2C: 1 I1 (IPS-93657), 1 M1 (IPS-93658), 1 m1 (IPS-93659).

Measurements: Table 8.

Description of the material from ROM-2C

m1: The m1 has the same morphology in ROM-2B and ROM-2C. This tooth lacks the entoconid cristids, and only a tiny vestigial entoconid is present at the lingual side of the talonid of the m1. The talonid is shorter and somewhat wider than the trigonid. The trigonid basin is completely open to the lingual side. The pigmentation affects the highest parts of the tooth, notably the labial sides of the paralophid and the oblique cristid, and the posterior face of the protolophid. The oblique cristid is concave in lateral view. There is a narrow cingulid covering the labial base of this tooth.

I1: This tooth is not fissident and has a dorsal margin with a regular curvature. A vestigial pigmentation is discernible in both, apex and talon. The base of the tooth is covered at its labial part by a softly undulated cingulum.

M1: The M1 has rather pointed cusps, being the metacone the highest of them. The paracone is somewhat lower than the metacone, and as is the protocone with respect to the paracone. The hypocone is poorly developed. The posterior emargination is moderately pronounced.

Discussion

Paenelimnoecus is easily identified by its tiny size (similar to that of the smallest living shrew, *Suncus etruscus*) and the lack of entoconid cristids. The specific ascription, however, is not so straightforward. In principle, the measurements of the teeth discriminate between *P. repenningi* and *P. pannonicus*, purportedly being the former around a 15% larger than the latter (Bachmayer and Wilson 1970). However, such difference is not so evident when the measurements of the Austrian teeth from Kohfidisch (*P. repenningi*) are compared with the Hungarian material from Osztramos 7 and 9 or Csarnóta 2 (*P. pannonicus*) provided by Reumer (1984). Based on the new specimens found, Bachmayer and Wilson (1978) seem to provide the presence of vestigial but still discernible entoconids as a new character to identify *P. repenningi*, something that is rarely present in *P. pannonicus*, according to the descriptions of Reumer (1984).

Minwer-Barakat et al. (2010) identify *P. pannonicus* in the Pliocene of Tollo de Chiclana, also in the southeast of the Iberian Peninsula, characterised by the complete absence of both entoconid and entoconid cristids. Such is not the condition found in the material from the Fortuna Basin, in which the molars still preserve vestigial entoconids. The material of *Paenelimnoecus* from La Celia and Gargantones in the nearby area (Van Dam et al. 2014) could indeed belong to this same species, but the absence of diagnostic elements does not allow further precision.

Biostratigraphy

ROM-2B and ROM-2C share most taxa: *Occitanomys alcalai*, *Occitanomys* aff. *adroveri*, *Apodemus gudrunae*, *Stephanomys ramblensis*, *Apocricetus* aff *plinii*, *Ruscinomys* aff. *gilvosi*, *Eliomys* cf. *truci*, *Parasorex* sp., and *Paenelimnoecus repenningi*. In addition, the faunal list of ROM-2C includes *Pliopetaurista* sp. and *Heteroxerus* sp. ROM-3A is the poorest level described in this work, with the mere presence of *O. alcalai* and *S. ramblensis*.

Stephanomys ramblensis is the most characteristic late Turolian taxon in Spanish basins (Agustí and Llenas 1996). *Occitanomys adroveri* is widely distributed in the middle Turolian (MN12) of Iberian basins but it persists until the first part of the late Turolian (MN13) associated to *O. alcalai* in some localities such as OTU-1, OTU-3 (García-Alix et al. 2008b), CR-14, and CR-22 (Martín Suárez and Freudenthal 1998). The absence of *Paraethomys* despite the large number of fossils recovered suggests an age for these sites younger than the FAD of this genus in Europe, established in LIB-1 and Vvm at about 6.2 Ma (Garcés et al. 1998; Agustí et al. 2006; Gibert et al. 2013). The joint occurrence of *S. ramblensis*, *O. alcalai*, *O.* aff. *adroveri*, *A. gudrunae* and the absence of *Paraethomys* lead us to attribute the localities of Romerales to the base of the late Turolian (Figures 8 and 9).

The studied levels were deposited after the start of the First Messinian Mammalian Event (occurred somewhere between 7.3 and 6.8 Ma, corresponding to the MN12-MN13 and middle-late Turolian boundaries) suggested by Agustí et al. (2006) and recorded in the continuous sequence of the Fortuna Basin. It is characterised by the extinction of the genus *Huerzelerimys*, the apparition for the first time of *A. gudrunae* and *S. ramblensis*, the replacement of *Hispanomys* by *Ruscinomys*, and *Cricetulodon* and *Neocricetodon* by *Apocricetus*. The sites of Romerales are close in age to the levels in the Fortuna Basin where this event is recorded, like SIF-3, CH-17, CH-29 and CH-33 (Agustí et al. 2006). ROM-2B, ROM-2C and ROM-3A are younger than the localities of SIF-1 with the presence of a somewhat archaic fauna (under study), and Casa del Acero (Agustí et al. 1981; Garcés et al. 2001). The studied localities are also younger than CH-307 and BS-141 (Agustí et al. 2006), since they record taxa from the middle Turolian such as *Apodemus barbarae* and *Huerzelerimys turoliensis* Michaux, 1969. On the other hand, the localities of MS-3, 4 7, 8, 9, AU-3 (A-M), LIB-1, SIF-79 and SIF-61 (Agustí et al. 1983, 2006) with the occurrence of *Paraethomys* are younger than those of Romerales.

The localities of the Romerales section can be correlated with other sites from the Iberian Peninsula. Regarding the Crevillente Basin, the levels of CR-14 and CR-31 share some species such as *O. alcalai* and *S. ramblensis* (Martín Suárez and Freudenthal 1993, 1998). But one of the differences with Romerales is the presence of *O. adroveri* instead of its derived form *O.* aff. *adroveri*, and *Castromys inflatus* (Mein, Moissenet and Adrover, 1990) in CR-14 and CR-31. In the Fortuna Basin, *Castromys* appears later, in MS-1 and MS-D (Agustí et al. 1983, 2006) by the entry of *Castromys kowalskii* (Agustí and Llenas 1996), a more derived species than *C. inflatus* from Crevillente (Martín Suárez and Freudenthal 1994, 1998), Teruel (Mein et al. 1990) and Granada (García-Alix et al. 2008b, 2008c) basins. Another difference between Romerales and CR-14 and CR-31 is the record of *A. gudrunae*. Our localities may be correlated with the upper part of the *Castromys inflatus* Zone from Crevillente Basin (Martín Suárez and Freudenthal, 1998) despite the presence of *A. gudrunae*. In the Crevillente area this species appears simultaneously with *Paraethomys meini* Michaux, 1969, in CR-6 caused probably by a gap in the fossil record (Martín Suárez and Freudenthal, 1998).

The fauna in our levels is very similar to that of the late Turolian localities of VDC-3 and VDC-6, LG-5, VIL and ARQ-1 in the Teruel area with the common occurrence of *S. ramblensis*, *O. alcalai* and *A. gudrunae*, and an intermediate *Apocricetus* between *A. plinii* and *A. alberti* (Freudenthal et al. 1998), which in LG-5 seems to be closer to *A. alberti* (van de Weerd 1976; Mein et al. 1990; Adrover et al. 1993a; Freudenthal et al. 1998). ROM-2B, ROM-2C and ROM-3A are probably coeval to these latter or slightly older. The main difference with them is the absence of *C. inflatus*, the presence of *O.* aff. *adroveri* and a somewhat archaic *S. ramblensis* relative to the type population of VLD-3. The site of LG-6 is somewhat older than Romerales according to the record of *Apodemus* cf. *barbarae* (Mein et al. 1990), while ARQ-2 and CEL-2 are younger due to the occurrence of *Paraethomys meini* (Figure 8).

Regarding the Granada Basin (García-Alix et al. 2008b, 2008c), our levels share with OTU-1 and OTU-3 a form of *O. adroveri* and *O. alcalai*, but the absence of *S. ramblensis* in these levels indicates an older age. On the other hand, the presence of the descendant of *A. gudrunae,* i.e. *A. gorafensis*, besides a more derived *Apocricetus*, and the absence of *O. adroveri* in PUR-23,

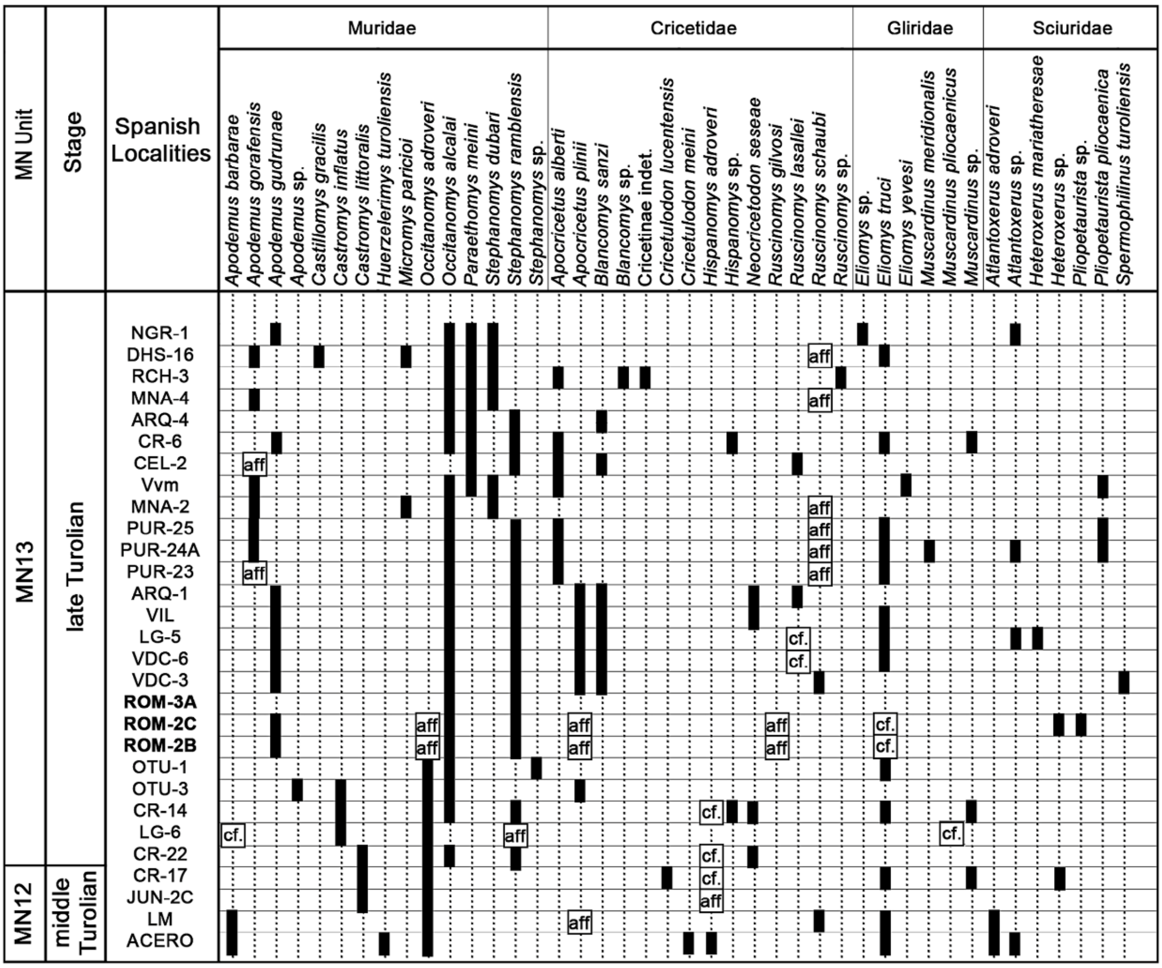


Figure 8. Distribution of rodent species studied in this work and, according to bibliography, of other species from middle and late Turolian. For the making of this figure the following synonymies have been taken in account: *Kowalskia meini* as *Cricetulodon meini*, *Kowalskia occidentalis* as *Apocricetus* aff. *plinii*, *Kowalskia lavocati* as *Neocricetodon seseae*, *Cricetus kormosi* either as *Apocricetus alberti* or *Apocricetus plinii* (according to Freudenthal et al. 1998), *Paraethomys anomalus* and *Paraethomys miocaenicus* as *Paraethomys meini*, *Valeremys turoliensis* as *Huerzelerimys turoliensis*, *Parapodemus barbarae* as *Apodemus barbarae*, *Karnimata inflata* as *Castromys inflatus*.

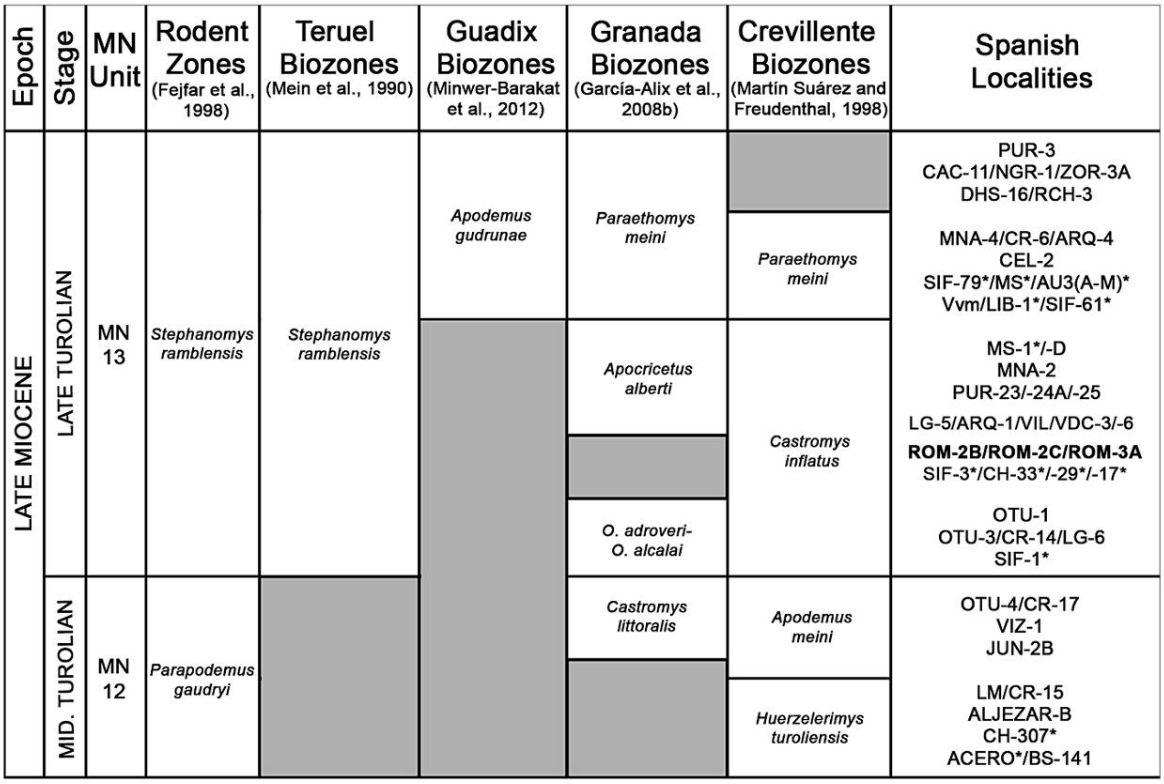
Abbreviations: NGR, Negratín; RCH, Rambla Chimeneas (Minwer-Barakat et al. 2009a, 2009b); DHS, Dehesa; MNA, Mina; PUR, Purcal; OTU, Otura; JUN, Canteras de Jun (García-Alix et al. 2008d); Vvm, Venta del Moro (Mansino et al. 2014, 2015b, 2016a, 2016b); CR, Crevillente (Martín Suárez and Freudenthal, 1998); ARQ, Arquillo; CEL, Celadas; LG-5, La Gloria 5; VDC, Valdecebro (Adrover et al. 1993a, 1993b); LG-6, La Gloria 5 (Mein et al. 1990); LM, Los Mansuetos (van de Weerd 1976); ACERO, Casa del Acero (Agustí et al. 1981; Agustí 1986).

PUR-24A and PUR25 suggests a slightly lower biostratigraphic position for these levels than that of Romerales. It is likely that the studied levels correlate with the Barren Interval of turbiditic gypsums without small mammal between the *Occitanomys adroveri-Occitanomys alcalai* Zone and the *Apocricetus alberti* Zone from the Granada Basin (García-Alix et al. 2008d).

To summarise, the levels from Romerales are older than the lowermost localities from the Guadix Basin like NGR-1 (Minwer-Barakat et al. 2009a) and RCH-3 (Minwer-Barakat et al. 2009b) where *P. meini* and *S. dubari* (the anagenetic descendant of *S. ramblensis*) have been identified.

Palaeoecology

Micromammals are more effective than macromammals when it comes to making paleoenvironmental inferences, since they have more specific ecological requirements, the energetic and physiological restrictions create a high degree of specialisation in small species, and micromammal species are more abundant than macromammal species (Hernández Fernández 2001). In this sense, micromammals have widely been used as palaeoclimatical and palaeoecological indicators. Studies of rodent assemblages in particular show interesting information on the past environmental and climatic conditions (Martín-Suárez et al., 2001; Minwer-Barakat 2005; Montuire et al. 2006; García-Alix et al. 2008a, among others). Neverthless, the palaeoecological and palaeoenvironmental trends (specially palaeo-humidity conditions) could be affected by the paleogeography of the area, recording physical landscape changes rather than global or regional climatic trends (García-Alix et al. 2013; Freudenthal et al. 2014; García-Alix 2015). Daams et al. (1999) proposed using



Epoch	Stage	MN Unit	Rodent Zones (Fejfar et al., 1998)	Teruel Biozones (Mein et al., 1990)	Guadix Biozones (Minwer-Barakat et al., 2012)	Granada Biozones (García-Alix et al., 2008b)	Crevillente Biozones (Martín Suárez and Freudenthal, 1998)	Spanish Localities
LATE MIOCENE	LATE TUROLIAN	MN 13	*Stephanomys ramblensis*	*Stephanomys ramblensis*	*Apodemus gudrunae*	*Paraethomys meini*	▨	PUR-3 CAC-11/NGR-1/ZOR-3A DHS-16/RCH-3
							Paraethomys meini	MNA-4/CR-6/ARQ-4 CEL-2 SIF-79*/MS*/AU3(A-M)* Vvm/LIB-1*/SIF-61*
					▨	*Apocricetus alberti*	*Castromys inflatus*	MS-1*/-D MNA-2 PUR-23/-24A/-25
						▨		LG-5/ARQ-1/VIL/VDC-3/-6 **ROM-2B/ROM-2C/ROM-3A** SIF-3*/CH-33*/-29*/-17*
						O. adroveri- *O. alcalai*		OTU-1 OTU-3/CR-14/LG-6 SIF-1*
	MID. TUROLIAN	MN 12	*Parapodemus gaudryi*	▨		*Castromys littoralis*	*Apodemus meini*	OTU-4/CR-17 VIZ-1 JUN-2B
						▨	*Huerzelerimys turoliensis*	LM/CR-15 ALJEZAR-B CH-307* ACERO*/BS-141

Figure 9. Proposed correlation between the studied localities and the local biozones in the Crevillente, Granada, Guadix and Teruel basins and its biostratigraphic position relative to other Spanish sites from the Late Miocene (Mein et al. 1990; Fejfar et al. 1998; Martín Suárez and Freudenthal 1998; García-Alix et al. 2008d; Martín-Suárez et al. 2000; Minwer-Barakat et al. 2012).

Abbreviations: PUR, Purcal; CAC, Cacín; NGR, Negratín; ZOR, Zorreras; DHS, Dehesa; RCH, Rambla Chimeneas; MNA, Mina; CR, Crevillente; ARQ, Arquillo; CEL, Celadas; SIF, Sifón; MS, Molina de Segura; Vvm, Venta del Moro; LIB, Librilla; AU, Autovía; VIL, Villastar; VDC, Valdecebro; CH, Chorrico; ROM, Romerales; OTU, Otura; LG, La Gloria; VIZ, Víznar; JUN, Canteras de Jun; LM, Los Mansuetos; ACERO, Casa del Acero; BS, Barranco de la Salada.

rodent associations with 100 or more m1 + m2 + M1 + M2 for palaeoecological studies based on micromammals. Hadly (1999) suggested that reconstructing the local mammalian community requires only a minimum sampling effort (200–250 specimens). Minwer-Barakat (2005) reduced this number to 100 because he only considered Rodentia and Insectivora. The small mammal sample of ROM-2B and ROM-2C consists of 131 and 414 specimens respectively. ROM-3A is discarded from this analysis due to its reduced sample (four individuals).

The determination of the ecological requirements of an extinct taxon is based on the phylogenetic relationships with extant species, dental-corporal modifications and association with taxa with known ecological preferences (García-Alix et al. 2008a). We have used the paleoecologic requirements established by Minwer-Barakat (2005) and García-Alix et al. (2008a) for rodents and insectivores (Table 9). *Apocricetus plinii* and *A. gudrunae* are considered the ancestors of *A.alberti* and *A. gorafensis* (Freudenthal et al. 1998; Martín Suárez and Mein 1998), so we assume ecological requirements similar to those of their descentants (Minwer-Barakat 2005; García-Alix et al. 2008a). Freudenthal et al. (2014) considered that *Eliomys* cannot be indicator of humidity since current representatives of this genus inhabit a range of different habitats, while *Pliopetaurista* lived in forested/wooded zones (de Bruijn 1999). Extant Xerini includes ground squirrels living in dry open habitats in the Palarctic and Sub-Saharan Africa (Krystufek et al. 2015), so we assume warm and dry conditions for *Heteroxerus*, an extinct Xerini.

Muridae is the most abundant and diverse small mammal family in ROM-2B and ROM-2C. Both associations are clearly dominated by the species *Stephanomys ramblensis* with a prevalence of 58.19% in the former and 66.46% in the latter (Table 9). The next most abundant taxon is the cricetid *Ruscinomys* aff. *gilvosi* with a relative abundance of 12.77% in ROM-2B and 17.48% in ROM-2C. This dominance of one species over others is indicating a low specific variability. As expected the values of the Shannon-Wiener index about the studies localities are not high ($H' = 1.37$ for ROM-2B and $H' = 1.14$ for ROM-2C). Usually low values in species diversity are associated with unstable ecosystems (Margalef 1974). Interestingly, the two most abundant species account for more than 70% of the micromammal association. Both groups present morphological features in the dental pattern associated with the stephanodonty (development of longitudinal ridges among molar cusps), which some authors interpreted as indicative of a diet based on fibrous components (van Dam and Weltje 1999; Renaud et al. 2005; Gomes Rodrigues et al. 2013;

Table 9. Relative abundances (number of specimens divided by the number of diagnostic elements) of each taxon with their palaeoecological affinities from the localities of ROM-2B and ROM-2C.

	RA (%)				
Species	ROM-2B	ROM-2C	Temperature	Humidity	Habitat
Occitanomys alcalai	7.31	4.74	W	H	E
Occitanomys aff. *adroveri*	3.60	3.51	C	D	E
Apodemus gudrunae	9.06	3.51	W	H	E
Stephanomys ramblensis	58.19	66.46	E	E	E
Apocricetus aff. *plinii*	0.87	2.25	W	E	OH
Ruscinomys aff. *gilvosi*	12.77	17.48	C	D	OH
Heteroxerus sp.	–	0.18	W	D	OB
Pliopetaurista sp.	–	0.18	E	H	F
Eliomys cf. *truci*	0.66	0.18	E	E	E
Parasorex sp.	6.99	1.08	E	E	E
Paenelimnoecus repenningi	0.55	0.45	E	H	E

Notes: C = cool; D = dry; E = eurytopic; F = forested; H = humid; OB = open/bare; OH = open/herbaceous; W = warm.

Table 10. Relative abundances expressed in percentage of the taxa from the localities ROM-2B and ROM-2C, according to their palaeoecological affinities.

	Temperature			Humidity			Habitat			
Locality	C	W	E	H	D	E	OB	OH	F	E
ROM-2B	16.38	17.25	66.38	16.92	16.38	66.70	–	13.65	–	86.35
ROM-2C	20.98	10.67	68.35	8.87	21.16	69.96	0.18	19.72	0.18	79.92

Notes: C = cool; D = dry; E = eurytopic; F = forested; H = humid; OB = open/bare; OH = open/herbaceous; W = warm.

Gómez Cano et al. 2013), so open grassland are expected as dominant habitat in the vicinity of ROM-2B and ROM-2C. Either way in this paper it is considered *S. ramblensis* as a eurytopic species for the habitat as Garcia-Alix et al. (2008a) and Minwer-Barakat (2005) indicated.

The small mammal association from ROM-2B and ROM-2C is mostly formed by taxa considered as eurytopic in terms of habitat preferences (86.35% and 79.92% respectively) like *O. alcalai*, *O.* aff. *adroveri*, *A. gudrunae*, *S. ramblensis*, *E. truci*, *Parasorex* sp. and *P. repenningi* (Table 10). The indicators of open and herbaceous habitats (*A.* aff. *plinii* and *R.* aff. *gilvosi*) consist of 13.65% in ROM-2B and 19.72% in ROM-2C. The woodland dwellers are poorly represented, being present only the flying squirrel *Pliopetaurista* sp. in ROM-2C with a prevalence of 0.18%. The open bare habitat representation is also very scarce (0.18%) being the only one the ground squirrel *Heteroxerus* sp. in ROM-2C. These results agree with a landscape dominated mainly by open grass meadows in the vicinity of ROM-2B and ROM-2C during the formation of these fossiliferous levels. The presence of a flying squirrel besides a ground one at ROM-2C indicates a fragmented habitat, consistent with fluctuating climate conditions (as is suggested by the low value of the Shannon-Wiener index and the great percentage of eurytopic species for habitat). According to these results, the open grass meadows where dominant during the early late Turolian in the surrounding of Romerales sites with a very scarce presence of forested patches at ROM-2C, probably close to the water reservoirs of palustrine-lacustrine origin.

Regarding the temperature, the faunal assemblage of both localities is dominated by eurytopic elements (66.38% in ROM-2B and 68.35% in ROM-2C). The indicators of warm climatic conditions (*O. alcalai*, *A. gudrunae*, *A.* aff. *plinii* and *Heteroxerus* sp.) represent 17.25% in ROM-2B and 10.67% in ROM-2C, whereas the taxa linked to cooler temperatures (*O.* aff. *adroveri* and *R.* aff. *gilvosi*) consist of 16.38% of the assemblage in ROM-2B and 20.98% in ROM-2C. There is a decrease of warm indicators from ROM-2B to ROM-2C. Although many identified taxa are not optimal indicators of temperature, the coexistence of species with different temperature requirements lead us to assume temperate conditions at the moment of formation of sites.

The taxa *S. ramblensis*, *A.* aff. *plinii*, *E.* cf. *truci* and *Parasorex* sp. are eurytopic regarding the humidity, with a prevalence of 66.70% and 69.96% in ROM-2B and ROM-2C respectively. *Occitanomys alcalai*, *A. gudrunae*, *Pliopetaurista* sp. and *P. repenningi* are indicators of wet conditions (19.92% in ROM-2B and 8.87% in ROM-2C), while *O.* aff. *adroveri*, *R.* aff. *gilvosi* and *Heteroxerus* sp. are considered as inhabitants of dry environments (16.38% in ROM-2B and 21.16% in ROM-2C). Therefore, a decrease of the moisture from ROM-2B to ROM-2C can be observed.

According to this analysis, the Fortuna Basin was mostly dominated by open grass meadows with a scarce development of forested environments under temperate climate during the base of the late Turolian. In addition, it seems to be a slight shift to colder and drier conditions from ROM-2B to ROM-2C. The low specific diversity, the dominance of relatively homogeneous grasslands, and the great prevalence of taxa able to tolerate a wide variety of habitats are consistent with the dominance of fluctuating (or unstable) climatic conditions during the pre-evaporite Messinian in the Fortuna Basin.

Our results for the base of the late Turolian in the Fortuna Basin are consistent with those obtained by García-Alix et al. (2008a) who deduced open herbaceous habitats and scarce forested environments under dry and cold-temperate conditions in the nearby Granada Basin during the middle-late Turolian transition, evolving towards wetter and warmer conditions with some oscillations during the late Turolian.

Conclusions

The rodent and insectivore assemblage from ROM-2B is formed by 131 specimens, the one from ROM-2C by 414 and the one from ROM-3A by 4. The faunal list of the richest level, ROM-2C, comprises 11 taxa: *Occitanomys alcalai*, *Occitanomys* aff. *adroveri*, *Apodemus gudrunae*, *Stephanomys ramblensis*, *Apocricetus* aff *plinii*, *Ruscinomys* aff. *gilvosi*, *Eliomys* cf. *truci*, cf., *Pliopetaurista* sp., *Heteroxerus* sp., *Parasorex* sp., and *Paenelimnoecus repenningi*. The faunal list of ROM-2B is very similar, except for the absence of the two sciurids in this locality. Finally, ROM-3A has yielded remains of just two murids: *S. ramblensis* and *O. alcalai*.

The faunal assemblages suggest a late Turolian age, posterior to the MN12-MN13 transition (at about 7.3–6.8 Ma) and prior to the first entry of *Paraethomys* (6.2 Ma). The studied localities are placed close to the Fortuna Basin localities of SIF-3, CH-17, CH-29 and CH-33, and above the sites of Casa del Acero, CH-307 and BS-141.

The amount of fossil remains yielded by the levels of ROM-2B and ROM-2C is enough to perform a palaeoecological analysis. The relative proportions of the species from these localities point out to the dominance of a relatively homogeneous open herbaceous habitat during the formation of the sites, with the presence of forest patches in ROM-2C. It is probable that the climate conditions were temperate. From ROM-2B to ROM-2C has been detected a slight decrease of temperature and humidity indicators. The low value of specific diversity of both ROM-2B and ROM-2C and the proportions of the taxa suggesting homogenous open grassland environment, allow us to infer unstable climatic conditions during the base of late Turolian in the Fortuna Basin.

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No potential conflict of interest was reported by the authors.

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VI. LA SUCESIÓN DE ROEDORES DE LA SECCIÓN DE SIFÓN DE LIBRILLA (CUENCA DE FORTUNA, SE ESPAÑA): IMPLICACIONES PARA EL LÍMITE MIO-PLIOCENO EN EL REGISTRO TERRESTRE DEL MEDITERRÁNEO

The rodent succession in the Sifón de Librilla section (Fortuna Basin, SE Spain): implications for the Mio-Pliocene boundary in the Mediterranean terrestrial record

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The rodent succession in the Sifón de Librilla section (Fortuna Basin, SE Spain): implications for the Mio-Pliocene boundary in the Mediterranean terrestrial record

The long and continuous continental section of Sifón de Librilla (Fortuna Basin, southern Spain) provides a detailed biostratigraphic record distributed along eight localities, in which the magnetostratigraphy has been unambiguously established. This section therefore provides a unique opportunity to cross biostratigraphic information with magnetostratigraphic data to establish a reliable frame to date sites. This 800-m-thick sequence extends from the latest Miocene to the early Pliocene, recording more than 2 Myr. In this work we provide a complete taxonomic survey of the recovered rodent remains, defining a new cricetid species named as *Hispanomys romeroi*. We also refine the phylogenetic relationships of the *Apodemus*, *Stephanomys*, *Paraethomys*, *Ruscinomys* and *Apocricetus* lineages. Considering the accurate age of the associations, we discuss the chronology of the first and last appearances of some species. In addition, this section clearly records the Mio-Pliocene boundary, allowing us to correlate between the marine and continental biostratigraphic scales. Taking advantage of this opportunity, we explore key biostratigraphic indicators for identifying the beginning of the Pliocene in the continental records, as well as for differentiating the MN13 and MN14 units, most specially the FOD of *Occitanomys brailloni*. According to this datum, we conclude that the Miocene-Pliocene boundary coincides with that of MN13-MN14 units.

Keywords: late Miocene, early Pliocene, MN13/MN14, biostratigraphy, chronology, marine/continental correlation.

Introduction

The composite section of Sifón de Librilla belongs to the Fortuna Basin (Murcia Province), in southeastern Spain (Fig. 1). The base of this section is located about 2 km to the north of the town of Librilla, at the southern edge of the Fortuna Basin (Garcés et al. 2001), Neogene basin situated at the contact between the Internal and the External Betic Zones.

Montenat and Crusafont (1970) led the first studies of the continental records in the Fortuna Basin, coming to light the late Turolian locality of Librilla. After the discovery of this site, some works on the vertebrate remains were published (Montenat 1973; de Bruijn et al. 1975; Montenat et al. 1975; Alberdi et al. 1981). Casa del Acero represents another classic locality of the Fortuna Basin, close to the Chícamo section (Agustí et al. 2001, 2006; Garcés et al. 2001). The mammal content of this middle Turolian site (late Tortonian, MN12) was studied by Agustí et al. (1981), followed by Agustí (1986) and Pons-Moyà (1987). The first geological and bioestratigraphical synthesis of the continental deposits of the Fortuna Basin was provided by Agustí et al. (1983), including also the late Turolian sequence of Molina de Segura (= Salinas de Molina in Agustí et al. 2006). On the other hand, the Fortuna Basin records evaporite beds over regressive marine packets beneath the continental sequence. The dating of these deposits has been widely discussed (Santisteban 1981; Santisteban and Taberner 1983; Muller and Hsu 1987; Muller and Schrader 1989; Ortí et al. 1993; Mankiewicz 1995; Playà et al. 1995; Dinarès-Turell et al. 1999; Krijgsman et al. 2000; Tent-Manclús et al. 2008).

Garcés et al. (1998, 2001) established a reliable time frame for the sedimentary infilling of the Fortuna Basin through detailed magnetostratigraphic studies that included continental packets from the middle Turolian (MN12) to the lower Ruscinian (MN14) (Barranco de la Salada, Río Chicamo, El Chorrico, Salinas de Molina and Sifón de Librilla). Based on the vertebrate fossil record and the magnetostratigraphic information, Agustí et al. (1999, 2006) established an accurate chronology for the main mammalian events that occurred in the western Mediterranean between 7.6 and 4.5 Ma. These authors published small-mammal lists from several sites, although they did not supply detailed information supporting their taxonomic determinations. So far, there are few works describing in detail the small-mammal remains found in the different fossil sites from the Fortuna Basin. In this line, Agustí et al. (1981) studied the vertebrate fauna from Casa del Acero; Agustí (1986) examined the cricetids from the same locality; Agustí and Llenas (1996) described the genus and species *Parasaidomys kowalskii* in MS-1. Furió and Agustí (2017) focused on the the insectivores from the Sifón de Librilla, El Chorrico and Salinas de Molina sections; and Piñero et al. (2017a) presented a complete survey of the rodents and insectivores from the Romerales section.

The continental sequence of Sifón de Librilla provides a reliable and detailed biostratigraphic record as it is exceptionally suitable for studying the evolution of small mammals during the late Miocene and early Pliocene. It represents more than 2 Myr of continental record (from 6.9 - 6.7 to 4.6 - 4.5 Ma), ranging from the lowermost MN13 to the base of the MN14 unit. Magnetostratigraphy is currently the most useful and widely available tool for providing independent age estimates of mammal faunas (Hordijk and de Bruijn 2009). There are few long stratigraphic sections that yield both micromammal and reliable paleomagnetic data. Fortunately, the Sifón de Librilla section is a very long and continuous sequence in which the magnetostratigraphy has been unambiguously established (Garcés et al. 1998, 2001; Agustí et al. 2006). In addition, Garcés et al. (2001) detected that in the Sifón de Librilla section the basal Pliocene transgression occurred just after the valley incision produced by the Messinian Salinity Crisis (MSC), which enables us to make a correlation between the marine and continental biostratigraphic scales. The first level containing small mammals, SIF-413, is immediately above the earliest Pliocene transgression.

In this paper, we present a complete taxonomic study of the rodents found in the localities of the Sifón de Librilla section (SIF-1, SIF-3, SIF-52, SIF-61, SIF-79, SIF-413, SIF-430 and SIF-P), and update their phylogenetic relationships. We also analyse the biostratigraphical implications for both detecting the Miocene-Pliocene boundary in the continental record, and differentiating the MN13 and MN14 mammal units. We also look at the chronological framework of the identified species.

Material, methods and abbreviations

The micromammal remains were extracted from a large amount of sediment recovered from different levels along the Sifón de Librilla section. All the sediment was screen-washed using superimposed 4.0, 1.0 and 0.5 mm mesh screens. The specimens described are currently kept at the *Institut Català de Paleontologia Miquel Crusafont* (ICP; Sabadell, Barcelona, Spain).

The material from the level SIF-1 comprises 139 teeth of at least seven rodent species, SIF-3 has yielded 104 teeth representing eight species, the sample of SIF-52 consist of 55 specimens ascribed to at least five taxa, SIF-61 comprises 158 molars assigned to nine different rodent species, SIF-79 has yielded 28 specimens comprinsing five taxa, the material from SIF-413 consists of 157 teeth representing nine rodent species, SIF-430 is the poorest level with only nine teeth belonging to three species, and the sample from SIF-P comprises 116 specimens ascribed to at least seven species.

All the measurements are expressed in millimeters and were taken on the occlusal plane of the teeth with the software DinoCapture 2.0, using photographs from the Digital Microscope AM4115TL Dino-Lite Edge. The teeth are illustrated by means of micrographs taken with an Environmental Scanning Electron Microscopy (ESEM) at the “Servei de Recursos Científics i Tècnics de la Universitat Rovira i Virgili” (Tarragona). The upper teeth are designates as P4, M1, M2 and M3 and the lower teeth as p4, m1, m2 and m3.

For the descriptions and measurements of the teeth of Murinae, we have followed van de Weerd (1976) and Martín Suárez and Freudenthal (1993), respectively. The nomenclature and measuring methods used in the descriptions of Taterillinae are those defined by Wood and Wilson (1936) and Minwer-Barakat (2005), respectively. The terminology employed for the description and the measuring methods of the teeth of Gliridae are those defined by Freudenthal (2004). Mein and Freudenthal (1971) have been followed for the descriptions and measurements of the Cricetidae teeth. The terms “preloph” and “prelophid” are taken from Freudenthal (1985).

Abbreviations: ACB, Almenara-Casablanca; ABS, Alcoi Barranc Sud; AC, Alcoi Cristian; AF, Alcoi Forn; AG, Alhaurín el Grande; AL, Alcoy; ALD, Aldehuela; ALJ, Aljézar; ARQ, Arquillo; AU, Autovía; Be, Bélmez; Bo, Botardo; BS, Barranco de la Salada; Bz, Baza; BUN, Bunker de Valdecebro; CAC, Cacín; CC, Concud Cerro de la Garita; CDA, Casa del Acero; CEL, Celadas; CH, Chorrico; CLC, Calicasas; CR, Crevillente; DHS, Dehesa; FV, Fuente del Viso; Go, Gorafe; JUN, Canteras de Jun; LB, La Bullana; LF, La Fontana; LIB, Librilla; LG, La Gloria; LM, Los Mansuetos; MCC, Moncucco Torinese; MDV, Masada del Valle; Masía del Barbo, MB; MNA, Mina; Mo, Moreda; MS, Molina de Segura; NGR, Negratín; ORR, Orrios; OTU, Otura; PC, Puerto de la Cadena; PER, Peralejos; PUR, Purcal; RCH, Rambla de Chimeneas; ROM, Romerales; SIF, Sifón de Librilla; TCH, Tollo de Chiclana; TO, Tortajada; VAR, Villalba Alta Río; VDC, Valdecebro; VER, Verduno; VIL, Villastar; VVm, Venta del Moro; YEG, Yeguas; ZOR, Zorreras.

IPHES, Institut Català de Paleoecologia Humana i Evolució Social; ICP, Institut Català de Paleontologia Miquel Crusafont.

c1, posterior accessory cusp; FOD, First Occurrence Datum; H, height; L, length; LOD, Last Occurrence Datum; MN, European Neogene land mammal units; MSC, Messinian Salinity Crisis; t1-t12, numbered tubercules from 1 to 12; tma, anterocentral cusp; W, width.

Geological setting

The Fortuna Basin is the result of a late Tortonian to present NE-SW strike-slip tectonics in the Eastern Betics, in the context of the convergence between the Iberian and African plates (De Larouzière et al. 1988; Montenat et al. 1990; Sanz de Galdeano 1990; Sanz de Galdeano and Vera 1992; Garcés et al. 2001; Agustí et al. 2006). Garcés et al. (1998, 2001) recognized three main units in the sedimentary infill of the Fortuna Basin: a Tortonian transgressive marine unit, a latest Tortonian regressive marine to transitional evaporitic unit, and a Messinian to Pliocene thick continental alluvial and lacustrine unit.

The Fortuna Basin underwent a rapid initial subsidence and a marine transgression during the Tortonian. This basin then became progressively isolated from the open Mediterranean Basin due to the uplift of the Internal Zones of the Betic chain that occurred during the late Tortonian. This marine-continental transition took place from 7.8 to 7.6 Ma, and the continental sediments are continuously recorded in the time span between 7.6 and 4.8 Ma (Garcés et al. 1998, 2001). The confinement and the incoming precipitation of evaporites in the Fortuna Basin in the latest Tortonian means that the Fortuna Basin cannot be included in a hypothetical Betic marine corridor during the late Messinian (Muller and Hsu 1987). Messinian marine sediments interfingered with late Turolian continental units can be found in the Fortuna Basin due to a marine connection in the southeastern margin (Mein et al. 1973). The sea level drop that occurred during the MSC at 5.96 Ma is recorded in the Librilla area by a valley incision followed by sudden gravel progradation. The normal marine conditions in the Mediterranean at the earliest Pliocene are represented in the Fortuna Basin by a short pulse of a very restricted transgression reported in the Sifón de Librilla section (Garcés et al. 2001; Agustí et al. 2006).

During the Messinian, the Fortuna Basin was a poorly drained, confined continental basin. Occasionally, the distal areas developed shallow lacustrine and palustrine environments (Agustí et al. 2006). The resulting palustrine-lacustrine sediments embedded over the confined shallow Fortuna Basin have provided rich small-mammal assemblages from the latest Tortonian (middle Turolian) to Messinian (late Turolian) and early Pliocene (early Ruscinian) along a number of continuous continental sections, one of which is the Sifón de Librilla section.

Sifón de Librilla represents an 800-m-thick sequence, which is divided into four members, from bottom to top (see Fig. 2; Garcés et al. 1998, 2001):

(1) a 400-m-thick alluvial-palustrine member, consisting of cyclic alluvial red sediments and palustrine organic-rich grey marls and minor lacustrine limestones. This member includes the localities of SIF-1, SIF-3, SIF-52, SIF-61, and SIF-79.

(2) a 30-m-thick prograding conglomeratic member, representing a marked basin-wide spread of the alluvial wedges fed from the western margin (External Betics).

(3) a 30-m-thick shallow marine member, comprising grey sandstones and marls with bivalves, echinoderms and benthonic foraminifera. They are indicative of early Pliocene age and shallow water depths. This represents the basal Pliocene marine conditions after the MSC transgression in the Mediterranean, being the first record of marine Pliocene sediments in the Fortuna Basin.

(4) a 350-m-thick upper alluvial member, consisting of channelized conglomerates and red silts. Clast composition also indicates a sediment supply from the western margin. The localities of SIF-413, SIF-430 and SIF-P are included in this member.

Systematic palaeontology

Order Rodentia Bowdich, 1821

Family Cricetidae Fischer, 1817

Subfamily Cricetinae Fischer, 1817

Genus *Neocricetodon* Schaub, 1934

Neocricetodon seseae Aguilar, Calvet and Michaux, 1995 (Figure 3(A) – (J))

Material and localities

SIF-1: 1 m1 (fractured; IPS-100780), 3 m2 (2 fractured; IPS-100781–IPS-100783), 3 m3 (1 fractured; IPS-100788–IPS-100790), 4 m12? (fractured; IPS-100784–IPS-100787), 1 M1 (IPS-100772), 3 M2 (1 digested; IPS-100773–IPS-100775), 4 M3 (2 fractured; IPS-100776–IPS-100779).

SIF-3: 3 m3 (1 fractured; IPS-100890–IPS-100892), 2 M1 (1 fractured; IPS-100883, IPS-100884), 1 M2 (IPS-100885), 4 M3 (1 digested, 1 fractured; IPS-100886–IPS-100889).

Measurements*:* Table 1.

Description of the material from SIF-1

m1: The fragmented molar displays a crest-like anteroconid. The anterolophid is simple and labial. No preserved roots.

m2: There is a well-developed labial anterolophid which reaches the base of the protoconid. The mesolophid is long, reaching the lingual wall of the tooth in one case while it is absent in two other teeth. The posterolophid reaches the posterior wall of the entoconid closing the posterosinusid. No preserved roots.

m3: Long labial anterolophid which reaches the base of the protoconid. A small lingual anterolophid is also present in one tooth and absent in the others. The mesolophid is of medium size in one case, very short in another, and it is absent in the third teeth. The sinusids are closed by basal cingulids. The posterolophid reaches the posterior wall of the entoconid closing the posterosinusid. There are two roots.

M1: The anterocone is formed by two lobes which are connected anteriorly. The anterolophule is double. The protolophule is double in one case and posterior in another. Medium sized mesoloph which in one case reaches the anterior wall of the metacone. The posterior metalophule is absent and the posteroloph connects directly to the posterior wall of the metacone. There are four roots.

M2: The labial and lingual anterolophs are well developed, the lingual one being slightly larger. There is a double protolophule. The mesoloph is medium sized. The sinuses are closed by basal cingula. As in the M1, the posterior metalophule is absent and the posteroloph connects directly to the posterior wall of the metacone. There are four roots.

M3: Well-developed labial and lingual anterolophs, the lingual one being longer. There is a double protolophule. The anterior metalophule reaches the anterior wall of the metacone closing a reduced posterosinus. No preserved roots.

Description of the material from SIF-3

m3: The m3 from SIF-3, besides the long labial anterolophid, develops a small lingual one. The mesolophid is medium sized and in one case connects to the posterior wall of the metaconid. As in SIF-1, the posterolophid reaches the posterior wall of the entoconid closing the posterosinusid.

M1: In the M1 from SIF-3, a preloph is observed in one case, which is no fused to the labial lobe of the anterocone. In the other case, it is fused to the anterocone forming a double anterolophule. The posterior protolophule is well developed, while a tiny anterior one can be observed at the base of the anterosinus. The mesoloph is medium sized and reaches the anterior wall of the paracone. As in SIF-1, the posterior metalophule is absent and the posteroloph connects directly to the posterior wall of the metacone.

M2: The M2 from SIF-3 is morphologically similar to that from SIF-1, and also has well developed labial and lingual anterolophs. However, in this case the lingual anteroloph is much longer than the labial one.

M3: The M3 from SIF-3 fits the size of the specimens from SIF-1 but the anterolophs are less developed: the labial one is short while the lingual one can hardly be distinguished at the base of crown.

Discussion

Aguilar et al. (1995) described *Neocricetodon seseae* based on scarce material coming from the Castelnou 1 site, in Southern France. The status of this species was confusing until Freudenthal et al. (1998) revised it. These authors realized that Castelnou 1 (a karstic site) probably contained mixed fauna and tried to determine the diagnostic morphological traits and intraspecific variability of this species. They also recognized this species in a number of Spanish sites, such as CR-11, CR-22, CR-25, ARQ-1, among others. Nevertheless, as these authors pointed out, *Neocricetodon seseae* is still a badly known species. As a significant feature, it differs from the almost coeval *Neocricetodon lavocati* (Hugueney and Mein, 1965) from the late Turolian of Lissieu as it is larger and has more reduced mesolophs and mesolophids. Its dimensions are very similar to those of *Neocriceton meini*, described from the CDA site in Fortuna Basin (Agustí 1986). Nevertheless, as evidenced by the sample from Sifón de Librilla, the retention of mesolophids and mesolophs in *Neocricetodon seseae* rules out an ancestor-descendant relationship with the species from CDA. In any case, a trend towards an increase in size, a reduction of mesolophs and mesolophids and a loss of the posterior metalophule can be recognized in *Neocricetodon seseae*, which could indicate a relationship with *Apocricetus plinii* (Freudenthal, Lacomba and Martín Suárez, 1991). However, more material of this species is needed in order to confirm this relationship.

Genus *Apocricetus* Freudenthal, Mein and Martín Suárez, 1998

Apocricetus alberti Freudenthal, Mein and Martín Suárez, 1991 (Figure 3(K) – (R))

Material and localities

SIF-52: 1 m1 (fractured; IPS-100945), 1 m2 (fractured; IPS-100946), 1 M3 (fractured; IPS-100943).

SIF-61: 2 m1 (1 fractured; IPS-101092, IPS-101093), 8 m2 (2 fractured; IPS-100994–IPS-100996, IPS-101094–IPS-101098), 5 m3 (1 fractured; IPS-101099–IPS-101103), 5 M1 (1 fractured; IPS-100991, IPS-101083–IPS-101086), 2 M2 (1 digested; IPS-100992, IPS-101087), 4 M3 (1 fractured; IPS-100993, IPS-101089–IPS-101091).

SIF-79: 1 M1 (fractured; IPS-101136), 2 M2 (1 digested; IPS-101137, IPS-101138).

Measurements*:* Table 2.

Description of the material from SIF-61

m1: The anteroconid is composed of two lobes in one specimen, and three in another fragmentary one. The anterolophulid is double in one individual, and simple and transverse in the other fragmentary one. A very short prelophid is present in one specimen. The mesolophid is absent. The posterolophid closes the posterosinusid. Two roots.

m2: There is a well-developed labial anterolophid which reaches the base of the protoconid. There is no lingual anterolophid. The mesolophid is also absent. The posterolophid is connected to the base of the entoconid closing the posterosinusid. In one tooth the posterolophid delimitates a tiny labial posterosinusid. Two roots.

m3: There is a well-developed labial anterolophid. A tiny lingual one can be distinguished at the base of the crown in two specimens. The mesolophid is absent. The posterolophid closes the posterosinusid. Two roots.

M1: The anterocone is composed of two lobes which are anteriorly connected. A small cingulum ridge can be observed in one tooth at the base of the anterior wall of the anterocone. Double anterolophule. The protolophule is double in two individuals, and posterior in one. A medium sized mesoloph is present, which in one case connects to the anterior wall of the metacone forming an anterior metalophule. The posterior metalophule is absent. the posterolophe connects directly to the metacone and closes the posterosinus. Four roots.

M2: Well-developed labial and lingual anterolophes. The protolophule is double, being the anterior one more developed than the posterior one. There is an anterior metalophule connected to the metacone, while the posterior metalophule is absent. The posterolophe is connected directly to the metacone and closing the posterosinus. Four roots.

M3: There is a well-developed labial anterolophule. A small lingual one can be distinguished at the base of the crown. Double protolophule. The anterior metalophule closes a reduced posterosinus. Three roots.

Description of the material from SIF-52 and SIF-79

The fragmentary m1 from SIF-52 possesses a wide and bilobated anteroconid. A transverse anterolophulid is connected to the labial lobe of the anteroconid, and there is no prelophid. The M2 from SIF-79 also displays well-developed labial and lingual anterolophes, the labial one displaying a higher than the lingual one. The protoluphule is also double, but in this case it is the posterior one which is better developed than the anterior one. As in most of the teeth from SIF-61, an anterior metalophule is present, connected to the anterior wall of the metacone. The highly worn M3 from SIF-79 presents the same features as those from SIF-61.

Discussion

The samples from SIF-52, SIF-61 and SIF-79, prior to the Messinian Salinity Crisis, agree in size with both the species *Apocricetus plinii* and *Apocricetus alberti*. Consequently, they are significantly smaller than other *Apocricetus* species, such as *Apocricetus barrierei* (Mein and Michaux, 1970). It also differs in a number of traits from this latter species, such as the prelophid being absent or very reduced and the retention of a double protolophule in the M3. This material resembles *A. plinii* or *A.* aff. *plinii* in a number of characters, such as the well-subdivided anteroconid, the retention of a small lingual anterolophid in one m3, and the presence of well-developed mesolophs in the upper molars. However, a number of derived characters preclude assigning the studied sample to *A. plinii*, including the presence in one case of a short prelophid, the total absence of ectomesolophids in the lower molars, the presence of a weak cingulum ridge in one M1 and the absence of a posterior metalophule. Thus, the sample from SIF-61 fits an archaic population of the species *A. alberti*.

In the Fortuna Basin, a small sample from ROM-2C was assigned to the species *Apocricetus* aff. *plinii* (Piñero et al. 2017a). This sample was characterized by a well-subdivided anteroconid, the retention of a small lingual anterolophid in one m3 and the presence of well-developed mesolophs in the upper molars, characters which are also present at SIF-61. However, besides its smaller size, *A.* aff. *plinii* from ROM-2C does not have the advanced characters present at SIF-61 mentioned above, such as the presence of a short prelophid and a weak cingulum ridge at the anterior wall of the anterocone. Therefore, the sample from ROM-2C corresponds to a more archaic population of *Apocricetus*. This result is consistent with the stratigraphically lower position of the Romerales section with respect to SIF-61.

Apocricetus* aff. *barrierei (Mein and Michaux, 1970) (Figure 3(S) – (AC))

Material and localities

SIF-413: 3 m1 (1 fractured; IPS-101276–IPS-101278), 1 m2 (IPS-101279), 3 m3 (IPS-101280, IPS-101271, IPS-101272), 1 M1 (IPS-101274), 2 M2 (IPS-101270, IPS-101275); 1 M3 (fractured; IPS-101273).

SIF-430: 1 m1 (fractured; IPS-101303), 1 m2 (IPS-101300), 1 M1 (fractured; IPS-101298), 1 M2 (fractured; IPS-101301), 1 M3 (IPS-101299).

SIF-P: 4 m1 (2 fractured; IPS-101394–IPS-101397), 8 m2 (2 digested, 2 fractured; IPS-101398–IPS-101405), 9 m3 (1 fractured; IPS-101406–IPS-101414), 5 M1 (1 digested, 2 fractured; IPS-101376–IPS-101380), 5 M2 (1 digested; IPS-101381–IPS-101385), 8 M3 (1 digested, 2 fractured; IPS-101386–IPS-101393).

Measurements: Table 2.

Description of the material from SIF-413

m1: The anteroconid is crest-like in two cases, and subdivided into one lingual cuspid and another central one in two other teeth. A short prelophid is present in two cases, being absent in the others. There is a double anterolophulid in all the cases, with a lingual branch directed towards the lingual lobe of the anteroconid, and a second one directed to the labial end of the anteroconid. The mesolophid is absent in all the cases. The posterolophid closes the posterosinusid. Two roots.

m2: The labial anterolophid is well developed, while there is no evidence of lingual anterolophid. There is no mesolophid. The sinusids are closed by basal cingulids. The posterolophid can be distinguished from the hypoconid, thus delimiting a tiny labial posterosinusid. Two roots.

m3: As in the m2, the labial anterolophid is well developed, with no evidence of a lingual one. Short mesolophid. The sinusids are closed by basal cingulids. The posterolophid closes the posterosinusid. Two roots.

M1: The anterocone is formed by two lobes. There is a double anterolophule and also a double protolophule. The sinuses are closed by basal cingula. There is an anterior metalophule, while the posterior one is absent. The posterolophe is connected directly to the metacone. Four roots.

M3: a fragmented M3 possesses a well-developed labial anterolophe.

Description of the material from SIF-P

m1: The anteroconid is large and subdivided into two cuspids. A small prelophid is present in one case and absent in the others. Double anterolophulid in all the cases, with a lingual branch directed towards the lingual cuspid of the anteroconid and a second one directed to the labial end of the anteroconid. The mesolophid is absent. The posterolophid closes the posterosinusid. Two roots.

m2: Well-developed labial anterolophid. The lingual anterolophid is absent. A small mesolophid is present in one case, while it is absent in the others. The sinusids are closed by basal cingulids. As in SIF-413, the posterolophid can be distinguished from the hypoconid, thus delimiting a tiny labial posterosenid. The posterolophid does not close the posterosinusid. Two roots.

m3: Well-developed labial anterolophid, while the lingual one is absent. A small mesolophid is present in three cases while it is absent in the others. The sinusids are closed by basal cingulids. The posterolophid closes the posterosinusid. Two roots.

M1: The anterocone is subdivided into two cusps which are anteriorly connected. Double anterolophule. A small anterior protolophule can be distinguished at the base of the anterosinus in two cases, while it is absent in the others. The sinuses are closed by basal cingula. The anterior metalophule is present, while the posterior one is absent. The posterolophe is connected directly to the metacone. Four roots.

M2: Well-developed labial anteroloph in all the specimens. In two of them there is also a well-developed lingual anteroloph, delimiting a lingual anterosinus. A small lingual anteroloph is present in another case. The anterior metalophule. There is no entoloph, therefore the posterior protolophule, the anterior metalophule, the posterior arm of the protocone and the anterior arm of the metacone design a X-like shape. Anterior metalophule, while the posterior one is absent. The posterolophe is connected directly to the metacone. Four roots.

M3: The labial anteroloph is well-developed, and the lingual one is absent. A small entoloph is present, therefore the posterior protolophule, the anterior metalophule, the posterior arm of the protocone and the anterior arm of the hypocone design a H-like shape. The anterior metalophule closes a very reduced posterosinus. Three roots.

Discussion

The samples from SIF-413, SIF-430 and SIF-P, after the Pliocene flooding, are larger in size than the samples assigned to *Apocricetus alberti* from previous levels, partially overlaping the size of the species *Apocricetus barrierei.* However, they coincide with the dimensions found at CR-6, the type locality of *A. alberti* (Freudenthal et al. 1998). Despite their larger dimensions, these samples could fit into *A. alberti*, as most of the m1 still lack a prelophid, and thus the two anterolophulids connect directly (in *A. barrierei* 100% of the molars present prelophid; Mansino et al. 2014; Piñero et al. in press). Assignment of the material from SIF-413, SIF-430 and SIF-P to *A. alberti* would contradict the simple, gradualistic phylogenetic scheme commonly assumed for the genus *Apocricetus*. In this way, provided the common absence of anterior protoluphle in the M2 and M3, we prefer to refer the material from the above mentioned levels to *Apocricetus* aff. *barrierei*.

Subfamily Cricetodontinae Stehlin and Schaub, 1951

Genus *Hispanomys* Mein and Freudenthal, 1971

Hispanomys **cf.** ***adroveri*** Agustí, 1986 (Figure 4(A) – (D))

Material and localities

SIF-1: 1 m2 (fractured; IPS-100792), 1 m3 (IPS-100791).

SIF-3: 2 m1 (fractured; IPS-100895, IPS-100896), 1 m2 (IPS-100894), 2 m3 (IPS-100897, IPS-100898), 1 M1 (fractured, IPS-100893).

Measurements: Table 3.

Description of the material

m1: Only two fragments are preserved from SIF-3. The posterolophid is rounded and separated from the hypoconid. It reaches the posterior wall of the entoconid at the base of the crown.

m2: This molar is represented by a fragmented tooth from SIF-1 and a complete one from SIF-3. The specimen from SIF-3 is highly worn and the only distinguishable feature is the absence of anterolophid. The anterolophid is also lacking in the fragmented m2 from SIF-3. The mesolophid is transverse and well developed, reaching the posterior wall of the metaconid. The posterolophid is fused to the hypoconid, not reaching the posterior wall of the anteroconid.

m3: This piece is represented by one tooth from SIF-1 and two teeth at SIF-3, one of them highly worn. In all the cases the anterolophid is absent. Both the specimens from SIF-1 and SIF-3 display a well-developed mesolophid, which in the case of SIF-1 is connected to the posterior wall of the metaconid at the base of the crown. In the less worn specimen from SIF-3, the mesolophid is fused to the posterior wall of the metaconid. In both cases the posterosinusid is open.

M1: There is only one fragmented specimen in SIF-3, lacking the anterocone. It corresponds to a highly worn specimen which presents well developed ectolophs.

Discussion

The dimensions and hypsodonty of the small sample from SIF-1 and SIF-3 are similar to those of the species *Hispanomys adroveri*, previously described from the CDA locality in the Fortuna Basin (Agustí 1986). The presence of *Hispanomys adroveri* in middle Turolian deposits was surprising, as it indicated an independent evolution from the Teruel-Alfambra Basin, in which a species of *Ruscinomys*, i.e. *Ruscinomys schaubi* Villalta and Crusafont, 1956, was the characteristic species of the middle Turolian (MN12). Later, the presence of *H. adroveri* in levels of similar age was also confirmed in the Crevillente Basin (Freudenthal et al. 1991). The presence of a form close to *Hispanomys adroveri* at SIF-1 and SIF-3 indicates that, even so, this species or a closely related form persisted until the late Turolian (MN13) in the Fortuna Basin.

Hispanomys romeroi n. sp. (Figures 4(E) – (L); 5(A) – (F))

Derivatio nominis: This species is named after Dr. Gregorio Romero, paleontologist from the region of Murcia, in recognition of the facilities that he provided for the paleontological research at the Fortuna Basin.

Diagnosis: Large species of *Hispanomys*. The anterocone is subdivided by a deep groove that reaches the base of the crown. A lingual spur can be present in the lingual lobe of the anterocone. The posterior wall of the protocone is projected backwards. In the lower molars, there are well-developed mesolophids which are connected to the posterior wall of the metaconid.

Diferential diagnosis: *Hispanomys romeroi* is larger and more hypsodont than most of the species allocated in this genus: *Hispanomys thaleri* (Hartenberger, 1965), *Hispanomys aragoniensis* (Freudenthal, 1966), *Hispanomys nombreviallae* (Freudenthal, 1966), *Hispanomys peralensis* van de Weerd, 1976 and *Hispanomys daamsi* Agustí, Casanovas-Vilar and Furió, 2005. It differs from *Hispanomys freudenthali* Weerd, 1976 in the larger size, the presence of a deep groove in the anterior wall of the anterocone, a reduced M3, poorly developed or absent anterolophids and long mesolophids that reach the posterior wall of the metaconid. It differs from *Hispanomys adroveri* Agustí, 1986 in the more accentuated it has higher hypsodonty and the reduced M3. Moreover, *Hispanomys romeroi* is smaller and much less hypsodont than most of the species of *Ruscinomys*, such as *Ruscinomys lasallei* Adrover, 1969, *Ruscinomys europaeus* Depéret, 1890, and *Ruscinomys schaubi* Villalta and Crusafont, 1956. Moreover, it differs from the latter species by the presence of a deep groove in the anterior wall of the anterocone, the reduced M3 and the long mesolophids, which reach the posterior wall of the metaconid. It is much larger and has less accentuated hypsodonty than *Ruscinomys gilvosi* Adrover, Mein and Moissenet, 1988.

Type locality: SIF-61

Holotype: An isolated M1 from SIF-61 (IPS-101104), deposited at ICP.

Other localities: SIF-52, SIF-79.

Material and localities

SIF-52: 2 m1 (1 fractured; IPS-100949, IPS-100950), 1 m2 (fractured; IPS-100952), 1 m3 (IPS-100953), 1 M1 (fractured; IPS-100947), 1 M2 (IPS-100948).

SIF-61: 6 m1 (IPS-100984–IPS-100986, IPS-101107–IPS-101109), 4 m2 (1 fractured; IPS-100988–IPS-100990, IPS-101110), 5 M1 (2 fractured; IPS-100980–IPS-100983, IPS-101104), 2 M3 (IPS-101105, IPS-101106).

SIF-79: 1 m2 (IPS-101139).

Measurements: Table 3.

Description of the material from SIF-61

m1: The anteroconid is rounded with no anterolophid. The long mesolophid reaches the posterior wall of the metaconid, being fused to it in one specimen. A small and rounded posterolophid can be distinguished from the hypoconid at earlier stages of wear. As wear advances, the posterolophid connects to the posterior wall of the entoconid closing the posterosinusid.

m2: The anterolophid is absent. There is a well-developed and transverse mesolophid fused to the posterior wall of the metaconid. The posterolophid cannot be distinguished from the hypoconid and never reaches the posterior wall of the entoconid.

M1: A deep groove which reaches the base of the crown divides the anterocone into two rounded lobes. The labial lobe is slightly larger than the lingual lobe in one of the individuals. In the other case, a small spur can be observed in the lingual lobe. The well-developed anterior ectoloph reaches the anterior wall of the paracone, without fusing to it. The posterior ectoloph, well developed as well, is always fused to the anterior wall of the metacone. In the less worn specimens, the posterior wall of the protocone is projected backwards. The posteroloph is fused to the hypocone.

M3: This molar has a very simple design, reduced to two interconnected rombs. The anterior romb includes the protocone and the paracone, although none of these cusps can be distinguished. A deep sinus separates this anterior romb from the posterior one. As in the case of the anterior romb, neither the hypocone nor the metacone can be recognized as separated cusps.

Description of the material from SIF-52

m1: The only m1 from SIF-52 agrees in morphology with those from SIF-61, but a very small labial anterolophid can be observed, while the mesolophid only reaches the posterior wall of the metaconid at the base of the crown and the posterolophid does not close the posterosenid. In the only highly worn and fragmented m2 from SIF-52, the only distinguishable feature is the absence of anterolophid *m3*: This piece is only represented by one highly worn specimen, in which the only recognizable feature is the absence of anterolophid.

M1: The only fragmented M1 from SIF-52 coincides in morphology with SIF-61. A small spur can be distinguished in the lingual lobe of the anterocone.

M2: This tooth is only represented by a highly worn specimen. In this molar, the anterolophs are absent.

Description of the material from SIF-79

M2: This tooth agrees with the morphology observed in SIF-61, the mesolophid being fused to a posterior spur on the posterior wall of the metaconid.

Discussion

Hispanomys romeroi mostly coincides in size and morpohology to two other Cricetodontinae species previously described in Fortuna Basin: *Hispanomys adroveri* from Casa del Acero (Agustí 1986) and *Ruscinomys* aff. *gilvosi* from Romerales (Piñero et al. 2017a). *Hispanomys romeroi* shares several morphological traits with *Hispanomys adroveri*, including the presence of a deep groove at the anterior wall of the anterocone, the posteriorly projected protocone and the long mesolophids, which reach the posterior wall of the metaconid (Fig. 5). These features make it possible to differentiate these two species from the coeval *Ruscinomys schaubi* from the Teruel-Alfambra Basin. At the same time, *H. romeroi* has some derived features with respect to *H. adroveri*, such as higher hypsodonty and a reduced M3, which are much more *Ruscinomys*-like. Therefore, *H. romeroi* fits as a feasible *in situ* descendant of *H. adroveri.* Morphologically *H. romeroi* also resembles in some ways *Ruscinomys* aff. *gilvosi*, described from the almost coeval site of Romerales, in Fortuna Basin, as they both have a deep groove on the anterior wall of the anterocone and show a similar development of long mesolophids (Fig. 5). In particular, the M3 of the two species are very similar, showing the same simplified pattern. In fact, *H. romeroi* could have been a feasible ancestor for *R. gilvosi;* however, Romerales is located in a lower stratigraphic position than SIF-61 and is older than the first entry of the murid *Paraethomys* into the Fortuna Basin, while SIF-1 already has *Paraethomys,* which makes it highly improbable that there is a phylogenetic relationship between the two species. The presence of *R.* aff. *gilvosi* in levels below SIF-61 clearly indicates that the evolution of *Hispanomys* and *Ruscinomys* in the latest Miocene was much more complex than previously thought.

Ruscinomys* cf. *lasallei Adrover, 1969 (Figure 4(M) – (N))

Material and localities

SIF-413: 3 m1 (2 fractured; IPS-101283–IPS-101285), 2 m3 (1 fractured; IPS-101281, IPS-101282).

Measurements: Table 3.

Description of the material

m1: The anteroconid is small and rounded. The anterolophid is absent. The mesolophid is small and transverse and does not reach the metaconid. The posterolophid is largerly fused to the hypoconid and does not reach the posterior wall of the entoconid.

m3: The anterolophid is absent. There is a small and transverse mesolophid which reaches the posterior wall of the metaconid. The posterosenid remains open.

Discussion

The Cricetodontinae present in SIF-413 fits the morphology of *Ruscinomys* rather than that of *Hispanomys*, given its highly hypsodont molars and simplified dental pattern. These molars resemble in size and morphology those of several early populations of *Ruscinomys lasallei*, such as those described from the sites of PUR-3 and AGU-1C (García-Alix et al. 2008a). An alternative assignment to *Ruscinomys schaubi, Ruscinomys gilvosi* or *Ruscinomys bravoi* Adrover and Mein, 1996, is ruled out because of their smaller size, whereas ascribing it to *Ruscinomys europaeus* is discounted due to the larger size of the latter. We therefore assign the two studied molars to *Ruscinomys* cf. *lasallei*. The scarcity of remains led us to use an open nomenclature.

***Ruscinomys* sp.**

Discussion

The presence of a form of *Ruscinomys* close to *Ruscinomys lasallei* in SIF-430 and SIF-P is attested by several fragments that do not allow a specific determination. However, the great hypsodonty of the fragments, the large size and the enamel thickness make it possible to ascribe these specimens to the genus *Ruscinomys*.

Family Muridae Illiger, 1811

Subfamily Murinae Illiger, 1811

Genus *Occitanomys* Michaux, 1969

Occitanomys adroveri (Thaler, 1966) (Figure 6(A) – (I))

Material and localities

SIF-1: 11 m1 (7 fractured, 1 digested; IPS-100736–IPS-100746), 12 m2 (7 fractured; IPS-100747–IPS-100758), 13 m3 (2 fractured, 1 digested; IPS-100759–IPS-100771), 17 M1 (8 fractured; IPS-100695–IPS-100711), 10 M2 (1 fractured; IPS-100712, IPS-100721), 14 M3 (3 fractured; IPS-100722–IPS-100735).

SIF-3: 7 m1 (2 fractured; IPS-100839–IPS-100845), 6 m2 (3 fractured; IPS-100846–IPS-100851), 3 m3 (1 fractured; IPS-100852–IPS-100854), 6 M1 (3 fractured; IPS-100829–IPS-100834), 3 M2 (IPS-100835–IPS-100837), 1 M3 (IPS-100838).

Measurements: Table 4.

Description of the material from SIF-1

m1: There is no tma. The anteroconid is slightly asymmetrical. The longitudinal crest is present in all specimens (except in IPS-100745), being low and sometimes difficult to appreciate. It is connected to the protoconid in 6 cases, while in 3 is joined to the metaconid-protoconid union. The labial cingulum is usually well developed with up to two accessory cuspids. The c1 is medium or big-sized, subtriangular and in contact with the hypoconid. The posterior heel is elongated and displaced posterolingually. Two roots.

m2: The longitudinal crest is present in 4 out of 12 individuals. The labial cingulum is moderate or well developed. There are medium-sized c1 and c2. The posterior heel is oval or oval-compressed and sometimes very weak. The anterolabial cuspid is high and oval. Two roots.

m3: The anterolabial cuspid is always present but in some cases reduced. It is low and most times elongated, developing from the posterolingual side of the protoconid (even from the metaconid in IPS-100763) to the anterolabial part. The c1 is present only in 3 out of 12 specimens. The longitudinal crest is observed in one molar. Two roots.

M1: The t1 is displaced backward. It is isolated in 3 out of 13 observable cases. In the rest the t1 is connected to t2 by a low crest. The union t1-t2 is lower than that of t2-t3. There is t1bis. The connection t1-t5 is basal or absent. The posterior spur of t3 is poorly developed, connecting in some individuals weakly the t3 with the t5. The t4 and t5 are joined by a low crest. The t12 is present in most of specimens as a salient angle of t8. There are three roots.

M2: The t1 is bigger than the t3. In some specimens there is a t1bis, usually oval-compressed and connected to the lingual side of the t5. The t1 is isolated in half of cases, in the other half the small posterior spur of t1 is in contact with the t5. The t3 is round or oval and isolated. The t12 is reduced or absent. Three roots.

M3: The t1 and t5 are united by a medium crest. The t3 is absent. The t8 is round or oval and can be isolated or connected to the t6 and even to the t4. The t4, t5 and t6 are connected. One molar bears a small t9 (IPS-100728). Three roots.

Description of the material from SIF-1

The m1 from SIF-1 differs slightly from that of SIF-3, especially in the longitudinal connection, which is absent in 3 out of 6 cases. When it is present, it can be connected to the protoconid (1 specimen) or to the metaconid (2 remaining). The posterior heel is oval in 2 out of 5 visible cases. The m2 of SIF-1 does not have longitudinal spur. The M1 displays somewhat stronger connections than those from SIF-3. The remaining features of the studied specimens from SIF-1 and SIF-3 are similar.

Discussion

The studied material differs from *O. alcalai* Adrover, Mein and Moissenet, 1988 in the larger size (PER-E; Adrover et al. 1988). There is no overlap in size with the *O. alcalai* populations from the SIF section. In addition, the studied lower teeth display a more asymmetrical anteroconid and more developed longitudinal crests than those of *O. alcalai*, and the upper teeth have relatively less developed t1 and t3 spurs, and a somewhat higher crown in M1. Furthermore, the teeth of *Stephanomys ramblensis* van de Weerd, 1976 are larger and more stephanodont than those of *O. adroveri* from SIF, with higher connections and the presence of t2bis (VLD-3; van de Weerd 1988). The crown-height of the studied material is between *O. alcalai* and S. *ramblensis*. The oldest species of the genus, such as *Occitanomys hispanicus* (Michaux, 1971) and *Occitanomys sondaari* van de Weerd, 1976, are distinguished from *O. adroveri* from SIF by their smaller size, less developed t1bis and lower t6-t9 union (MB-2B, TO-A; van de Weerd 1976). *Occitanomys brailloni* Michaux, 1969 can be differentiated from the studied samples of *O. adroveri* by its larger size, more developed longitudinal connections in both the lower and upper molars, more reduced t12 and more swollen tubercles (Layna; Michaux 1969; Martín Suárez 1988).

The shape and size of the studied specimens agree with those of *O. adroveri* from its type locality, LM (Thaler 1966; van de Weerd 1976). These samples have many similarities, such as a great frequency of well-developed longitudinal spurs in m1 and m2, the elongated posterior heel, the presence of t1bis in most M1, the t1 separated from t2 or joined by a low crest, the t12 as a small salient angle of t8, and the postero-labial spur on the t1 directed toward the t5. In addition, the studied material is similar in size to that of *O. adroveri* from OTU-1, OTU-3 (García-Alix et al. 2008b), CR-7, CR-8, CR-17 (Martín Suárez and Freudenthal 1993), CDA (Agustí et al. 1981), CC-2, CC-3, TO (van de Weerd 1976) and ALJ-B (Adrover 1986).

We have compared the collection of *O. adroveri* from SIF-1 and SIF-3 directly with that of the specimens from Casa del Acero (Agustí et al. 1981) and with *O*. aff. *adroveri* from ROM-2C and ROM-2B (Piñero et al. 2017a) stored at the *Institut Català de Paleontologia Miquel Crusafont* (Sabadell, Barcelona). These localities are also situated in the Fortuna Basin. We have detected a slight increase in size from the Middle Turolian (MN12) of CDA to SIF-3, while the size of the early Late Turolian (MN13) populations of *O.*

aff. *adroveri* are similar to that of *O. adroveri* from SIF. There is a slight decrease in the relative width from CDA to SIF-3. In Romerales, this value increases to become similar to that of CDA in the upper teeth, whereas the relative width of the lower teeth is stable. In terms of morphology, there is a slight increase in the stephanodonty and crown-height in the upper molars, with greater development of the spurs of t1 and t3 from CDA to ROM-2C, and the latter is close to *Stephanomys ramblensis*. The t12 tends to decrease in size from CDA to SIF-3, and the frequency of the longitudinal crest in the lower molars decreases over time. Nevertheless, in Romerales it increases again. Martín Suárez and Freudenthal (1993) also detected a trend towards an increase in size and in the stephanodonty in *O. adroveri* from older to younger levels in the Crevillente Basin.

Some authors consider *Occitanomys adroveri* to be the ancestor of *Stephanomys ramblensis* (Michaux 1971; García-Alix et al. 2008b; Mansino et al. 2017a). However, Freudenthal and Martín Suárez (1999) considered *Stephanomys stadii* Mein and Michaux, 1979, to be the ancestor of *S. ramblensis*. García-Alix et al. (2008b) suggested that this relationship was not clear and *S. stadii* was an alternative descendant of *O. adroveri*. To this hypothesis, we must add that the specimens of *O.* aff. *adroveri* from ROM-2C and 2B have similarities with the oldest *Stephanomys*. These samples seem to correspond to an intermediate form between *O. adroveri* and *S. ramblensis*, but this cannot be so because the cited species coexists with a clearly *S. ramblensis* population (Piñero et al. 2017a). This fact precludes the interpretation of an anagenetic lineage leading from *O.* aff. *adroveri* to *S. ramblensis*, and thus *S. ramblensis* can be better interpreted as an immigrant in the Fortuna Basin. Similarly, van de Weerd (1976) considered that *S. ramblensis* is an immigrant in the Spanish-French faunistic province. In the same way that *S. stadii* could be a descendant of *O. adroveri* who acquired a morphology type "*Stephanomys*" alternatively to *S. ramblensis*, *O. adroveri* from the Fortuna Basin (*O. adroveri* CDA – *O. adroveri* SIF-1, 3 – *O.* aff. *adroveri* ROM-2C, 2B) may have undergone a similar process. According to Adrover (1986), some Mediterranean climatic conditions could induce the development of stephanodonty several times. We support the ancestor – descendant relationship between *O. adroveri* and *S. ramblensis* proposed by García-Alix et al. (2008b). However, most probably this process took place outside the Fortuna Basin.

Occitanomys alcalai Adrover, Mein and Moissenet, 1988 (Figure 6(J) – (S))

Material and localities

SIF-1: 1 M1 (IPS-100685).

SIF-3: 4 m1 (2 fractured, 1 digested; IPS-100863–IPS-100866), 1 m2 (IPS-100867), 1 m3 (IPS-100868), 2 M1 (1 fractured; IPS-100855, IPS-100860), 6 M2 (2 digested; IPS-100856–IPS-100859, IPS-100861, IPS-100862).

SIF-52: 1 m1 (fractured; IPS-100931), 4 m2 (1 fractured; IPS-100932–IPS-100935), 2 m3 (IPS-100936, IPS-100937), 3 M1 (2 fractured; IPS-100924, IPS-100925), 3 M2 (1 fractured; IPS-100927–IPS-100929), 1 M3 (IPS-100929).

SIF-61: 3 m1 (1 fractured; IPS-100965, IPS-101030, IPS-101031), 2 m2 (1 digested; IPS-101032, IPS-101033), 3 m3 (1 digested; IPS-100966, IPS-101034, IPS-101035), 5 M1 (3 fractured; IPS-100964, IPS-101024–IPS-101027), 2 M2 (IPS-101028, IPS-101029).

SIF-79: 2 m1 (fractured; IPS-101132, IPS-101133), 2 m2 (1 fractured; IPS-101134, IPS-101135), 2 M1 (1 fractured; IPS-101127, IPS-101128), 3 M2 (fractured; IPS-101129–IPS-101131).

SIF-413: 1 m1 (IPS-101163), 2 m2 (1 digested; IPS-101164, IPS-101165), 1 m3 (IPS-), 1 M1 (IPS-101162).

Measurements: Table 5.

Description of the material from SIF-61

m1: The tma is absent. The anteroconid is nearly symmetrical and connected to the metaconid-protoconid pair. There is a hint of longitudinal spur. The wide and continuous labial cingulum is separated from the protoconid by a valley, reaching the labial face of the hypoconid. The c1 is large and may be isolated or connected to the hypoconid by a spur. Apart from the c1, up to two accessory cuspids can be present. The posterior heel is small or medium-sized and varies from oval to very elongated. There are two roots.

m2: There is no longitudinal crest. The anterolabial cuspid is large and isolated. The posterior heel is round, small and low. The labial cingulum is moderated. There is a medium-sized and isolated c1. Other small accessory labial cuspid can be present. Two roots.

m3: The protoconid and metaconid are symmetrical. The longitudinal crest is absent. The anterolabial cuspid and c1 may be very weak or absent. There are two roots.

Description of the material from SIF-3

M1: The t1 has a backward position with respect to the t3. The t1bis is well developed. The t2bis is absent. The t1 bears a spur that contacts basally with the t5. The posterior spur of the t3 is reduced. The t1-t2 and t4-t5 unions are lower than those of t2-t3 and t5-t6. The t6 and t9 are connected. There is a medium-sized t12. Three roots.

M2: The t1 is in contact with the anterolingual side of t5 by a low spur. The t1bis is present in 3 out of 6 specimens as a double t1. The t3 is small, round and connected basally to t1. The t9 is well developed. Only one specimen has a reduced t12. Three roots.

Description of the material from SIF-52

M3: The t1 is connected very basally to the t5. The t3 is absent. The t5 is in contact with the t4 and t6. The t8 is isolated. The roots are not preserved.

Description of the remaining material

The morphological pattern of the material from SIF-3 and SIF-61 obeys well to that observed in the saples from the rest of levels from the SIF sequence. However, we will remark some differences resulted by the morphological variability of *O. alcalai*: The M1 may develop a small t2bis (IPS-100685, SIF-1). The posterior spur in t3 can be well developed (IPS-100685, SIF-1; IPS-101025, SIF-61) or absent (IPS-101024, SIF-61; IPS-101162, SIF-413). The t1 can appear separated from the t5 due to the absence of posterior spur (IPS-100926, SIF-52). The t1 may be separated from the t3 but united to the t5 (IPS-101127, SIF-79) or completely isolated (IPS-101162, SIF-413). The t2-t3 may be very low (IPS-101162, SIF-413). In the M2, the posterior spur of the t1 can be better developed than those from SIF-3 (IPS-100927, IPS-100928 (N, Fig. 6), IPS-100929, SIF-52). The longitudinal connection of m1 and m2 is absent in most of specimens, but it can appear as a longitudinal spur (one out of 3 m1 from SIF-3; 3 out of 4 m2 from SIF-52; 1 out of 2 m2 from SIF-79) or as a complete crest reaching the protoconid (IPS-100866, SIF-3). In the m1 the anteroconid is separated from the metaconid-protoconid complex (IPS-101163, SIF-413), and may be subtriangular (IPS-101163, SIF-413; IPS-100866, SIF-3) or very weak (IPS-101133, SIF-79). The labial cingulum of m2 may be weak, the c1 absent (IPS-100867, SIF-3; IPS-100934, SIF-52), and the posterior heel oval (IPS-100867, SIF-3; IPS-100932, IPS-100935, SIF-52; IPS-101134, SIF-79) or very weak (IPS-100935, IPS-100934, SIF-52; IPS-101135, SIF-79; IPS-101164, SIF-413). Due to the scarcity of remains, this heterogeneity can only be observed in the SIF section when the material from the different localities is compared. But when large populations such as VVm are observed, the morphological variability becomes clear. (Mansino et al. 2017a).

Discussion

The studied material differs from *O. hispanicus* in the better development of the t6-t9 connection. The material of *O. alcalai* from SIF is similar is size to *Occitanomys sondaari* but unlike that species, our molars have better developed labial cingula in the lower molars, and t1bis and t6-t9 connection in the upper teeth without any isolated t4 or t9. *Occitanomys adroveri* has larger size, more frequency and better development of longitudinal crests in the lower molars, as well as the t1 in a relatively more anterior position and a somewhat higher crown in the M1. *Occitanomys brailloni* can be distinguished from the studied sample of *O. alcalai* by its larger size and greater development of longitudinal connections.

The studied specimens keep a fairly stable size along the sequence. Generally, their dimensions are somewhat smaller than those of *Occitanomys alcalai* from its type population (PER-E, Adrover et al. 1988). However, they fit well with the lower half of the size range of that species from sites such as VDC-3 (van de Weerd 1976; Adrover et al. 1993), VDC-6 (Adrover et al. 1993) and CR-6 (de Bruijn et al. 1975; Adrover et al. 1988). In addition, the teeth morphology is consistent with some of the diagnostic characters of *O. alcalai* proposed by Adrover et al. (1988), including the relatively high crown, well-developed t1bis, absence of isolated tubercles, well-developed spurs in the upper molars, and symmetrical anteroconid. Although the lack of longitudinal spurs or crests in the lower molars of *O. alcalai* is considered diagnostic by these authors, there are populations (apart from the studied in this work) that show reduced or complete longitudinal spurs in some molars, such as those from LG-5, VDC-6 (Adrover et al. 1993), PUR-4 (García-Alix et al. 2008b), VVm (Mansino et al.

2017a) and ROM-2C (Piñero et al. 2017a). According to the size and morphology we ascribe the studied specimens to *Occitanomys alcalai*.

Occitanomys alcalai is the rodent species with the longest stratigraphic range in the SIF section. It extends continuously from the oldest level (SIF-1) to the oldest Pliocene locality (SIF-413). However, the material is scarce and it does not become a dominant species at any locality. On the other hand, *O. alcalai* is identified in the fossil record throughout the entire Late Turolian (MN13). This species has been also found in some early Ruscinian (MN14) localities, such as PUR-7, CLC-3, CLC-4, CLC-5 and PUR-13 in the Granada Basin (García-Alix et al. 2008b), AF-1'07 in the Alcoy Basin (Mansino et al. 2015a), and PER-E, LG-4, CEL-3, CEL-4, CEL-7, and CEL-9 in the Teruel Basin (Adrover et al. 1988, 1993). The fossil record of *O. alcalai* disappears in somewhat younger levels characterized by the presence of *Trilophomys,* as it is Go-4 (Martín Suárez 1988).

Despite the morphological heterogeneity, some variation has been observed when Miocene specimens are compared with Pliocene specimens (SIF-413): slight increase in crown-height linked to a lower inclination of tubercles, and relatively slender cuspids. Also worth mentioning is the particularly small size of the specimens from SIF-413. Perhaps the possible competition induced by the entrance of *O. brailloni* triggered these slight changes in *O. alcalai*. In fact, SIF-413 is the only locality in which *O. alcalai* coexists with *O. brailloni*. The entry of this taxon together with the arrival of *Castillomys* observed in SIF-P could have led to the premature extinction of *O. alcalai* in Fortuna Basin.

Occitanomys brailloni Michaux, 1969 (Figure 6(T) – (X))

SIF-413: 2 m2 (IPS-101171, IPS-101172), 3 M1 (one fractured; IPS-101167–IPS-101169), 1 M2 (IPS-101170),

SIF-P: 1 m2 (IPS-101309), 4 M1 (2 fractured; IPS-101304–IPS-101307), 1 M2 (IPS-101308).

Measurements: Table 6.

Description of the material from SIF-413

m2: There is a hint longitudinal crest in 1 out 2 specimens. The labial cingulum is well-developed. Up to three weak accessory cuspids can be present. The posterior heel may be very weak or oval and low. The anterolabial cuspid is not preserved in any case.

M1: The t1-t2 union is low. The connection between t1 and t5 may be very basal or somewhat higher throughout a distal spur. The t3 has a posterior spur directed towards the t4-t5 intersection but does not connect the t5. Its length is variable. The t1bis and t2bis are present in only one molar (IPS-101167). The t4-t5 connection is low. The t6 is closer to the t9 than to the t3. The t12 is reduced.

M2: The t1 is much larger than t3 and both are isolated. There is no t1bis. The t9 is smaller than the t4. The t6-t9 union is weak. The t12 is reduced.

Description of the material from SIF-P

The material recovered from SIF-413 and SIF-P has similar morphological traits. Nevertheless, the total absence of t1bis and t2bis in the M1 from SIF-P is remarkable. In the only m2, the longitudinal spur is absent and there are three accessory cuspids. However, the main difference lies in the M2: the tooth of SIF-P (IPS-101308) has the t1 and t5 joined, the t4 and t5 are united much basally, the t9 is bigger, and the t12 is absent.

Discussion

The stephanodonty of the studied teeth is more developed than in *Apodemus* but less advanced than in *Stephanomys* and *Castillomys*. In addition, its medium size, the presence of a t1 placed posteriorly, and the strongly inclined t6 that is much closer to t9 than to t3 are characteristic of *Occitanomys* (Michaux 1969; Martín Suárez and Mein 1991).

The molars found in SIF-413 and SIF-P fall within the size range of *O. brailloni* from Layna (type locality) and resemble it in morphology, showing many similarities in most of the specimens, such as the t1 connected to t5, a distal spur in t3 that does not reach the t5, reduced t12 in M1, small t3 and large t1 often linked to the t5 in the M2, as well as the presence of a longitudinal spur in m2 (Michaux 1969). Further, the measurements are very close to those of *O. brailloni* from Go-A (Ruiz Bustos et al. 1984) and Bz-1 (Piñero et al. in press) in the Guadix-Baza Basin, ARQ-3 (Adrover 1986) in the Teruel Basin, Nîmes

(Michaux 1969) in France, and Kardia (van de Weerd 1979) in Greece. On the contrary, the size is clearly bigger than *O. hispanicus*, *O. sondaari*, *O. alcalai*, *O. debruijni* and *O. vandami* (Michaux 1971; van de Weerd 1976; Adrover et al. 1988; de Giuli 1989; Suata-Alpaslan 2009). Accordingly, we identified these teeth as *Occitanomys brailloni.*

We must mention some “archaic” features shown by the studied populations as opposed to Layna (late Pliocene), including a lesser degree of stephanodonty: lower t1-t5 connection, weaker t1-t3 and t4-t5 unions and occasional t1bis in the upper molars, and a less-developed longitudinal crest in the lower molars. The slightly larger t12 and the more developed accessory cuspids are also remarkable. Certainly, *O. brailloni* from the SIF sequence represents the oldest record so far of the species.

The material was compared directly with the younger population of *O.* cf. *brailloni* from Baza-1. Although they show many similarities, the differences are similar to those mentioned with Layna in accordance with their older evolutionary stage: lower crown-height, less development of t1bis, lower t1-t5 union and slightly smaller t12 in M1 and M2, and less-developed accessory cuspids in m2. The difference in size is not significant.

Michaux (1969) indicated a middle and late Pliocene distribution for *O. brailloni*. Today we know that its temporal range starts earlier, as it has been identified in numerous early Pliocene localities (van de Weerd 1979; Ruiz Bustos et al. 1984; Adrover 1986; Guerra-Merchán and Ruiz Bustos 1991; Guerra-Merchán et al. 1991, 2013; Piñero et al. in press).

***Genus** Castillomys* Michaux, 1969

Castillomys gracilis van de Weerd, 1976 (Figure 6(Y) – (Z))

Material, locality and measurements

SIF-P: 1 M1 (IPS-101310) (L: 1.58 mm; W: 1.09 mm), 1 M2 (IPS-101311) (L: 1.08 mm; W: 0.98 mm).

Description of the material from SIF-P

M1: The t1 is placed in a rather posterior position and connected to the lingual face of the t5. The t1-t2 union is low. The posterior spur of t3 is weak. The t1bis and t2bis are absent. The t3 is far apart from t6. The t3 and t6 are similar in size to the t1 and the t4. There is no t7.

The t8 is higher than the t4. The t12 is almost indistinguishable and appears as a salient angle of t8. The roots are not preserved.

M2: The t1 is comma-shaped and separated from the t5. The t3 is very small and isolated. The t6-t9 connection is very narrow. The t12 is absent. There are no preserved roots.

Discussion

The SIF section has only yielded two molars displaying the typical traits of the genus *Castillomys*: small size, absence of t7 and development of posterior spur in t1 and t3. Both were found in the youngest locality of the sequence, the Pliocene SIF-P. These teeth are distinguishable from the species *Castillomys crusafonti* Michaux, 1969, *Castillomys rivas* Martín Suárez and Mein, 1991, and *Castillomys africanus* Coiffait, 1991, because the studied specimens are smaller and have less-developed t1-t5 and t3-t5 connections than these species. The t1 and t4 of the two studied molars are as developed as the t3, t6 and t9, thus differing from those of *Castillomys margaritae* Antunes and Mein, 1989. However, the poor development of the posterior spur on the t3 of the M1, and the presence of an isolated t3 in the M2 are in accordance with *Castillomys gracilis.* In addition, the size values fit the range of *C. gracilis* from its type locality, Caravaca, and the morphology is similar as well (van de Weerd 1976). We compared the studied material directly with that of *C. gracilis* from Bz-1 and found that both the morphology and size are similar. For these reasons, we ascribed it to *Castillomys gracilis*.

The genus *Castillomys* was created by Michaux (1969) for a group of Pliocene and early Pleistocene Muridae from SW Europe (Martín Suárez and Mein 1991). Adrover et al. (1993) considered it an immigrant group, at least in the Teruel Basin. The oldest site with *C. gracilis* in that region is LG-4 from the early Ruscinian (MN14). Indeed *C. gracilis* is well represented in early Ruscinian levels from the Iberian Peninsula, such as Go-1, Go-4, Bo-C, Bo-D (Martín Suárez 1988) and Bz-1 (Piñero et al. in press) in the Guadix-Baza Basin; CLC-3, CLC-4, PUR-13 (García-Alix et al. 2008b) in the Granada Basin; AL-2C, LB-2B (Mansino et al. 2013, 2015b) in the Alcoy Basin; ORR-1 (van de Weerd 1976), ALD (Adrover 1986) in the Teruel Basin. However, it has also been reported at sites assigned to the late Miocene age, including DHS-16 in the Granada Basin (García-Alix et al. 2008b), Salobreña (Aguilar et al. 1984), and ACB-M (Agustí et al. 2011). The specimens of ACB-M, stored at ICP, have been revised and it was found that they fit better with *O. alcalai* than with *Castillomys gracilis*.

The only specimen found in DHS-16 corresponds to a worn M2 (García Alix et al. 2008b). The measurements are close to the minimum values of *O. alcalai* from Vvm (Mansino et al. 2017a) and the morphology may also fit this species; and therefore we consider that its ascription to *Castillomys gracilis* is doubtful. The morphology of *O. alcalai* shows great variability as our results and those of Mansino et al. (2017a) indicate. The locality of Salobreña has yielded only two specimens ascribed to *Castillomys gracilis* that are neither figurated nor described, and were identified before *O. alcalai* was described, so we therefore recommend a review.

In 1976, van de Weerd defined *Castillomys crusafonti gracilis*. Later, Martín Suárez and Mein (1991) elevated it to species level (*Castillomys gracilis*) and proposed the following anagenetic evolutionary lineage: *Castillomys gracilis* – *Castillomys crusafonti* – *Castillomys rivas*, in which an increase in size and a better development in the longitudinal connections both in lower and upper molars can be observed from oldest to youngest populations. *Castillomys gracilis* and *C. rivas* are located on the opposite points of variability of this line, whereas *C. crusafonti* shows an intermediate size and morphology between them.

Genus *Castromys* Martín Suárez and Freudenthal, 1994

Castromys* cf. *littoralis Martín Suárez and Freudenthal, 1994 (Figure 6(AA) – (AB))

Material, measurements and locality

SIF-61: 1 m3 (IPS-100963) (L: 1.28 mm; W: 1.25 mm), 1 M2 (IPS-100962) (L: 1.63 mm; W: 1.54 mm).

Description

m3: The molar is broad. The well-developed anterolabial cuspid is low and round. The protoconid-metaconid pair has a slightly trilobate occlusal surface. The hypoconid-entoconid complex is transversely widened and labially compressed. There are no preserved roots.

M2: The t1 is large and isolated. There is no t1bis. The t3 is small and isolated. There is no posterior spur in t1 or t3. The t7 is absent. The t4 is connected to t8 by a low and narrow crest. The t5 is very broad. The t4-t5 connection is lower than that of t5-t6. The well-developed t9 is similar in size to the t3, but smaller than the t6. The t9 is separated from the t6 by a narrow and deep valley. The t12 is reduced and emplaced between the t8 and t9. The roots are not preserved.

Discussion

The separation of t6 and t9 by a deep valley in the only M2, the presence of t12, the well-developed t9, the t4-t8 connection, the broad central cusps, the absence of t7 and longitudinal connections, the broad m3 and its well-discernible anterolabial cuspid are typical features of the genus *Castromys*.

Castromys inflatus (Mein, Moissenet and Adrover, 1990) and *Castromys kowalskii* (Agustí and Llenas, 1996) are quite larger than the studied material. *Castromys juniensis* (Padial Ojeda and Ruiz Bustos, 1989) and the teeth from SIF-61 are similar in size, but the presence of t12 in the studied M2 differs from that species. Otherwise, the morphological traits of this M2 are consistent with *Castromys littoralis* from its type locality, CR-17 (Martín Suárez and Freudenthal 1994): large isolated t1 without t1bis, small t3 similar in size to t9, absence of posterior spur in t1 and t3, very low union of t4 and t8 by a narrow crest, very broad t5, t9 smaller than t6, slightly trilobate occlusal surface of m3, and transversely widened hypoconid-entoconid complex. Moreover, the size of the two studied molars is very close to the minimum values of the mentioned species from CR-17. The representatives of *C. littoralis* from CR-22, JUN-2B, JUN-2C, VIZ-1, and OTU-4 (Martín Suárez and Freudenthal 1994; García-Alix et al. 2008b) are clearly bigger. The small population of *Castromys* from SIF-61 seems to be a relict representation of *C. littoralis*; however, the scarcity of material leads us to attribute it to *Castromys* cf. *littoralis*.

The youngest population of *C. littoralis* found so far is that from the middle Turolian locality of OTU-4 in the Granada Basin (García-Alix et al. 2008b), where it is associated with *O. adroveri*. This contrasts with the presence of *C.* cf. *littoralis* in SIF-61, where it appears together with *Paraethomys meini*. Therefore, these two studied specimens become the latest representatives of the genus *Castromys* identified so far, and the biostratigraphical range of the genus is extended until the arrival of *Paraethomys*.

The first and only reference to *Castromys* in Fortuna Basin is that of *C. kowalskii* found in MS-1 and MS-D (Agustí et al. 1983, 2006; Agustí and Llenas 1996), localities prior to the entry of *Paraethomys*. According to Freudenthal and Martín Suárez (1999), the genus

Castromys is related to the large *Apodemus meini*. Martín Suárez and Freudenthal (1998) indicated an ancestor-descendant relationship between *C. littoralis* and *C. inflatus* according to the complete record of superposed levels in Crevillente Basin. Similarly, García-Alix et al. (2008b) observed these species in superposed localities in Granada Basin. *Castromys kowalskii* is a derived form of *C. inflatus* that developed a t6-t9 connection (Agustí and Llenas 1996; Agustí et al. 2006).

The reappearance of a species close to *C. littoralis* together with *Paraethomys* suggests that it is an immigrant population rather than an "in situ" descendant of *C. littoralis* from the middle Turolian Spanish localities.

Genus *Stephanomys* Schaub, 1938

Stephanomys ramblensis van de Weerd, 1976 (Figures 7(A) – (I), 8(B) – (D))

Material and localities

SIF-1: 1 m1 (IPS-100691), 2 m2 (fractured; IPS-100692, IPS-100693), 1 m3 (fractured; IPS-100694), 4 M1 (fractured; IPS-100682–IPS-100684, IPS-100686), 1 M2 (IPS-100687), 3 M3 (IPS-100688–IPS-100690).

SIF-3: 8 m1 (5 fractured, 1 digested; IPS-100815–IPS-100822), 4 m2 (2 fractured; IPS-100823–IPS-100826), 2 m3 (fractured; IPS-100827–IPS-100828), 13 M1 (5 fractured; IPS-100796–IPS-100807), 6 M2 (IPS-100808–IPS-100813), 1 M3 (IPS-100814).

SIF-52: 6 m1 (5 fractured; IPS-100912–IPS-100917), 3 m2 (2 digested; IPS-100918–IPS-100920), 3 m3 (1 fractured; IPS-100921–IPS-100923), 8 M1 (5 fractured, 1 digested; IPS-100899–IPS-100906), 4 M2 (IPS-100907–IPS-100910), 1 M3 (IPS-100911).

SIF-61: 4 m1 (IPS-101014, IPS-101015, IPS-100958, IPS-100959), 6 m2 (2 fractured; IPS-101016–IPS-101019, IPS-100960, IPS-100961), 4 m3 (IPS-101020–IPS-101023), 9 M1 (3 fractured; IPS-100997–IPS-101003, IPS-100954, IPS-100955), 8 M2 (1 fractured; IPS-101004–IPS-101010; IPS-100956), 4 M3 (1 digested; IPS-101011–IPS-101013, IPS-100957).

SIF-79: 1 m2 (IPS-101126), 1 M1 (IPS-101125).

Measurements: Table 7.

Description of the material from SIF-61

m1: One out of three specimens shows a small and low tma. The complete longitudinal crest is connected to the center of the metaconid-protoconid pair. The anteroconid may be symmetrical or slightly asymmetrical. The protoconid and hypoconid are slightly situated posteriorly relative to the metaconid and entoconid respectively. The long and narrow posterior heel reaches the posterolingual side of the entoconid. The labial cingulum is moderate. The subriangular or oval c1 is small, and can be connected to the hypoconid by a small spur. Another accesory labial cuspids is distinguished at the level of the protoconid. There are two roots.

m2: The anterolabial cuspid is large, oval and connected to the protoconid by a small spur. The labial cingulum is reduced. There are a small c1 and up to two accessory labial cuspids. The longitudinal crest is complete and connected to the metaconid-protoconid junction. The posterior heel is laminar or oval. There are two roots.

m3: The anterolabial cuspid is low and reduced in three out of four individuals. One specimen has a reduced c1. The longitudinal connection is strong and complete in three molars. In the other it is weak and displaced labially, towards the protoconid. There are two roots.

M1: The t1 is situated posteriorly relative to the t3. There is a crest connecting t1 and t5 in one out of nine specimens, a reduced spur in other five, while three specimens have no posterior spur or crest on the t1. The t3 contacts the t5 through a crest in four molars; and there is a spur in other one, and the remaining three teeth have no t3-t5 connection in three individuals. The t1bis is developed in all specimens. The t2bis is present in two teeth, being medium-sized in one specimen and weak in the other one. The t1-t2 connection is strong in all individuals but low in one of them. The t12 is absent in one specimen; in the rest of the molars, it is reduced to a more or less developed salient on the posterolabial part of the t8. There are three roots.

M2: The t1 is large and comma-shaped, reaching basally the anterolingual side of the t5. In one out of eight specimens, the t1 is connected to the posterolingual face of the t5 by a crest, and in four by a spur. The t3 is small and round or oval. There is a longitudinal crest connecting t3 and t5 in one molar, and a spur in other two. There is no t3-t5 connection in five specimens. Three out of eight individuals bear an oval t1bis. The t12 is present in four molars as a salient angle of t8, and absent in the others. There are three roots.

M3: The t1 is isolated in one tooth and connected to t5 in others three. The t3 is absent except in one individual in which is very reduced and displaced posteriorly (IPS-101012). There is always a t4-t5-t6 connection. The t9 is fused to t8 forming an isolated complex in three specimens. In one molar it is connected to the t6 by a low crest (E, Fig. 7). There are two roots.

Description of the material from SIF-1, SIF-3, SIF-52 and SIF-79

The populations from SIF-1, SIF-3, SIF-52, and SIF-79 share the main traits of the specimens from SIF-61 characteristic of the genus *Stephanomys*: high crown, development of longitudinal crests in the lower teeth, and presence of posterior crests and spurs on the t1 and t3 in the upper teeth. They differ only in the high and strength of the crests, in the inflation of the tubercles, in the frecuency of posterior spurs and crests of t1 and t3 in the upper teeth (Table 8), in the presence of a longitudinal crest directed to the protoconid in two m1 from SIF-3 (IPS-100816 and IPS-100819), in the weak longitudinal connection in one m2 (IPS-100825) from the mentioned level, and in the variability of the shape of the posterior heel of the m1 (laminar, oval, triangular).

Discussion

The Pliocene and Pleistocene species of *Stephanomys* are larger, have a higher crown and more pronounced stephanodonty than the studied populations (Gmelig-Meyling and Michaux 1973; Ruiz Bustos et al. 1984; Adrover 1986; Bachelet and Castillo Ruiz 1990; López-Martínez et al. 1998; Minwer-Barakat et al. 2005, 2011; García-Alix et al., 2008b; among others). The mean values of the studied molars are always below lower than those of *Stephanomys numidicus* Coiffait, Coiffait and Jaeger, 1985, and *Stephanomys debruijni* de Giuli, 1989, and are similar to those of *Stephanomys stadii* Mein and Michaux, 1979. Nevertheless, the former *S. stadii* has less accentuated stephanodonty in the upper molars, lower longitudinal crests in the lower molars and lesser asymmetry between labial and lingual cuspids in the m1. The size of the studied teeth overlaps with that of *Stephanomys dubari*

Aguilar, Michaux, Bachelet, Calvet and Faillat, 1991, but they differ in the morphology: the studied teeth are lower crowned, and have lower and less frequent longitudinal connections than those of *S. dubari*. The molars of *Occitanomys adroveri* are smaller and have lower and less frequent longitudinal crests than the material *S. ramblensis* from SIF. The m1s from SIF, unlike those of *O. adroveri*, usually have the longitudinal connection joined to the protoconid-metaconid junction. The M1s and M2s of *O. adroveri* have less accentuated stephanodonty, lack a t2bis, and are relatively narrower than those of *S. ramblensis*. In addition, the t12 of *O. adroveri* is smaller, better individualized and more frequent than that of *S. ramblensis*.

The dimensions of the teeth fit the size range and have similar average values as those of *S. ramblensis* from its type locality VDC-3 (van de Weerd 1976). The measurements also agree very well with those of *S. ramblensis* from ROM-2C and ROM-2B (Piñero et al. 2017a), MDV-7 (van de Weerd 1976), VIL, VLD-6 (Adrover et al. 1993) and PUR-23 (García-Alix et al. 2008b). In addition, the moderate size, development of longitudinal connections, and hypsodonty are consistent with this species. Accordingly, the specimens of *Stephanomys* from the Miocene succession of the SIF section are identified as *S. ramblensis*.

Stephanomys dubari Aguilar, Michaux, Bachelet, Calvet and Faillat, 1991 (Figures 7(J) – (N), 8(E)).

Material and localities

SIF-413: 7 m1 (1 fractured, 1 digested; IPS-101149–IPS-101155), 6 m2 (3 fractured; IPS-101156–IPS-101161), 3 m3 (1 fractured; IPS-101161a–IPS-101161c), 4 M1 (2 fractured, 1 digested; IPS-101140–IPS-101143), 2 M2 (IPS-101144, IPS-101145), 3 M3 (IPS-101146–IPS-101148).

SIF-430: 1 M1 (fractured; IPS-101297).

Measurements: Table 7.

Description of the material from SIF-413

m1: There is no tma. The anteroconid is slightly asymmetrical. It is in contact with the protoconid-metaconid junction by a narrow ridge. The longitudinal crest is complete and connected to the intersection of the protoconid and metaconid. The posterior heel may be oval-compressed or laminar. It reaches the posterolingual side of the entoconid. The moderately developed labial cingulum has a small oval or subtriangular c1 in contact to the hypoconid. There are up to two small accessory labial cuspids. There are two roots.

m2: The oval or subtriangular anterolabial cuspid is high and connected to the protoconid by a small crest. The labial cingulum is poorly developed. The c1 is reduced. There are no accessory labial cupids. The complete longitudinal crest is connected to the metaconid. The posterior heel is oval-compressed. It may bear a small crest reaching the posteriolingual face of the entoconid. There are two roots.

m3: The small anterolabial cuspid can be laminar or oval and high or low. It is connected to the anterior side of the protoconid. The c1 is small and low. There is a longitudinal crest connected to the metaconid-protoconid union. There are two roots.

M1: The t1 is situated backward. The t1-t2 union is lower than that of t2-t3. There are always connections between t1 and t5, and t3 and t5. They are crests in three individuals, and spurs in the other. The t1bis is well-developed in all specimens. The t2bis is present but less developed than the t1bis. A medium-height crest connects the t4-t5-t6-t7-t9-t8. The posterior side of the molar is only preserved in one specimen (IPS-101142), in which the t12 is present as a small salient angle of the t8. There are three roots.

M2: The t1 is large and comma-shaped. It connects to the t5 by a crest in one molar, and a spur in the other. The t1bis is crest-like connecting basally to the anterolingual side of the t5. The small and oval t3 is connected to t5 by a posterior crest. The t12 is very small. There are three roots.

M3: The t1 is connected to the t5. There is no t3. There is always a t4-t5-t6 connection. The t9 is present in two out three specimens. It is fused to the t8 forming a complex. The t8 is connected to the t4-t6 junction. There are two roots.

Description of the material from SIF-430

The only specimen yielded by SIF-430 is a fragment of a M1 corresponding to the lingual part of the tooth. The heigh of the crests and the crown-height are similar to those of the material from SIF-413.

Discussion

The studied specimens have the main features of *Stephanomys*: high-crown, medium-heigh longitudinal crests in the lower molars, and moderate stephanodonty in the upper molars.

The studied material is close in size to *S. ramblensis* from some populations, including those of VLD-3 (van de Weerd 1976), LG-5, VIL, and VLD-6 (Adrover et al. 1993). The measurements are also similar to those of *S. stadii* (see Mein and Michaux 1979). However, they can be differentiated by morphological criteria because the specimens from SIF-413 have a more pronounced stephanodonty and hypsodonty. They show a higher frecuency of complete longitudinal crests in the upper molars, and stronger and higher longitudinal connections in the lower teeth. The African *S. numidicus* has a tma in m1, and is slightly larger than the studied population (Coiffait et al. 1985). The size of *S. debruijni* is also bigger and, unlike the material from SIF, it has a small tma and a less developed posterior heel in m1, and a more backward t1 in M1 (de Giuli 1989). In comparison with *S. cordii*, the specimens of *Stephanomys* from SIF-413 and SIF-430 are slightly smaller (Figure 9), display less frequency of complete longitudinal crests in the M1 and M2 (Table 8), and have lower crowns and crests. The other *Stephanomys* species from the Pliocene and Pleistocene are larger, have higher crowns and more pronounced stephanodonty than the material from SIF-413 (Minwer-Barakat et al. 2011).

Nonetheless, these molars are fairly similar on average to those of *S. dubari* from its type locality, Castelnou 3 (Aguilar et al. 1991), and other late Turolian localities, such as Vvm (Mansino et al. 2017a), BRA-5B, CAC-9, DHS-16, and DHS-14 (García-Alix et al. 2008b). The size of *S. dubari* from the early Ruscinian levels of PUR-13 (García-Alix et al. 2008b), PER-E (Adrover et al. 1988), and LG-4 (Adrover et al. 1993) is slightly larger than the studied specimens. In addition, the morphology is consistent with that species. Accordingly, we identify the *Stephanomys* from SIF-413 and SIF-430 as *S. dubari*.

Aguilar et al. (1991) defined *Stephanomys dubari* as an intermediate species between *S. ramblensis* and *S. cordii*. This species has a wide biostratigraphic range. It has been reported in late Miocene sites, like Vvm (Mansino et al. 2017a) in the Cabriel Basin; NGR-1 (Minwer-Barakat et al. 2009a) in the Guadix Basin; MNA-4 and DHS-16 (García-Alix et al. 2008b) in the Granada Basin; and ZOR-3A (Martín Suárez et al. 2000) in the Sorbas Basin. The temporal distribution of *S. dubari* extends up to the early Pliocene, as it has been recorded in the localities PUR-4, PUR-13, CLC-3, CLC-4 (García-Alix et al. 2008b) in the Granada Basin; AF-1´07 (Mansino et al. 2015a) in the Alcoy Basin; LB-3, LB-2B (Mansino et al. 2015b) in the Cabriel Basin; LG-4 (Adrover et al. 1993), and PER-E (Adrover et al. 1988) in the Teruel Basin; and SIF-413 in the Fortuna Basin.

Stephanomys cordii Ruiz Bustos, 1986 (Figures 7(O) – (T), 8(F))

Material and locality

SIF-P: 7 m1 (1 fractured, 1 digested; IPS-101360–IPS-101366), 4 m2 (1 fractured, 1 digested; IPS-101367–IPS-101370), 5 m3 (2 fractured; IPS-101371–IPS-101375), 11 M1 (1 fractured, 2 digested; IPS-101340–IPS-101350), 6 M2 (1 digested; IPS-101351–IPS-101356), 3 M3 (IPS-101357–IPS-101359).

Measurements: Table 7.

Description of the material

m1: There is no tma. The slightly asymmetrical anteroconid is connected to the protoconid-metaconid union. The protoconid and hypoconid are displaced posteriorly relative to the metaconid and entoconid respectively. The complete and high longitudinal crest is somewhat displaced towards the metaconid. The labial cingulum is moderately or poorly developed. The c1 is small, low, subtriangular and connected to the hypoconid by a small crest. There are no others accessory labial cuspids. The posterior heel is subtriangular and isolated. There are two roots.

m2: The anterolabial cuspid is oval and connected to the protoconid and a small labial cingulum. There is no c1 in any specimen. The complete longitudinal crest is connected to the metaconid. The posterior heel is low, small and can be oval or elongated. There are two roots.

m3: There is a crest-shaped anterolabial cuspid connected basally to the protoconid. The c1 is very small and low. There is a complete longitudinal crest slightly displaced towads the protoconid. There are two roots.

M1: The t1 is displaced backward. The position of t1 and t3 is rather symmetrical respect the t2. The t1bis and t2bis are always present. All the specimens have a well-developed t1-t5 and t3-t5 longitudinal crests. There is a high crest connecting the t4-t5-t6-t9-t8. The t4-t8 connection is low. The t12 appears as a salient angle of the t8 in seven out of eight specimens. There are three roots.

M2: The comma-shaped t1 is large. The t1bis is crest-like and contacts basally to the anterolingual face of t5. There are posterior crests on the t1 and the t3 connected to the t4-t5 and t5-t6 union crests, respectively. A small t12 is present only in one out of five specimens. There are three roots.

M3: The t1 is joined to t5. The t3 is absent. There is a t4-t5-t6 connection. The t8 is connected to the union of t4 and t6 by a low crest. The roots are not preserved.

Discussion

The crown height, the high longitudinal crest in the lower molars, and the posterior crests of t1 and t3 in the upper teeth are characteristic of the genus *Stephanomys*.

The *Stephanomys* specimens from SIF-P have the largest size, the highest longitudinal crests both in upper and lower teeth, and the highest crown of all the studied levels from the SIF sequence. These features allow us to distinguish the material from SIF-P from the species *S. ramblensis*, *S. stadii*, *S. numidicus* and *S. debruijni* (van de Weerd 1976; Mein and Michaux 1979; Coiffait et al. 1985; Giuli 1989). In contrast, the studied specimens are smaller than other Pliocene species like *Stephanomys vandeweerdi* Adrover, 1986, *Stephanomys donnezani* (Depéret, 1890), *Stephanomys calveti* Bachelet and Castillo Ruiz, 1990, *Stephanomys thaleri* López-Martínez, Michaux and Hutterer, 1998, and *Stephanomys balcellsi* Gmelig Meyling and Michaux, 1973. The studied M1 and M2 have higher and more frequent longitudinal connections than those of *S. dubari*. Furthermore, *S. dubari* has lower average size values. Some of the specimens from SIF-P fall within the size range of *Stephanomys minor* Gmelig Meyling and Michaux, 1973 from Mo-1A and Mo-1B (Castillo Ruiz 1990), but they differ from the quoted species in the tubercular shape of the posterior heel. The measurements of the studied molars also match those of some specimens of *Stephanomys margaritae* from ARQ-3 (Adrover 1986). However, one of the diagnostic traits of the latter species is the size of the M2 (Adrover 1986), and the M2 from SIF-P are smaller than those of *S. margaritae* from several localities such as ALD (Adrover 1986), VAR (Adrover et al. 1988) and Go-5 (Martín Suárez 1988).

The size of the teeth from SIF-P lies within the range of variation of *S. cordii* from its type locality, Alcoy (Cordy 1976), and AL-2D (Mansino et al. 2013). In addition, the studied specimens have the main traits that Cordy (1976) used to identify *Stephanomys medius*: symmetric disposition of t1 and t3 with respect to t2 in M1, reduced labial cingulum in the lower molars, tubercular posterior heel in the m1 and the m2, and a longitudinal crest displaced to the protoconid in the m3. López Martínez et al. (1998) considered *S. medius* as a “nomen nudum”, and determined that the correct denomination was *Stephanomys donnezani cordii*. Later, García-Alix et al. (2008b) elevated this taxon to species level, and called it *Stephanomys cordii*. According to both the morphological and biometrical criteria, we ascribe the specimens from SIF-P to this species.

We have compared the population of *S. cordii* from SIF-P directly with that from Bz-1 (Piñero et al. in press), currently stored at the IPHES and the ICP, observing that they are very similar in size and morphology. The main difference lies in the somewhat lower crown of the specimens from SIF-P. In addition, the M3 under study are slightly larger, and the m3 have less developed c1 and anterolabial cuspid, and slightly less labially displaced longitudinal connection. This is consistent with the relatively older age of SIF-P.

Minwer-Barakat (2005) proposed the evolutionary line *S. ramblensis* – *S. dubari* – *S. cordii* – *S. margaritae* – *S. vandeweerdi*. These ancestor-descendant relationships explain the overlap in size between the studied population and some samples of both *S. dubari* and *S. margarita*e. This lineage undergoes a continuous increase in size, crown height and stephanodonty over time. *Stephanomys cordii* has been recorded in early Ruscinian localities such as Alhaurín el Grande-1 (Guerra-Merchán et al. 2013) in the Málaga Basin; Aljibe 3 (Guerra-Merchán et al. 1991), YEG (Minwer-Barakat 2005), Go-A (Ruiz Bustos et al. 1984), Bz-1 (Piñero et al. in press) in the Guadix-Baza Basin; AL-2C, AL-2D (Mansino et al. 2013) in the Alcoy Basin; and CEL-9 (Adrover et al. 1993) in the Teruel Basin.

Remarks about the genus Stephanomys from the Sifón de Librilla section

In the sequence of SIF, the molars of *S. ramblensis* from the youngest levels (SIF-52, SIF-61 and SIF-79) have stronger and more pronounced longitudinal crests both in lower and upper molars, more swollen and bulkier tubercles, and broader t1bis and t12 in M1 than those of *S. ramblensis* from the oldest localities (SIF-1 and SIF-3). Some specimens from SIF1 and SIF3 display features resembling *O. adroveri* such as the size of the cusps, shape of the molars (see A, B, Fig. 8), displacement of the longitudinal crest towards the protoconid (two out of seven m1 from SIF-3), and the weak longitudinal connection in the m2 (one out of four specimens from SIF-3). In contrast, one out of two molar from the youngest level with *S. ramblensis* (SIF-79), has a morphology similar to that of *S. dubari*, since that m2 has a very strong and thick longitudinal crest connected to the metaconid. However, its crown-height resembles that of *S. ramblensis*. The other tooth, an M1, fits the size and morphology of *S. ramblensis*.

The frequency of the different development stages of the longitudinal connections in t1 and t3 of the studied M1 and M2 is heterogeneous over time, but always within the expected morphological variability of the species *S. ramblensis*. In the M1, the development of longitudinal connections is similar in the t1 and the t3; on the contrary, in the M2 the longitudinal connection of the t3 is more frequent than that of the t1. There is no increase in the number of spurs or crests along the samples assigned to *S. ramblensis*, all of them corresponding to Miocene levels (except when the M2 from SIF-1 is compared with the rest). On the contrary, such an increase is clearly evident when the populations are compared with those attributed to *S. dubari* and *S. cordii* (Table 8).

A preliminary analysis of the size data did not reveal any remarkable changes from the oldest (SIF-1) to the youngest (SIF-79) populations of *S. ramblensis*. In fact, specimens from intermediate levels, like SIF-52, show the highest values for some tooth positions (M1, m2, m3 and width in m1 and M2). However, if a trend line is established in the length and width values, a slight trend towards an increase size over time is detected (except in the m3 and the length of the M1). In any case, this increase cannot be used as a biochronological criterion to compare localities, since there are older levels that have larger populations than younger levels. There is no clear trend in the relative width of the molars. Anyhow, it can not be overlooked that these small inconsistences in the overall trend to an increase in size can be due to the small sample size.

Summarizing, the sequence of the SIF section has a very complete and continuous record of *Stephanomys*. All the samples from the Miocene levels have been ascribed to *S. ramblensis*, from the oldest populations in SIF-1 and SIF-3 (where it still coexists with its probable ancestor *O. adroveri*), to the last representatives of that species in SIF-79, before it evolved into *S. dubari*. An increase in size, crown and crest height, and stephanodonty has been observed from *S. ramblensis* via *S. dubari* towards *S. cordii* (Fig. 9; Table 8). Minwer-Barakat (2005) noted that this increase continues throughout the Pliocene. In addition, the presence of specimens displaying some archaic traits closer to *O. adroveri* in SIF-1 and SIF-3 supports the line *O. adroveri – S. ramblensis – S. dubari – S. cordii*, previously proposed by García-Alix et al. (2008b) (Fig. 8).

Genus *Apodemus* Kaup, 1826

Apodemus gudrunae van de Weerd, 1976 (Figure 10(F) – (L))

Material and localities

SIF-1: 4 m1 (1 fractured; IPS-94708–IPS-94711), 9 m2 (2 fractured; IPS-100665–IPS-100673), 8 m2 (2 fractured; IPS-100674–IPS-100681), 3 M1 (fractured; IPS-94703–IPS-94705), 1 M2 (IPS-94706), 1 M3 (IPS-94707).

SIF-3: 2 m1 (IPS-100878, IPS-100879), 2 m2 (IPS-100874, IPS-100880), 1 m3 (IPS-100881), 3 M1 (1 fractured; IPS-100875–IPS-100877).

SIF-61: 1 m1 (IPS-100972), 1 M2 (IPS-101082).

SIF-413: 4 m1 (3 fractured; IPS-101261–IPS-101264), 5 m2 (IPS-101265–IPS-101269), 3 M1 (1 worn, 1 fractured; IPS-101256–IPS-101258), 2 M2 (IPS-101259, IPS-101260).

Measurements: Table 9.

Description of the material from SIF-1

m1: The well-developed tma is round and isolated. The anteroconid complex is symmetrical. It is connected to the protoconid-metaconid junction. The labial cingulum is well developed. The c1 is large and round. There are up to three accessory labial cuspids. The medium-sized posterior heel is oval and lingually displaced. There is no longitudinal connection. There are two roots.

m2: The anterolabial cuspid is round and may be large or small. The c1 is round and smaller than the posterior heel, which is medium sized and oval. There is another small accessory labial cuspid attached to the protoconid. There is a cingulum ridge between the anterolabial cuspid and the c1. There are two roots.

m3: The anterolabial cuspid is present as a very small protuberance in three out of eight specimens. There is a small and low c1 in six of them. There are two roots.

M2: The round t1 is much bigger than the oval t3. The t7 is elongated and connected to the t8. It is separated from the t4 by a narrow and shallow valley. The t6-t9 connection is weak. The large t12 is connected to t8 but separated from t9. The roots are not preserved.

M3: The large and oval t1 is connected to t5. There is no t3. The t4-t5-t6 are connected. The t8 and t9 are fused. This complex has a spur directed to t6. The roots are not preserved.

Description of the material from SIF-3

M1: The t1 is connected to t2 but isolated from the t5. The t1-t2 union is very weak in one specimen (IPS-100875). The t3 has a short posterior spur directed to the t5-t6 intersection. The elongated t7 is connected to the t8. It is separated from the t4 by a shallow and narrow valley in one out of three specimens (IPS-100875), and connected to the t4 in the rest. The well-developed t12 is connected to the t8 and separated from the t9. The t8 is connected to the t9 by a crest. There are three roots.

The remaining material of *A. gudrunae* from SIF-3 shares the main traits of that from SIF-1. The only difference fall in the two m1 (IPS-100878, IPS-100879), which have the anteroconid separated from the protoconid-metaconid pair, being the two anteroconid lobes also separated.

Description of the material from SIF-61

The population from this level is very similar to that of *A. gudrunae* from SIF-1 and SIF-3. It is only remarkable the similarities between the m1 from SIF-61 (IPS-100972) and those from SIF-3. In both levels, the m1 shows the two lobes of the anteroconid separated, and the anteroconid complex separated from the protoconid-metaconid pair.

Discussion

The well-developed t7, the large tma, and the well-developed labial cingulum of the studied molars allow their ascription to the genus *Apodemus*. In general, *Apodemus barbarae* (van de Weerd, 1976) and the studied molars are close in size. Nonetheless, the presence of a well-developed t7 and the complete union between t6 and t9 in all the studied specimens rule out the ascription to this species. *Apodemus gorafensis* Ruiz Bustos, Sesé, Dabrio, Peña and Padial, 1984, *Apodemus meini* Martín Suárez and Freudenthal, 1993 and *Apodemus jeanteti* Michaux, 1969 are larger than the specimens of *A. gudrunae* from the SIF section. In addition, the presence of a large tma in the m1 differs from *A. jeanteti*, whereas the well-developed t7 in the upper teeth differ from *A. meini*. *Apodemus lugdunensis* (Schaub, 1938) is notably smaller than our populations. The studied m2 have thicker enamel, a greater posterior heel (with oval or round shape), and better-developed accessory labial cuspids than those of *O. adroveri*. The m3 has a more frequent and larger c1 than that of *O. adroveri*. *Apodemus atavus* Heller, 1936 can be distinguished from the studied samples mainly by its smaller size.

All studied populations fall within the size variability of *A. gudrunae* from its type locality, VDC-3 (van de Weerd 1976). The size is also fairly similar to that of *A. gudrunae* from ROM-2C and ROM-2B (Piñero et al. 2017a), NGR-1 (Minwer-Barakat et al. 2009a), LF (van de Weerd 1976), LG-5, and VDC-6 (Adrover et al. 1993). In addition, the specimens of SIF-1, SIF-3, SIF-61 share many features with those of VDC-3, including the t1 connected to t2 but separated from t5 in M1, elongated t7 in M1 and M2, presence of a narrow and shallow valley between t7 and t4 in some individuals, weak t6-t9 connection in some specimens (two out of three M2: those from SIF-1 and SIF-61), symmetrical anteroconid complex, and large tma and c1 in m1. For these reasons, we identify *A. gudrunae* in the Miocene levels from the SIF section.

Apodemus* cf. *gudrunae van de Weerd, 1976 (Figure 10(M) – (O))

Material and localities

SIF-413: 4 m1 (3 fractured; IPS-101261–IPS-101264), 5 m2 (IPS-101265–IPS-101269), 3 M1 (1 worn, 1 fractured; IPS-101256–IPS-101258), 2 M2 (IPS-101259, IPS-101260).

Measurements: Table 9.

Description of the material

The studied population shares most of traits showed by *A. gudrunae* from SIF-1, SIF-3 and SIF-61. The main differences fall in the presence of an individualized t7 in one M2 (IPS-101259), whereas it is connected to t8 and t4 in the other (IPS-101260); strong t6-t9 union in both M2; tma connected to the labial lobe of the anteroconid in one out two specimens in which it is preserved; and poorer development of the labial cingulum in both m1 and m2.

Discussion

The specimens from SIF-413 agree in size with the maximum values of *A. atavus* from ARQ-3 (Adrover 1986), Mo-1A, Mo-1B (Castillo Ruiz 1990), TCH-1B (Minwer-Barakat et al. 2005), PUR-13, CLC-3 (García-Alix et al. 2008b) and Alozaina (Aguilar et al. 1993). The single m1 from SIF-413 is much shorter than the medium value of *A. gudrunae* from its type locality (VDC-3, van de Weerd, 1976), and, on the contrary, its length is just identical to the mean value of *A. atavus* from TCH-1B (Minwer-Barakat et al., 2005). The scarce upper molars from SIF-413 fit the size range of *A. gudrunae* from VDC-3, but are smaller than the mean values of that locality. In general, the size of the *Apodemus* from this level is intermediate between that of *A. gudrunae* and *A. atavus*. In addition, this population shows some derived features resembling *A. atavus,* such as a barely isolated t7 in one out of two M2, and the connection of the metaconid to the lingual lobe of the anteroconid by a low crest. However, all the individuals differ from *A. atavus* in the proximity or connection between t4 and t7 in M1 and M2, the complete union of t6 and t9 in the upper teeth, and the medium-sized posterior heel of m2. Both the size and morphology seem to be closer to *A. gudrunae* than to *A. atavus*, but taking into account the scarcity of material and the lack of solid morphological criteria, we prefer to be cautious and use open nomenclature.

Apodemus gorafensis Ruiz Bustos, Sesé, Dabrio, Peña and Padial, 1984 (Figure 10(P) – (Y))

Material and localities

SIF-3: 1 m1 (IPS-100873), 1 M1 (IPS-100869), 1 M2 (IPS-100870), 2 M3 (IPS-100871, IPS-100872).

SIF-52: 1 m1 (fractured; IPS-100939), 1 m2 (IPS-100940), 2 m3 (IPS-100941, IPS-100942), 1 M1 (worn and fractured; IPS-100938).

SIF-61: 3 m1 (2 fractured; IPS-101043–IPS-101045), 3 m2 (IPS-101046–IPS-101048), 4 m3 (2 fractured; IPS-101049–IPS-101052), 2 M1 (IPS-101036, IPS-101037), 3 M2 (IPS-101038–IPS-101040), 2 M3 (1 worn and fractured; IPS-101041–IPS-101042).

Measurements: Table 10.

Description of the material from SIF-61

m1: There is a round and isolated tma. The anteroconid is symmetrical. It is separated from the protoconid-metaconid complex. The protoconid and hypoconid are slightly displaced posteriorlly respect to the metaconid and entoconid. In two specimens (IPS-101044, IPS-101045), the hypoconid is in contact with the entoconid but the enamel is not fused. The labial cingulum is well developed. The c1 is round and large. It is bigger than the oval posterior heel and may be connected to the hypoconid. There are up to four accessory labial cuspids. There are two roots.

m2: The anterolabial cuspid is oval and large. It is connected to the well-developed labial cingulum, and basally to the anterior face of the protoconid. The posterior heel may be oval or oval-compressed. It is in central position or slightly displaced lingually. The c1 may be small or medium-sized. There are up to two accessory labial cuspids. The cingulum can be attached to the labial side of the protoconid. There are two roots.

m3: There is no c1. The anterolabial cuspid may be crest-like, very low and reduced, or absent. The protoconid and metaconid may be fused or contacting. There is no longitudinal connection. There are two roots.

M1: the t1 is slightly displaced backward respect to t2 and t3. It is separated from the t5. The t1-t2 connection is lower than that of t2-t3. There is a hint of t2bis. The t3 develops a small posterior spur directed to the t5-t6 intersection. The t6 is the most inclined tubercle. The well-developed and elongated t7 is in contact with the t4. The separation between the t1 and t4 is wide and deep. The t6 and t9 are connected. The t12 is well developed, connected to t8 but separated from t9. There is a small extra cusp lingually placed between t1 and t4 in one specimen (IPS-101036). There are two small and round extra cusps in the other individual (IPS-101037). One of them is located between the t2 and t3, whereas the other in the anterior face of the t2. There roots are not preserved.

M2: There is a t1bis in a hardly worn specimen (IPS-101039), attached to the t1 and similar in size to the t3. In the other specimens (IPS-101038; IPS-101039), the t1 is clearly larger than the t3 and develops an anterior spur directed to the posterior face of the t2. The small t3 is round and isolated. The medium-sized t7 is elongated and basally connected to the t8. It is separated from the t4 by a shallow or medium-deep valley. The t12 is low and connected to the t8. It extends basally up to the posterior side of the t9. The t6 and t9 are very close together in one specimen (IPS-5). In the other two there is a weak connection between these cusps. The roots are not preserved.

M3: The large and oval t1 is basally connected to the t5 by a spur. The t3 is shown as a small bulge of the enamel. The t4, t5, t6, and t8 are connected. The roots are not preserved.

Description of the material from SIF-3 and SIF-52

The studied material from SIF-3 and SIF-52 shares most of the morphological features described for the SIF-61 population, but there are some differences: the only M1 from SIF-3 (IPS-100869) has a little separation between t6 and t9, and it has a small extra cusp in the deep valley between t1 and t4. One out of two M3 (IPS-100871) from SIF-3 has a well-developed, small and round t3. The other M3 is a worn specimen (IPS-100872) in which the t4, t5, t6, and t8 are connected forming a central depression. The only m1 from SIF-3 (IPS-100873) has a very large and isolated tma, and the hypoconid and metaconid separated. The two lobes of the anteroconid are in contact but the enamel is not fused. In the fragmentary m1 from SIF-52 (IPS-100939), the two lobes of the anteroconid are separated, and they are also separated from the protoconid-metaconid pair. There are no accessory labial cusps in the m2 from SIF-52 (IPS-100940) and the c1 is much reduced.

Discussion

The presence of a t1bis in M2 is not common in *Apodemus*. However, the studied teeth share the rest of the main morphological characteristics of the mentioned genus: presence of a well-developed t7 and t12, t6-t9 union, t1 in an anterior position, longitudinal crest usually absents in the lower molars, and presence of tma (Martín Suárez and Mein 1998).

The large *Apodemus* from SIF-3, SIF-52 and SIF-61 is larger than the Miocene *A. lugdunensis*, *A. barbarae* and *A. meini* (Schaub 1936; van de Weerd 1976; Martín Suárez and Freudenthal 1993). The medium-small *A. atavus, Apodemus mystacinus* (Danford and Alston, 1877)*, Apodemus sylvaticus* (Linnaeus, 1758) and *Apodemus flavicollis* (Melchior, 1834) have a smaller size than the studied specimens. Our individuals are larger than *A. gudrunae*, and differ from it in some morphological traits: greater development of t7, presence of extra cusps in some M1, smaller t12 in the M2 and presence of t1bis in some of these molars, better development of the t3 in the M3, relatively smaller tma in the m1, fewer connections between the cusps in the m1 and the m2, and absence of c1 in the m3. Our specimens are similar in size to *A. jeanteti*; however, they differ from this species in the presence of a thick tma in the m1, the development of a posterior spur in the t3 of the M1, the more backward position of the t1 with respect to the t3 in the M1, and the weaker t6-t9 connection in the upper teeth. The dimensions of *A. gorafensis* from SIF resemble those of *Apodemus agustii* Martín Suárez, 1988 from its type locality, Cañada del Castaño-1, but the relative width of M1 and m1 of the mentioned species is greater. In addition, *A. agustii* has a less pronounced stephanodonty in the upper molars, and a funnel delimited by the anteroconid, protoconid and metaconid in m1. The measurements of the material from SIF are a little larger than those of *A.* aff. *gorafensis* from PUR-23 (García-Alix et al. 2008b) and CEL-9 (Adrover et al. 1993).

The populations from SIF-3, SIF-52 and SIF-61 fit the size and the morphology of *Apodemus gorafensis* from the type locality, Gorafe A (Ruiz Bustos et al. 1984), displaying an elongated t7, greater inclination of t6 in relation to the other tubercles in the M1 and M2, posterior spur in the t3 of the M1, weak t6-t9 connection in the M2, large tma and c1 in m1, and a well-developed labial cingulum. The measurements are also close to those of *A. gorafensis* from Vvm (Mansino et al. 2017a), and other localities of the Guadix-Baza Basin (Martín Suárez 1988; Piñero et al. in press), Granada Basin (García-Alix et al. 2008b), and Alcoy Basin (Mansino et al. 2013, 2015a). The studied populations maintain some archaic features, such as the t4-t7 connection in the M1, the separation between t6 and t9 in some individuals, presence of t1bis in some M2, the separation of the anteroconid lobes and the metaconid-protoconid pair in some m1, and the presence of up to four accessory labial cuspids in m1 (instead of three like in the type population of *A. gorafensis*).

Remarks about the genus Apodemus from the Sifón de Librilla section

Two species of *Apodemus* are distinguished in the SIF section: *A. gudrunae* (small-sized form), and *A. gorafensis* (large-sized form). The small *Apodemus* appears for the first time in the studied section in SIF-1, and the large *Apodemus* in the somewhat younger locality of SIF-3. The two species co-occur in SIF-3 and SIF-61.

Following Martín Suárez and Mein (1998), *A. barbarae* from the middle Turolian (MN12) is the most probable ancestor of *A. gudrunae*. When the *A. barbarae* population from

CDA is compared directly with the *A. gudrunae* samples from SIF-1 and SIF-3, the transitional traits that derived into *A. gudrunae* become evident (Fig. 10): slight increase in size; increase in the relative frequency of M1 with a t7, and to a lesser degree of M2 (all the specimens from the SIF succession have a t7, whereas it appears only in 60% of the M1 and 50% of M2 from CDA); greater percentage of t6-t9 union in M1 and M2; transition from the dominance of an oval-comprised posterior heel to a rounder one in the m1; greater connection between the anteroconid and the metaconid-protoconid complex; better development of accessory labial cuspids in the m1 and m2; and increase in the apparition of the c1 in the m3.

Along the SIF section, the populations of *A. gudrunae* and its related form *A.* cf. *gudrunae* undergo a relative decrease in size, a greater development of t7 in M1 and M2 and a trend towards its individualization, a little reduction of the t12, a decrease in the number of accessory labial cusps, a reduction in the labial cingulum in m1 and m2, a reduction of the tma, and a better anteroconid-metaconid union. These morphological and size derivations expressed by *A. gudrunae* over time seem to indicate a progressive evolution towards *Apodemus atavus* by means of a developmental delay during the Pliocene, as Martín Suárez (1988) suggested. However, the citation of *A. atavus* in the late Miocene of the Granada Basin (García-Alix et al. 2008b) refutes this hypothesis.

The data provided by the SIF section indicate that *Apodemus gorafensis* emerged in the late Miocene when *O. adroveri* was still present. Martín Suárez and Mein (1998) proposed that *A. gudrunae* was the most probable ancestor of *A. gorafensis*. They suggest that the size increase and the reduction in the longitudinal connections between the cusps in *A. gudrunae* over time gave rise to *A. gorafensis*. Another possibility is that this species was an immigrant or the result of a rapid cladogenetic process in agreement with its coexistence with *A. gudrunae* in SIF-3 and SIF-61. Previously, Mansino et al. (2017a) stated that the supposed ancestor and descendant coexisted for some time.

García-Alix et al. (2008b) considered *Apodemus* aff. *gorafensis* from PUR-23 to be an intermediate form between *A. gudrunae* and *A. gorafensis*. In accordance with the older age of SIF-3 (with the occurrence of *O. adroveri* and *Hispanomys* cf. *adroveri*), the specimens from PUR-23 should be a rather small population of *Apodemus gorafensis* with some archaic characteristics. Thus, *A. gorafensis* from SIF-3 becomes the oldest population of that species cited so far. The age of SIF-3 and SIF-61 explains the presence of archaic traits in some specimens. From the individuals of SIF-3 to those of SIF-61 we can observe a better t6-t9 connection in the M1 and M2, a smaller t3 in M3, an increase in the hypoconid-entoconid connection, a better union between the lobes of the anteroconid in the m1, and a slightly smaller tma.

Martín Suárez (1988) and García-Alix et al. (2008b) reported a trend towards increasing size in the *A. gorafensis* populations from the Guadix-Baza and Granada Basins over time. However, this tendency is not observed in the SIF section. In fact, the oldest specimens of *A. gorafensis* represented by the late Miocene population of SIF-3 are even larger than those of the early Pliocene localities of PUR-4 (García-Alix et al. 2008b) and AL-2C (Mansino et al. 2013).

The biostratigraphical range of *A. gorafensis* continues along the Pliocene of the Iberian Peninsula and southern France (Martín Suárez and Mein 1998) until it becomes extinct beside other large-sized *Apodemus* (*A. jeanteti*), coinciding with the spread of the arvicolids (Martín Suárez 1988). Since then, only the medium and small-sized *Apodemus* remain, which is true to this day.

***Genus** Paraethomys* Petter, 1968

Paraethomys meini Michaux, 1969 (Figures 11(A) – (H), 12(A) – (E), 12(G) – (L))

Material and localities

SIF-61: 8 m1 (2 digested, 2 fractured; IPS-101064–IPS-101069, IPS-100973, IPS-100974), 12 m2 (1 digested, 2 fractured; IPS-101070–IPS-101077, IPS-100975–IPS-100978), 5 m3 (IPS-101078–IPS-101081, IPS-100979), 8 M1 (1 digested, 2 fractured; IPS-101053–IPS-101059, IPS-100967), 7 M2 (3 fractured; IPS-101060–IPS-101062, IPS-100968–IPS-100971), 1 M3 (IPS-101063).

SIF-79: 1 m1 (IPS-101121), 3 m2 (1 fractured; IPS-101122–IPS-101124), 4 M1 (2 fractured; IPS-101112–IPS-101115), 4 M2 (1 fractured; IPS-101116–IPS-101119), 1 M3 (IPS-101120).

SIF-413: 18 m1 (3 digested, 5 fractured; IPS-101219–IPS-101236), 19 m2 (2 digested, 2 fractured; IPS-101237–IPS-101255), 5 m3 (1 fractured; IPS-101173–IPS-101177), 14 M1 (3 digested, 5 fractured; IPS-101178–IPS-101191), 18 M2 (3 digested, 4 fractured; IPS-101192–IPS-101209), 9 M3 (4 digested, 2 fractured; IPS-101210–IPS-101218).

SIF-430: 1 m1 (IPS-101296), 1 M2 (IPS-101295).

Measurements: Table 11.

Description of the material from SIF-413

m1: There is a very small tma in one out of 16 specimens. The anteroconid is slightly asymmetrical. A reduced longitudinal spur is present in 12 out of 17 individuals. There is a small and round enamel islet between the anteroconid complex and the protoconid-metaconid pair in eight out of 16 individuals. The labial cingulum may be weak or moderate. The posterior heel is oval or elongate and lingually displaced. It is similar in size to the c1. There are up to three small accessory labial cusps. There are two roots.

m2: The anterolabial cuspid may be big or medium-sized. It may be round, subtriangular or oval. The oval posterior heel may be weak or moderate. There is a small longitudinal spur in nine out of 19 specimens. The labial cingulum is weakly or moderately developed. There is a c1 in 11 out of 18 individuals. Another two accessory labial cuspids can be present. There are two roots.

m3: There is no longitudinal spur. There is a reduced anterolabial cupids in two out of five molars. The c1 and other labial cuspids are absent. There are two roots.

M1: The t1 is in more backward position than the t2 and t3. There is a low t1-t2 connection. The t1 has a very basal posterior spur directed towards t5 in five out of 11 specimens (C, D, Fig. 12). The t2 and t3 are united. There is a small distal spur on the t3 directed to the t2-t3 intersection in nine out of 11 individuals (D, Fig. 12); in three of them, the spur almost reaches that intersection, whereas in the others it is short. The t4-t5 union is lower than that of t5-t6. The t6 and t9 are joined by a narrow crest. The t4-t8 connection is very low. There is a small t12. There are three roots.

M2: The t1 is larger than the round t3. There is a low posterior spur on the t1 in four out of 14 specimens. The t9 is absent in 11 individuals, inflated in the others four (K, Fig. 12). The t12 is absent. There are three roots.

M3: The t1 is isolated and similar in size to the t8. The t3 is absent. The t4, t5 and t6 are united. The t6 is also joined to the t8 in all individuals but one (IPS-101210). Most of specimens have a complete t4-t5-t6-t8 union, forming a closed depression. This funnel is softly broad in the t4-t8 and t8-t6 contact. There are three roots.

Description of the material from SIF-61 and SIF-79

All the molars from these two levels have a similar morphology to those from SIF-413. The main differences fall in the frecuencies of some features (Tables 13 and 14). In addition, there is a medium-sized or large t12 in two M1 from SIF-61 (A, B, Fig. 12), and a very small t12 in the two M2 of this locality (H, Fig. 12).

Discussion

The studied material is consistent with the typical traits of the genus *Paraethomys*: union between t6 and t9, reduced of absent t9 in the M2, absence of tma in the m1, weak or moderate labial cingulum in the lower molars, presence of a small funnel of enamel in some m1, and reduced or absent anterolabial cupids in the m3.

The studied specimens are quite a bit smaller than *Paraethomys abaigari* Adrover, Mein and Moissenet, 1988. Moreover, the distal spurs on the t1 and t3 are better-developed in this latter. *Paraethomys jaegeri* Montenat and de Bruijn 1976 is even larger than *P. abaigari* and also has more developed distal spurs on the t1 and t3. *Paraethomys belmezensis* Castillo Ruiz 1992 differs from *P. meini* from the SIF sequence by the presence of a well-developed tma connected to the lingual lobe of the anteroconid. Like *P. meini* from Vvm (Mansino et al. 2017a), the presence of a reduced spur on the t3 in the M1 from SIF resembles that of *Paraethomys lissasfensis* Geraads 1998 from the Lissasfa site (late Miocene, North Africa). Nevertheless, the slightly smaller size of our material, the absence of a deep valley between t2 and t3, and the fact that not all the M2 have an inflated t9 (Table 14) allow distinguishing the material from SIF from *P. lissasfensis*.

The populations from SIF-61 and SIF-79 are a little smaller than *P. meini* from its type locality, Séte (Adrover 1986; Michaux 1969), but this species reaches a relatively large size in MN15 sites such as this latter (Mansino et al. 2017a). However, the specimens from the studied Miocene levels are similar in size and morphology to *P. meini* from Vvm (Mansino et al. 2017a), MNA-4 (García-Alix et al. 2008b), CR-6 (de Bruijn et al. 1975), NGR-1 (Minwer-

Barakat et al. 2009a), RCH-3 (Minwer-Barakat et al. 2009b), *Paraethomys anomalus* de Bruijn, Dawson and Mein, 1970 from Maritsa (Adrover 1986), and *Paraethomys miocaenicus* jaeger, Michaux and Thaler, 1975, from LIB (Brandy 1979). These two mentioned species are considered synonymous in several works (Montenat and de Bruijn 1976; van de Weerd 1976; Adrover 1986; Minwer-Barakat et al. 2005; García-Alix et al. 2008b; Mansino et al. 2015a; Piñero et al. in press; among others). The slightly larger material from SIF-413 agrees in size with *P. miocaenicus* from Khendek el Ouaich (Adrover 1986), and *P. meini* from PER-E (Adrover et al. 1988), LG-4, CEL-9 (Adrover et al. 1993), and PUR-4 (García-Alix et al. 2008b), ABS-3A (Mansino et al. 2015c), VER (Colombero et al. 2013), and MCC-5 (Colombero et al. 2014).

The measurements of the M3 and the lower molars are clearly smaller than those of the large *Paraethomys* found in SIF-P. Nonetheless, the maximum values of the M1 and M2 from SIF-413 overlap with the minimum values of the population from SIF-P. In addition, the large variability in size of the studied M1 may mean that the sample is formed by two species. Therefore, we calculated the coefficient of variability proposed by Freudenthal and Martín Suárez (1990) for the range variability of the M1 from SIF-413. The results (length M1 V’ = 19.09; width M1 V’ = 9.09) suggest that the sample is homogeneous, because their values represent a normal variability coefficient. This allows us to attribute the *Paraethomys* specimens from SIF-413 to one single population of *P. meini.*

From the older to the younger populations it is possible to see an increase in the variability in size of M1, a slight decrease in the relative width of M1 and a reduction in its t12, a reduction in the t9 and t12 in the M2 (Fig. 12), and an increase in the frequency of a reduced longitudinal spur in the m1.

Paraethomys* aff. *abaigari Adrover, Mein and Moissenet, 1988 (Figures 11(I) – (M), 12(F), 12(M))

Material and locality

SIF-P: 9 m1 (1 digested, 6 fractured; IPS-101325–IPS-101333), 3 m2 (2 fractured; IPS-101334–IPS-101336), 3 m3 (IPS-101337–IPS-101339), 5 M1 (3 fractured; IPS-101312–IPS-101316), 6 M2 (1 digested, 3 fractured; IPS-101317–IPS-101322), 2 M3 (IPS-101323, IPS-101324).

Measurements: Table 12.

Description of the material

m1: There is a slightly asymmetric anteroconid. The tma is absent. Two out of five specimens have a round islet of enamel between the anteroconid and the protoconid-metaconid. The anteroconid complex and the metaconid-protoconid pair are separated in one specimen (IPS-101329). All the individuals have a reduced longitudinal spur. The labial cingulum is moderately developed. The c1 is large, subtriangular, and connected to the protoconid by a low crest. Other two accessory labial cuspids are present. The medium-sized posterior heel can be oval or oval-compressed. There are two roots.

m2: The anterolabial cuspid is high and connected basally to the labial cingulum. There is a reduced longitudinal spur in two out three specimens. The labial cingulum is weak. There is neither c1 nor other accessory labial cuspids. The posterior heel is oval. It is weak in one individual (IPS-101334). The roots are not preserved.

m3: The anterolabial cuspid is absent. The hypoconid and entoconid are separated from the protoconid-metaconid pair. There is a weak labial cingulum in two out of three molars. One specimen (IPS-101338) develops an accesory labial cuspid in the labial side of the hypoconid-entoconid complex. There are two roots.

M1: The t1 is in backward position. The t2-3 union is higher than that of t1-t2. All the specimens have a distal spur in t1 connected to t5. It is high in two specimens and low in other three. They have also a distal spur in t3 directed to the t5-t6 intersection. It reaches this intersection in three out of five specimens. The t4-t5 union is lower than that of t5-t6. The connection between t4 and t8 is low. There is a high t6-t9 connection. A small or medium-sized t12 is present. There are three roots.

M2: The t1 is large. There is a very low posterior spur in the t1 directed to the t5 in three out of four individuals. In one worn specimen (IPS-101318) the t1 connects to the posterolingual side of the t5 (IPS-101318). The t3 is small, round and isolated. The t9 is absent in all the specimens. There are not preserved roots.

M3: The t1 is isolated. There is no t3. The t4, t5 and t6 are connected. The t8 is connected basally to them forming a closed depression. The roots are not preserved.

Discussion

The population found in SIF-P has the common traits of the genus *Paraethomys* cited above. It is bigger than *P. meini* and has more developed distal spurs on t1 and t3, and a somewhat stronger connection between t6 and t9 in the M1. *Paraethomys lissasfensis* is also smaller, whereas *P. jaegeri* is larger. *Paraethomys belmezensis* resembles the studied material in size but it has a well-developed tma in the m1.

The studied individuals fit the main characteristics of *Paraethomys abaigari*: presence of distal spurs in the t1 and t3 (less developed in the t1), high t6-t9 connection in the M1, large t1 with posterior spur in the M2, presence of a reduced longitudinal spur in the m1, moderate labial cingulum, large c1 and moderate posterior heel in the m1. However, the size of the specimens from SIF-P is slightly smaller than those of VAR (type locality) and La Judería (Adrover et al. 1988). As a result, we determined this population as *Paraethomys* aff. *abaigari*. In addition, the studied specimens agree with the size of *P*. aff. *abaigari* from ABS-2, ABS-3, ABS-3A, AC-0 (Mansino et al. 2015c), LB-2B, LB-3 (Mansino et al. 2015b), PUR-13, CLC-5A (García-Alix et al. 2008b), CEL-9, and LG-4 (Adrover et al. 1993). The specimens from AL-2C and AL-2D (Mansino et al. 2013) are slightly larger than our individuals. We compared *P*. aff. *abaigari* from Bz-1 (currently deposited in IPHES) directly with the studied material and found that they are fairly similar in morphology, but the specimens from Bz-1 have somewhat more derived characteristics: moderately more developed distal spurs on the t1 and t3 in the M1, slightly smaller t12 in the M1, better-developed union between the anteroconid and the protoconid-metaconid pair, and weaker labial cingulum in the m3. In addition, our specimens are a bit smaller, which is consistent with the slightly younger age of Bz-1.

Remarks about the genus Paraethomys from the Sifón de Librilla section

The *Paraethomys* dispersal is probably associated with the entry of *Paracamelus* into southern Spain (Agustí et al. 2006). The presence of the two taxa in European Messinian levels can be explained as being part of this dispersal event probably from northern Africa (Pickford et al. 1994; Garcés et al. 1998; Agustí et al. 2006; García-Alix et al. 2016). In fact, Geraads (1998) related the North African *P. lissasfensis* to the Iberian *Paraethomys* forms.

Some populations of *P. meini* near the Mio-Pliocene boundary, such as those from Moncucco Torinese (Colombero et al. 2014), Verduno (Colombero et al. 2013), PUR-4 (García-Alix et al. 2008b), PER-E (Adrover et al. 1988), and AF-1'06 (Mansino et al. 2015a), display a great size variability, like the specimens from SIF-413. García-Alix et al. (2008b) and Mansino et al. (2015a) suggested that this could be due to the presence of two different *Paraethomys* species. However, as occurs in SIF-413, a second species cannot be clearly distinguished within these assemblages, but rather they seem to be transitional populations towards a larger species.

The continuous record of *Paraethomys* in the SIF sequence allows us to observe an increase in size from the Miocene to the Pliocene populations. Although the specimens of *P. meini* from SIF-61 and SIF-79 remain similar in size, the M1 from SIF-413 becomes larger. The maximum values of the mentioned tooth overlap with the minimum values of *P.* aff. *abaigari* from SIF-P. Our data suggest that the large *P.* aff. *abaigari* can be the result of a local anagenetic process from the small *P. meini*, rather than it being an immigrant. This process would have been led by a continuous increase in size and a slight decrease in the relative width of the M1, joined to an increase in the development of longitudinal spurs in the upper teeth, a reduction of the t9 and t12 in the M2, and an increase in the frequency of a small distal spur in the m1 and m2 (Fig. 12; Tables 13, 14). Adrover et al. (1988) found that *P. abaigari* and *P. jaegeri* had greater development than *P. meini* of the posterior spurs in the t1 and t3 in the upper molars. We propose the phyletic lineage *P. meini* – *P.* aff. *abaigari* – *P. abaigari* – *P. jaegeri*, marked by a size increase and a progressive better development of the posterior spurs in the t1 and t3 along the early Pliocene.

In some of the earliest Ruscinian sites from the Teruel Basin, including CEL-14, CEL-5, CEL-5A, LG-4 and CEL-9 (Adrover et al. 1993), two species of *Paraethomys* are associated: the small-sized *P. meini* and the large-sized *Paraethomys* aff. *abaigari*. Contemporaneous and younger localities also have two coexisting *Paraethomys* species, for example PUR-13 and CLC-5A in the Granada Basin (García-Alix et al. 2008b), Bz-1 in the Guadix-Baza Basin (Piñero et al. in press), and Alcoy 2, AL-2C, AL-2D and LB-2B in the Alcoy Basin (Esteban Aenlle and Lacomba 1988; Mansino et al. 2013, 2015b). However, only one form of *Paraethomys*, *P.* aff. *abaigari*, is recognized in SIF-P. Hitherto, this is the only population of *P.* aff. *abaigari* that does not co-occur with *P. meini*. The absence of *P. meini* in SIF-P is consistent with the ancestor – descendant relationship between the small and large

Paraethomys. The last occurrence of *P. meini* in the Fortuna Basin corresponds to the level SIF-430.

Family Gerbillidae Alston, 1876

Subfamily Taterillinae Chaline, Mein and Petter, 1977

Genus *Debruijnimys* Castillo and Agustí, 1996

***Debruijnimys* sp.** (Figure 11(N) – (S))

Material and locality

SIF-413: 2 m1 (1 fractured; IPS-101287, IPS-101292), 1 m2 (fractured; IPS-101288) 2 M1 (fractured; IPS-101286, IPS-101290), 1 M2 (fractured; IPS-101291), 1 M3 (IPS-101289).

Measurements: Table 15.

Description of the material

m1: In the fragmented specimen, damaged in the anterior part,, a connection is observed between the anteroconid and the metaconid. The protoconid and metaconid are connected, but they are not fused. The connection between the protoconid and hypoconid is not established at the present stage of wear. A small posterolophid is attached to the posterior wall of the hypoconid. In the complete specimen, highly worn, a labial anterolophid can be observed. The protoconid and metaconid are widely confluent. A well-developed crest is present between the protoconid and the hypoconid. The hypoconid and the entoconid are widely confluent, forming a romb-like transversal ridge. A small posterolophid appears fused to the hypoconid.

M1: The best preserved specimen lacks the anterior wall, but it can be still observed that the anterocone was probably not very large. The protocone is widely confluent with the paracone, forming a transverse ridge. The metacone is attached to the hypocone, but in a more anterior position. There is no connection between the hypocone and the protocone. In a second fragment, only the posterior part of the tooth is preserved. Transverse ridges are present at the posterior wall of the protocone and the anterior wall of the hypocone, thus connecting the two cusps. The hypocone and metacone are widely confluent, the metacone placed in a more anterior position and delimiting a very superficial posterosinus.

M2: The only specimen does not preserve the posterior part. There is no evidence of anterolophs. The protocone and paracone are widely confluent, a posterior constriction delimiting both cusps. Although damaged, it seems that hypocone and metacone were also widely confluent. The anterior wall of the metacone is projected forwards and is almost connected to the posterior wall of the paracone.

M3: This piece is represented by a highly worn specimen in which the only distinguishable feature is the persistence of a very tiny mesosinus at the labial wall of the tooth.

Discussion

The presence of a very archaic member of *Debruijnimys* has already been recorded at the AL-4B site (Agustí and Casanovas-Vilar 2003). The species from SIF-413 can be clearly differentiated from *Debruijnimys almenarensis*, because of the shape of the anterocone in the M1 and particularly the shape of the anteroconid in the m1. In this way, it ressembles the type-species *Debruijnimys julii* Castillo and Agustí, 1996 from the Pliocene of Asta Regia. However, the species represented at SIF-413, although clearly related to the species from Asta Regia-3, is smaller and has less developed transversal ridges in the lower molars. The material from SIF-413 coincides in size and morphology with the above mentioned AL-4B population. In particular, the complete m1 from SIF-413 fits the m1 from AL-4B almost exactly, figured by Agustí and Casanovas-Vilar (2003; Fig. 1, 9), while the damaged m1 also fits the second figured m1 from AL-4B (Fig. 1, 8). The smaller size and simplified dental pattern of *Debruijnimys* sp. from SIF-413 corroborate the idea that this species cannot be a descendant of *Debruijnimys almenarensis* (Agustí, 1990) according to the morphological features of m1, and that a second gerbil dispersal took place in the Iberian Peninsula during the Messinian (Agustí 1990; Agustí and Casanovas-Vilar 2003).

Family Gliridae Muirhead, 1819

Subfamily Dryomyinae de Bruijn, 1967

Genus *Eliomys* Wagner, 1840

Eliomys truci Mein and Michaux, 1970 (Figure 13(A) – (I))

Material and localities

SIF-1: 1 m1-2 (IPS-100794), 1 M3 (IPS-100793).

SIF-61: 1 M3 (IPS-101111).

SIF-413: 1 m1-2 (IPS-101294), 1 M1 (IPS-101293).

SIF-P: 1 d4 (IPS-101419), 1 m2 (fractured; IPS-101416), 1 m3 (IPS-101417), 1 P4 (IPS-101418).

Measurements: Table 16.

Description of the material

d4: A very worn d4 from SIF-P displays a subtriangular occlusal outline. The only character which can be hardly distinguished is the presence of a vestigial anterotropid.

m1-2: In the complete specimen from SIF-1, the labial end of the anterolophid is fused to the protoconid and the metalophid. There is a small lingual anterotropid. The centrolophid is discontinuous, with a lingual segment connected to the metalophid and a labial one fused to the mesolophid. The posterotropid is very long. A second fragmented tooth from this level presents a short centrolophid. The specimen from SIF-413 coincides with that of SIF-1, but the anterotropid is lacking. A long centrolophid and a long posterotropid are also present. The protoconid, the mesoconid and the hypoconid are directed forwards.

m3: In the specimen from SIF-P, a short anterolophid not connected to the protoconid is present. The centrololophid is very short. The posterotropid is very small. As in the m1-2, the protoconid, the mesoconid and the hypoconid are directed forwards.

P4: In the specimens from SIF-P, a short anteroloph is present. A small precentroloph is present in one case and a very short and vestigial one in another. The posteroloph is long and fused to the protocone.

M1-2: The occlusal surface is concave. The endoloph is continuous, although the connection between the metaloph and the posteroloph is weak. The precentroloph is long and labially fused to the protoloph. The postcentroloph is short and isolated. The posteroloph is labially connected to the metaloph.

M3: In the specimen SIF-1 a continuous endoloph is present. The precentroloph is short, whereas the postcentroloph is longer. The tooth from SIF-61 is notably larger and proportionally wider than that of SIF-1, but the postcentroloph is absent.

Eliomys* cf. *intermedius Friant, 1953 (Figure 13(J))

Material, localitiy and measurements

SIF-P: 1 M1-2 (fragmented; IPS-101415) (L: 1.34 mm).

Description of the material

M1-2: A large fragmented M1-2 indicates the presence of a second species of *Eliomys*, accompanying *Eliomys truci*. A continuous endoloph can be recognized. This specimen is characterized by a very long postcentroloph. The posteroloph does no reach the metacone.

Remarks about the genus Eliomys from the Sifón de Librilla section

From SIF-1 to SIF-P, most of the levels have yielded scarce remains of a small species of *Eliomys* that fits the size and morphology of *Eliomys truci*. In SIF-P, a second and larger species, identified as *Eliomys* cf. *intermedius*, joins the former species. The somewhat larger specimens from SIF-413 could also fit as the species *Eliomys yevesi*, considered to be the direct ancestor of *Eliomys intermedius* by Mansino et al. (2015d). However, continuity in size and morphology can be observed in the *Eliomys truci* material from the Sifón section, until de abrupt entry of *E*. cf. *intermedius* in SIF-P. We therefore assume that the small *Eliomys* present in the Sifón section corresponds to the same species, *Eliomys truci*, and that *E*. cf. *intermedius* is an immigrant into the Fortuna Basin.

Genus *Muscardinus* Kaup, 1829

Muscardinus vireti Hugueney and Mein, 1965 (Figure 13(K))

Material, locality and measurements

SIF-3: 1 M1 (IPS-100882) (L: 1.63 mm; W: 1.32 mm).

Description of the material

M1: This tooth displays six tranversal ridges, corresponding to the anteroloph, the protolophe, the precentrolophe, the *postcentroloph*, the metaloph, and the posteroloph. All of them are long ridges, ranging from the labial to the lingual border of the tooth, being their lingual ends slightly directed backward. A small lingual ridge is also present between the protolophe and the precentroloph. The anteroloph is isolated. An endoloph connects the lingual ends of the protoloph, the precentrolophe, the postcentroloph and the metaloph. The posteroloph is isolated, not joining the endoloph.

Discussion

In the *Fortuna* Basin, *Muscardinus vireti* was previously found at the La Hornera site (Agustí et al. 1983, 2006). The specimen from La Hornera (an M1; L, Fig. 13) is similar in size and morphology to the M1 from SIF-3, except for the absence of the small lingual ridge between the protolophe and precentroloph. As SIF-3, La Hornera is older than the first entry of *Paraethomys meini*. The presence in both localities of *Muscardinus vireti*, a taxon which is absent from all the other levels in Fortuna Basin, suggests that the two localities are probably coeval and reflect similar environmental conditions.

Biostratigraphic correlations

The localities of the Sifón de Librilla section can be correlated with other sites from the Iberian Peninsula on the basis of their rodent assemblages.

SIF-1 and SIF-3

SIF-1 and SIF-3 share most taxa: *Stephanomys ramblensis*, *Apodemus gudrunae*, *Occitanomys alcalai*, *Occitanomys adroveri*, *Hispanomys* cf. *adroveri*, and *Neocricetodon seseae*. In addition, the rodent list of SIF-1 includes *Eliomys truci*, whereas that of SIF-3 includes *Apodemus gorafensis* and *Muscardinus vireti*. The two localities are comparable to the oldest associations attributed to the MN13 unit. These localities, beside CH-17, CH-29 and CH-33 in Fortuna Basin (Agustí et al. 2006), mark the start of the first Messinian

Mammalian Event (MME-1; occurred somewhere between 7.3 and 6.8 Ma, corresponding to the MN12-MN13 boundary (middle-late Turolian boundary) proposed by Agustí et al. (2006).

Stephanomys ramblensis is considered the most characteristic late Turolian taxon in Spanish basins (Agustí and Llenas 1996; Daams et al. 1998), whereas *Occitanomys adroveri* is a typical element from the middle Turolian (MN12) in the Spanish continental record. Nevertheless, this latter species reaches the early late Turolian associated with *Occitanomys alcalai* at sites such as OTU-1, OTU-3 (García-Alix et al. 2008b), CR-14, CR-22, and CR-31 (Martín Suárez and Freudenthal 1998). Therefore, SIF-1 and SIF-3 can be correlated with the *Occitanomys adroveri*-*Occitanomys alcalai* Biozone from the Granada Basin (García-Alix et al. 2008c), and the base of the *Castromys inflatus* Biozone from the Crevillente Basin (Martín Suárez and Freudenthal 1998). In the former biozone, other species, like *Neocricetodon seseae*, *Hispanomys* sp., *Eliomys truci*, and *Muscardinus* sp., were reported; some of these species or closely related forms are also present in SIF-1 and SIF-3. *Hispanomys* is considered to have been replaced by *Ruscinomys* during the MN12/MN13 transition (Agustí et al. 2006). However, molars ascribed to the fromer genus have been reported at the base of MN13 in CR-14 and CR-6 (Martín Suárez and Freudenthal 1998). The presence of *H.* cf. *adroveri* in SIF-1 and SIF-3 confirms the persistence of this genus in the late Turolian.

The LG-6 site in the Teruel Basin is somewhat older than SIF-1 and SIF-3 according to the occurrence of *Apodemus* cf. *barbarae* (Mein et al. 1990). These sites are correlated with the lower part of the *Stephanomys ramblensis* Biozone from the Teruel Basin (Mein et al. 1990).

ROM-2C and ROM-2B in the Fortuna Basin (Piñero et al. 2017a) have many elements in common with SIF-1 and SIF-3, like *Stephanomys ramblensis*, *Occitanomys alcalai*, *Apodemus gudrunae*, and *Eliomys* cf. *truci*. However, the occurrence of a more derived form of *Occitanomys adroveri* (*O.* aff. *adroveri*) in ROM and *Hispanomys* cf. *adroveri* in SIF-1 and SIF-3, indicates that ROM-2C and ROM-2B are younger. The La Hornera association (Agustí et al. 1983) is very similar to that of SIF-3, with the presence of *Apodemus gudrunae*, *Stephanomys ramblensis*, *Hispanomys* sp., and *Muscardinus vireti*, suggesting that they have a similar stratigraphical position.

SIF-52

The locality of SIF-52 includes records of *Stephanomys ramblensis*, *Occitanomys alcalai*, *Apodemus gorafensis*, *Hispanomys romeroi*, and *Apocricetus alberti*. The first two elements have also been found in ROM-2C and ROM-2B; however, these sites contain *Occitanomys* aff. *adroveri* and *Apocricetus* aff. *plinii*, so it can be supposed that SIF-52 is slightly younger. SIF-52 also resembles AU-2R, the last locality in El Chorrico section before the arrival of *Paraethomys* to the Iberian Peninsula, it was therefore accumulated shortly before the second Messinian Mammalian Event (MME-2; Agustí et al. 2006).

SIF-52 may be correlated with the upper part of the *Castromys inflatus* Zone from the Crevillente Basin (Martín Suárez and Freudenthal 1998). The rodent list from SIF-52 is very similar to that of the late Turolian sites of VDC-3 and VDC-6, LG-5, VIL and ARQ-1 in the Teruel Basin (attributed to the *Stephanomys ramblensis* Biozone), with the common presence of *Stephanomys ramblensis*, *Occitanomys alcalai* and an intermediate *Apocricetus* between *A. plinii* and *A. alberti* (Freudenthal et al. 1998), which in LG-5 seems to be closer to *A. alberti* (van de Weerd 1976; Mein et al. 1990; Adrover et al. 1993; Freudenthal et al. 1998). The main difference between them is the absence of *Castromys inflatus*, a species that has not been identified so far in the Fortuna Basin.

Like the localities PUR-23, PUR-24A, PUR-25 in the Granada Basin (García-Alix et al. 2008c), SIF-52 also has *Stephanomys ramblensis*, *Occitanomys alcalai*, *Apodemus gorafensis* (*A*. aff. *gorafensis* in PUR-23) and *Apocricetus alberti*, while *Paraethomys* is still absent. This suggests that these localities from the Granada Basin have a similar biostratigraphic position as SIF-52.

SIF-61 and SIF-79

The fauna of SIF-61 and SIF-79 comprises *Stephanomys ramblensis*, *Occitanomys alcalai*, *Paraethomys meini*, *Apocricetus alberti*, and *Hispanomys romeroi*. Moreover, SIF-61 includes *Apodemus gudrunae*, *Apodemus gorafensis*, *Castromys* cf. *littoralis*, and *Eliomys truci*. SIF-61 and LIB-1 are the first localities that record the MME-2 (Garcés et al. 1998; Agustí et al. 2006). The nearby site of MS-9, in the Fortuna Basin, has yielded a similar small-mammal association, with the occurrence of *Stephanomys ramblensis*, *Paraethomys* *meini*, *Apodemus gudrunae* and *Apocricetus alberti* (Agustí et al. 1983, 2006), suggesting it has a similar age.

Likewise, the CR-6 level has elements common to SIF-61 and SIF-79, such as *Occitanomys alcalai, Stephanomys ramblensis, Paraethomys meini* and *Apocricetus alberti*, so they can be correlated to the *Paraethomys* Biozone from the Crevillente Basin (Martín Suárez and Freudenthal 1998). In addition, CR-6 shares with SIF-61 *Apodemus gudrunae* and *Eliomys truci*, indicating that they have a close age.

SIF-61 and SIF-79 share *Occitanomys alcalai*, *Paraethomys meini* and *Apocricetus alberti* with Vvm, in the Cabriel Basin, to which *Apodemus gorafensis* is added in the case of SIF-61 (Montoya et al. 2006; Mansino et al. 2014, 2017a). Their similar rodent associations suggest a similar biostratigraphical position.

The first occurrence of *Paraethomys meini* in the Granada Basin was reported in MNA-4 (García-Alix et al. 2008b), so SIF-61 and SIF-79 have a close biostratigrafical position than the localities attributed to the *Paraethomys meini* Biozone of the Granada Basin (García-Alix et al. 2008c).

SIF-413 and SIF-430

SIF-413 contains *Stephanomys dubari*, *Paraethomys meini*, *Apodemus* cf. *gudrunae, Occitanomys alcalai*, *Occitanomys brailloni*, *Debruijnimys* sp., *Apocricetus* aff. *barrierei*, *Ruscinomys* cf. *lasallei*, and *Eliomys truci*. Only *Stephanomys dubari*, *Paraethomys meini*, *Apocricetus* aff. *barrierei* and *Ruscinomys* sp. are reported in SIF-430, although these sections are very close in age. These associations lead us to place SIF-413 and SIF-430 at the base of the MN14 unit (earliest early Ruscinian).

The small mammal assemblage from the nearby site of PC (Piñero et al. 2017b) is very similar to those of SIF-413 and SIF-430. Similar taxa have been recognized in this level: *Debruijnimys* sp., *Paraethomys* cf. *meini*, *Stephanomys* cf. *dubari*, and *Ruscinomys lasallei*. According to biostratigraphical criteria, these sections are close in age. SIF-413 and SIF-430 were deposited after the third Messinian Mammalian Event (MME-3; Agustí et al. 2006), which involved rodents of African affinities, like members of the genera *Myocricetodon* and *Debruijnimys,* entering the western Mediterranean. This dispersal event is directly related to the MSC.

The nearby La Alberca site also contains a small-mammal association similar to those from SIF-413 and SIF-430, with the occurrence of *Stephanomys dubari*, *Ruscinomys lasallei*, *Paraethomys meini*, and *Apocricetus alberti* (Montenat 1973; Freudenthal et al. 1998). Following de Bruijn et al. (1975), the La Alberca site is late Miocene in age. These authors based their dating on the association of planktonic foraminiferans found in higher and lower marine sediments between which the continental site is intercalated. The La Alberca site is therefore older than SIF-413 and SIF-430. This is consistent with the absence of gerbils in La Alberca.

The PUR-3 locality, in the Granada Basin, resembles SIF-413 in that it has *Paraethomys meini*, *Stephanomys dubari*, *Occitanomys alcalai,* and *Ruscinomys* cf. *lasallei* (García Alix et al. 2008c). However, PUR-3 lacks *O. brailloni*, which suggests that this locality has an older age than SIF-413 and SIF-430. On the contrary, PUR-4 resembles SIF-413 in the presence of *Occitanomys alcalai*, *Stephanomys dubari*, *Paraethomys meini*, and two species closely related to *Ruscinomys lasallei* and *Apocricetus barrierei*. Thus, SIF-413 and SIF-430 can be correlated with the lower part of the *Apocricetus barrierei* Biozone in the Granada Basin (García-Alix et al. 2008c).

Likewise, the small-mammal association from SIF-413 and SIF-430 can be correlated with the *Apocricetus barrierei* Biozone that Mansino et al. (2017b) proposes for the Alcoy Basin. The AF-1'07 level resembles SIF-413 in that it contains *Paraethomys meini*, *Occitanomys alcalai*, *Stephanomys dubari* and *Apocricetus barrierei* (Mansino et al. 2015a).

SIF-413 and SIF-430 can be partly correlated with the upper part of the *Stephanomys ramblensis* zone of the Teruel Basin (Mein et al. 1990), in which the ARQ-4 locality (Adrover et al. 1993) shares with SIF-413 the presence of *Paraethomys meini*, *Occitanomys alcalai* and *Ruscinomys* cf. *lasallei*, although the absence of *O. brailloni* and the identification of *Stephanomys ramblensis* in ARQ-4 suggests that it is older than SIF-413.

The SIF-413 and SIF-430 sites can be compared with the *Apodemus gudrunae* zone of the Guadix Basin, in which the reference locality is NGR-1 (Minwer-Barakat et al. 2012). This locality resembles SIF-413 in that *Stephanomys dubari*, *Paraethomys meini*, *Occitanomys alcalai*, *Ruscinomys* sp., and *Eliomys* sp have been recorded in it. However, the presence of *Debruijnimys almenarensis, Myocricetodon jaegeri* and a murid clearly assigned to *Apodemus gudrunae* in NGR-1, and the absence of *O. brailloni*, suggests that it is somewhat older than SIF-413 and contemporaneous to the MME-3 (Agustí et al. 2006).

SIF-P

SIF-P contains *Stephanomys cordii*, *Paraethomys* aff. *abaigari, Castillomys gracilis, Occitanomys brailloni, Apocricetus* aff. *barrierei, Ruscinomys* sp., *Eliomys* cf. *intermedius* and *Eliomys truci*. The SIF-P association includes typical elements of the MN14 unit, such as *Paraethomys* aff. *abaigari*, *Castillomys gracilis*, *Stephanomys cordii, O. brailloni* and *Apocricetus* aff. *barrierei*. We attribute SIF-P to the base of MN14, previous to the entry of *Trilophomys*.

The associations from LB-3 and LB-2B (Mansino et al. 2015b), located in the Cabriel Basin, contain *Stephanomys dubari*, whereas the SIF-P association includes *Stephanomys cordii*. Nevertheless, they have many elements in common, especially SIF-P and LB-2B, and share *Paraethomys* aff. *abaigari*, *Castillomys gracilis*, *Occitanomys brailloni*, *Ruscinomys* sp., a related form close to *Apocricetus barrierei,* and *Eliomys intermedius*. We therefore consider that LB-3 and LB-2B are close in age to SIF-P, although LB-3 and LB-2B are somewhat younger according to the presence of *Stephanomys cordii*. The SIF-P site is correlated to the *Paraethomys* aff. *abaigari* Biozone from the Alcoy Basin (Mansino et al. 2017b), and is close in age to ABS-8, AC-0B, and AC-0, sharing *Paraethomys* aff. *abaigari* and a taxon close to *Stephanomys cordii* (Mansino et al. 2015c).

SIF-P is close in age to some sites from the Teruel Basin, such as CEL-14, CEL-5, LG-4 and CEL-9, with the common occurrence of *Paraethomys* aff. *abaigari* (Mein et al. 1990; Van Dam et al. 2006), among others. As a result, SIF-P can be correlated with the two *Paraethomoys* + *Promimomys* Biozones from the Teruel Basin (Mein et al. 1990). PER-E is somewhat older than SIF-P since a large *Paraethomys* cannot be distinguished with clarity (Mein et al. 1990).

SIF-P is similar to PUR-13 from the Granada Basin in that they both contain *Castillomys gracilis*, and *Paraethomys* aff. *abaigari*, but the presence of *Stephanomys dubari* instead of *Stephanomys cordii* in PUR-13 suggests that it is older than SIF-P. This latter can be correlated to the *Paraethomys* aff. *abaigari* Biozone from the Granada Basin (García-Alix et al. 2008c).

The sites of Go-A (Ruiz Bustos et al. 1984), Go-1 (de Bruijn 1974), Bz-1 (Piñero et al. in press), Go-4 (Martín Suárez 1988), in the Guadix-Baza Basin; CEL-6, CEL-12 (Mein et al. 1990), ALD (Adrover 1986), VAR (Adrover et al. 1988), in the Teruel Basin; and AL-2C, AL-2D (Mansino et al. 2013) in the Alcoy Basin, have many elements in common with SIF-P. However, all of them are characterized by the presence of *Trilophomys*, so they are younger than the top of the SIF section. To finish, the Bo-C and Bo-D localities in the Guadix-Baza Basin are close in age to SIF-P given the presence of *Stephanomys cordii* and *Castillomys gracilis* (Martín Suárez 1988; Piñero et al. in prep).

Chronostratigraphic framework of the rodents from the Sifón de Librilla section

In the section of Sifón de Librilla, there is a very complete and continuous record of rodents that, in combination with the reliable paleomagnetic study carried out by Garcés et al. (2001), allows us to establish a set of first and last occurrences for the species found along the SIF sequence. We will now tentatively give age estimates for the First Occurrence Datum (FOD) and Last Occurrence Datum (LOD) of some of these species. These estimates are based on both the paleomagnetic correlation presented by Garcés et al. (2001), and other paleomagnetic studies from other sites of similar ages to the sequence from SIF, such as BUN and BUN-4/5 (Van Dam et al. 2001), PUR-3 and PUR-4 (García-Alix et al. 2008c; Martín Suárez et al. 1998), ZOR (Martín Suárez et al. 2000), Vvm (Montoya et al. 2006; Gibert et al. 2013; Mansino et al. 2014, 2017a), PC (Piñero et al. 2017b), FV (Opdyke et al. 1997), Bo-C and Bo-D (Martín Suárez 1988; Piñero et al. in prep) and LB-3 and LB-2B (Mansino et al. 2015b). The Fig. 14 shows the distribution of the species identified in the studied levels and the age of each site as stated by Garcés et al. (2001) and Agustí et al. (2006).

Genus Neocricetodon

SIF-1 and SIF-3 both include *Neocricetodon seseae*, which allows us to establish its FOD at 6.9 – 6.7 Ma. The LOD is probably in Vvm (at about 6.2 – 6.0 Ma), but the ascription is doubtful (Montoya et al. 2006).

Genus Apocricetus

SIF-52 has one of the first populations of *Apocricetus alberti* after it evolved from *Apocricetus* aff. *plinii*. Similarly, the PUR-23 site records *Apocricetus alberti* before the entrance of *Paraethomys meini*. The FOD of *A. alberti* has to be placed at sometime between ROM-2C (in which *Apocricetus* aff. *plinii* has been identified) and SIF-52, probably somewhat before 6.25 Ma. *Apocricetus alberti* and *Apocricetus barrierei* has been clasically considered two different stages within the evolution of an anagenetic lineage in which changes are gradual (Freudenthal et al. 1998). Anyhow, the oldest clearly population of *Apocricetus barrierei* has been detected at PUR-4, at about 5.2 – 5.3 Ma.

Genus Hispanomys

The species *Hispanomys adroveri* is considered typical of the MN12 unit (Agustí 1986; Agustí et al. 2006), but the close form *H.* cf. *adroveri* reaches the base of the MN13 in SIF-1 and SIF-3. The LOD of this taxon is therefore in SIF-3, at about 6.7 Ma. The genus *Hispanomys*, however, persists until SIF-79 (between 6.2 and 6.0 Ma) represented by the new species *H. romeroi*.

Genus Occitanomys

The LOD of *Occitanomys adroveri* is recorded in SIF-3, at the base of C3An.2n, at about 6.7 Ma. *Occitanomys alcalai* appears for the first time in SIF-1, at the top of C3Ar (at about 6.9 – 6.7 Ma), but it disappears in levels that are younger than SIF-P (Go-4; Martín Suárez 1988). The FOD of *Occitanomys brailloni* is recorded in SIF-413 (between 5.33 and 5.23 Ma), but its presence continues beyond the Sifón de Librilla section (along the Ruscinian).

Genus Stephanomys

The oldest evidence of *Stephanomys ramblensis* is that of SIF-1, at about 6.9 – 6.7 Ma, whereas the last specimens before they evolve into *Stephanomys dubari* are found in SIF-79. Both SIF-79 and Vvm have been included in chron C3An.1n (Garcés et al. 2001; Gibert et al. 2013). Therefore, the LOD of *Stephanomys ramblensis* and the FOD of *Stephanomys dubari* have to be placed sometime between 6.25 and 6.03 Ma. In turn, the transitional replacement of *S. dubari* by *S. cordii* took place sometime between LB-2B and Bo-C (at about 4.9 – 4.6 Ma).

Genus Paraethomys

According to Agustí et al. (2006) the FOD of *Paraethomys meini* in the Iberian Peninsula took place in the Fortuna Basin prior to MSC (at about 6.2 Ma). Contrary to this, Gibert et al. (2013) identified the first appearance of *Paraethomys* at the Vvm site, roughly 6.23 Ma. The FOD of *Paraethomys* aff. *abaigari* is uncertain since the PER-E site seems to have two specimens close to this species (García-Alix et al. 2008b). Similarly, the three molars of *Paraethomys* cf. *meini* found in the basal MN14 locality of PC (Piñero et al. 2017b) are very close in size to *P*. aff. *abaigari*, so we consider these specimens as a transitional population towards the large-sized *Paraethomys*. However, the FOD of *Paraethomys* aff. *abaigari* can be tentatively established in LB-3, at about 5.2 – 5.0 Ma, because this site has yielded some molars attributed to this form (Mansino et al. 2015a)

Genus Castillomys

The only samples of *Castillomys gracilis* identified in the late Miocene are those of Salobreña, ACB-M, and DHS-16 (Aguilar et al. 1984; Agustí et al. 2011; García-Alix 2006). Nonetheless, as we have discussed previously, the ascription of these material is doubtful, and they could correspond to *Occitanomys alcalai*. In this way, the FOD of *Castillomys gracilis* would be restricted to the Pliocene, as originally proposed by Weerd (1976) and Mein et al. (1990).

Genus Apodemus

The SIF sequence reports the FOD of *Apodemus gudrunae*. This species appears in SIF-1 (6.9 – 6.7 Ma), whereas its LOD is recorded in Bo-C, at about 4.8 – 4.6 Ma (Martín Suárez 1988; Piñero et al. in prep). The FOD of *Apodemus gorafensis* is recorded in SIF-3, at about 6.7 Ma, but its stratigraphic range extends beyond the SIF sequence (Martín Suárez and Mein 1998).

Genus Eliomys

The FV site records the FOD of *Eliomys intermedius* at about 4.9 Ma. *Eliomys truci* has been identified in older and younger levels than those from the SIF sequence (Daams and Freudenthal 1988; Minwer-Barakat et al. 2012).

The problem of MN13 – MN14 and its correlation with the Miocene – Pliocene boundary

The Mio-Pliocene boundary has been estimated at 5.33 (Gradstein et al. 2004, 2012). This limit is usually considered to coincide with the Turolian-Ruscinian or MN13-MN14 boundary (Hernández-Fernández et al. 2004; García-Alix et al. 2008c). However, several studies have questioned this equivalence because the upper part of the MN13 unit reaches the earliest Pliocene (Opdyke et al. 1997; Agustí et al. 2001; Piñero et al. 2017b). Thanks to the detection of the valley incision produced by the MSC in the SIF section and the presence of a marine Pliocene transgression, the late Miocene levels can now be clearly separated from the early Pliocene ones (Garcés et al. 2001; Agustí et al. 2006). SIF-413 is the first level rich in micromammal remains found just after the basal Pliocene transgression. Thus, the localities below are correlated with the late Miocene (SIF-1, SIF-3, SIF-52, SIF-61, SIF-79), and those found above are correlated with the early Pliocene (SIF-413, SIF-430, SIF-P).

Mein et al. (1990) defined the base of the MN14 in the Teruel Basin based on the entry of *Celadensia*. However, Agustí et al. (2001) proposed defining the base of MN14 in relation to the first apparition of the arvicolid *Promimomys* due to the occurrence of *Celadensia* in Baccinello (Italy), a MN13 locality (Rook and Torre 1995). *Promimomys* entered the Teruel Basin (recorded in CEL-9 and CEL-12) in approximately 5 Ma (Van Dam et al. 2006). However, the range of *Promimomys* within the Iberian Peninsula is limited to the Teruel region (Mein et al. 1990), so correlations with southern Iberian basins are difficult to establish. In the absence of arvicolids, Agustí et al. (2001) proposed distinguishing MN13 and MN14 in relation to the evolutionary stages of *Apodemus*, *Stephanomys*, *Paraethomys*, *Ruscinomys* and *Apocricetus*. However, the problem is that most of these lineages underwent gradual evolution throughout the late Miocene and early Pliocene, and no clear cut can be defined within them.

The stratigraphic range of *Apodemus gudrunae* is not limited to the late Turolian since this species has been found in the MN14 level of Bo-C (Martín Suárez, 1988), so this species cannot be used as an indicator of MN13. *Apodemus gorafensis* appears in the late Turolian level of SIF-3, and its record extends along the Ruscinian (Martín Suárez and Mein 1998). Therefore, this species cannot be used as a marker of MN13 or MN14, and merely indicates a late Turolian – Ruscinian age.

Stephanomys ramblensis has an exclusively late Turolian distribution (Agustí and Llenas 1996), whereas *Stephanomys dubari* is common in latest Turolian and earliest Ruscinian assemblages (García-Alix et al. 2008c; Mansino et al. 2015a). *Stephanomys cordii* has an exclusively MN14 distribution, evolving toward *Stephanomys margaritae* at the top of this unit (Adrover 1986; Mein et al. 1990). It is therefore an early Ruscinian indicator.

According to Morales et al. (2013), the appearance of a large *Paraethomys* (*P*. aff. *abaigari*, *P. abaigari*) besides a smaller one (*P. meini*) indicates the beginning of the subzone N2. Mansino et al. (2017b) considers this subzone to be early Ruscinian (MN14). Our work supports the appearance of *P*. aff. *abaigari* in the base of the MN14 unit, and it is therefore a key element of MN14.

Ruscinomys lasallei can be found both in MN13 and MN14 localities (Adrover et al. 1993; García-Alix et al. 2008a; Ruiz Bustos et al. 1984; Piñero et al. in press, 2017b; Mansino et al. 2013; among others), whereas *Ruscinomys europaeus* is recorded in both MN14 and MN15 levels (Adrover 1986; Castillo Ruiz 1990; Mein et al. 1990; Martín Suárez 1988; among others). *Apocricetus alberti* is typical of the latest Turolian (or MN13 unit), in agreement with several authors (Mein 1975; Fejfar and Heinrich 1990; Kälin 1999; Minwer-Barakat et al. 2009a), whereas *Apocricetus barrierei* is considered an early Ruscinian (or MN14) indicator (Mein et al. 1990; Freudenthal et al. 1998; Kälin 1999; García-Alix et al. 2008a, 2008c).

In the absence of the arvicolid *Promimomys,* we propose using the presence of *Occitanomys brailloni*, a typical Ruscinian species which is still present at SIF-413, the first level after the MSC, to correlate with the beginning of the MN14 unit. Otherwise, the joint presence of *Apocricetus alberti* and *Stephanomys dubari* is indicative of MN13.

The equivalence between the Mio-Pliocene boundary and the MN13-MN14 limit has been confirmed in this work. Our work indicates that the only element that can mark the beginning of the Pliocene in the continental record of southwestern Europe is *Occitanomys brailloni*. This taxon is the sole species from SIF-413 not found in Miocene levels. Its identification in SIF-413 corroborates its appearance in the earliest Pliocene. Consequently, *Occitanomys brailloni* becomes a key element for marking the Pliocene in the terrestrial record, and for the distinction between MN13 and MN14.

Conclusions

SIF-1 has yielded 139 rodent teeth, whereas SIF-3 contained 104 molars. These localities share most taxa: *Stephanomys ramblensis*, *Apodemus gudrunae*, *Occitanomys alcalai*, *Occitanomys adroveri*, *Hispanomys* cf. *adroveri*, and *Neocricetodon seseae*. In addition, SIF-1 includes *Eliomys truci*, whereas SIF-3 includes *Apodemus gorafensis* and *Muscardinus vireti*. Both levels are comparable to the oldest associations assigned to the MN13 unit, or earliest late Turolian.

SIF-52 has yielded 55 specimens, including the species *Stephanomys ramblensis*, *Apodemus gorafensis*, *Occitanomys alcalai*, *Hispanomys romeroi*, and *Apocricetus alberti*. This locality is correlated with the MN13 (late Turolian), shortly before the first entry of *Paraethomys* in the Iberian Penisnula.

The rodent list of SIF-61 (with 158 teeth) and SIF-79 (with 28 specimens) consists of *Stephanomys ramblensis*, *Occitanomys alcalai*, *Paraethomys meini*, *Apocricetus alberti*, and *Hispanomys romeroi*. In addition, SIF-61 includes *Apodemus gudrunae*, *Apodemus gorafensis*, *Castromys* cf. *littoralis*, and *Eliomys truci*. These associations suggest a late Turolian age, and record the first occurrence of *Paraethomys* in Western Europe.

The 157 specimens yielded by the early Pliocene level of SIF-413 are attributed to the species *Stephanomys dubari*, *Paraethomys meini*, *Apodemus* cf. *gudrunae*, *Occitanomys alcalai*, *Occitanomys brailloni*, *Debruijnimys* sp., *Apocricetus* aff. *barrierei*, *Ruscinomys* cf. *lasallei*, and *Eliomys truci*. SIF-430 only contained nine molars, identified as *Stephanomys dubari*, *Paraethomys meini* and *Apocricetus* aff. *barrierei*, and some fragments identified as *Ruscinomys* sp. These localities have been correlated with the earliest early Ruscinian (base of the MN14 unit).

The rodent assemblage from SIF-P is based on 116 molars, comprising the taxa *Stephanomys cordii*, *Paraethomys* aff. *abaigari*, *Castillomys gracilis*, *Occitanomys brailloni*, *Apocricetus* aff. *barrierei*, *Eliomys* cf. *intermedius* and *Eliomys truci*. Some fragments attest to the presence of *Ruscinomys* sp. This locality is correlated with the earliest Ruscinian (base of MN14).

The anagenetic evolutionary line *S. ramblensis* – *S. dubari* – *S. cordii* has been confirmed based on the material found in the Sifón de Librilla section.

The coexistence of *Apodemus gudrunae* and *Apodemus gorafensis* in the earliest late Turolian (basal MN13) locality of SIF-3, as well as the absence of a transitional population, suggest that *Apodemus gorafensis* is either an immigrant to Iberian Peninsula basins or the result of a rapid cladogenetic process rather than the anagenetic descendant of *Apodemus gudrunae*.

It has been proposed that *Paraethomys meini* is the ancestor of *Paraethomys* aff. *abaigari* as the result of an anagenetic evolutionary process marked by a size increase and better development of the posterior spur in t1 and t3 during the early Pliocene.

A new species of Cricetodontinae, i.e. *Hispanomys romeroi,* has been defined in the SIF-61 locality.

In the absence of the arvicolid *Promimomys,* the first occurrence of *Occitanomys brailloni* is the only valid element that makes it possible to distinguish the late Miocene from the early Pliocene in the continental record of Western Europe, as well as the MN13 from the MN14. According to this datum, the MN13-MN14 boundary can be considered equivalent to the Miocene-Pliocene boundary.

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Table 1. Measurements (mm) of the teeth of *Neocricetodon seseae* from SIF-1 and SIF-3.

Element	Locality	Length				Width			
		N	Min	Mean	Max.	N	Min.	Mean	Max.
M1	SIF-1	1		2.12		1		1.41	
	SIF-3	1		2.17		1		1.36	
M2	SIF-1	1		1.76		2	1.41	1.45	1.49
	SIF-3	1		1.76		1		1.41	
M3	SIF-1	3	1.53	1.57	1.60	2	1.45	1.47	1.49
	SIF-3	3	1.43	1.44	1.45	2	1.29	1.30	1.30
m2	SIF-1	1		1.77		3	1.34	1.38	1.41
m3	SIF-1	2	1.64	1.64	1.64	2	1.33	1.34	1.34
	SIF-3	2	1.76	1.81	1.85	3	1.40	1.43	1.46

Table 2. Measurements (mm) of the teeth of the genus *Apocricetus* from the Sifón de Librilla section.

Species	Elem.	Locality	Length				Width			
			N	Min	Mean	Max.	N	Min.	Mean	Max.
A. alberti	M1	SIF-61	4	2.28	2.35	2.43	4	1.40	1.49	1.54
A. aff. *barrierei*		SIF-413	1		2.64		1		1.66	
A. aff. *barrierei*		SIF-430					1		1.55	
A. aff. *barrierei*		SIF-P	2	2.54	2.58	2.61	2	1.53	1.58	1.62
A. alberti	M2	SIF-61	1		1.82		1		1.59	
A. alberti		SIF-79	1		1.95		2	1.55	1.55	1.55
A. aff. *barrierei*		SIF-413	2	1.87	1.91	1.94	1		1.49	
A. aff. *barrierei*		SIF-P	4	1.89	1.95	2.04	3	1.51	1.60	1.68
A. alberti	M3	SIF-61	3	1.37	1.51	1.70	2	1.24	1.28	1.31
A. aff. *barrierei*		SIF-430	1		1.67					
A. aff. *barrierei*		SIF-P	5	1.64	1.69	1.77	2	1.45	1.46	1.47
A. alberti	m1	SIF-61	1		2.21		1		1.28	
A. aff. *barrierei*		SIF-413	2	2.39	2.43	2.46	1		1.35	
A. aff. *barrierei*		SIF-P	2	2.36	2.42	2.47	2	1.33	1.38	1.43
A. alberti	m2	SIF-52					1		1.36	
A. alberti		SIF-61	5	1.66	1.78	1.86	7	1.31	1.41	1.45
A. aff. *barrierei*		SIF-413	1		1.71		1		1.39	
A. aff. *barrierei*		SIF-430	1		1.93					
A. aff. *barrierei*		SIF-P	4	1.97	2.01	2.06	4	1.50	1.57	1.61
A. alberti	m3	SIF-61	3	1.82	1.85	1.91	4	1.30	1.37	1.43
A. aff. *barrierei*		SIF-413	2	1.94	1.95	1.96	3	1.49	1.55	1.57
A. aff. *barrierei*		SIF-P	8	1.80	1.96	2.08	7	1.39	1.48	1.54

Table 3. Measurements (mm) of the teeth of the genera *Hispanomys* and *Ruscinomys* from the Sifón de Librilla section.

Species	Elem.	Locality	Length				Width			
			N	Min	Mean	Max.	N	Min.	Mean	Max.
H. cf. *adroveri*	M1	SIF-3					1		2.23	
H. romeroi		SIF-61	3	3.86	4.00	4.25	5	2.24	2.37	2.47
H. romeroi	M2	SIF-52	1		2.65		1		1.95	
H. romeroi	M3	SIF-61	2	1.89	1.91	1.93	2	1.47	1.56	1.65
Hispanomys sp.	m1	SIF-3					2	1.84	1.85	1.85
H. romeroi		SIF-52	2	2.80	2.82	2.84	1		2.00	
H. romeroi		SIF-61	6	2.83	2.98	3.13	6	1.85	1.95	2.00
R. cf. *lasallei*		SIF-413	1		3.23		2	2.00	2.05	2.10
H. cf. *adroveri*	m2	SIF-1	1		2.63					
H. cf. *adroveri*		SIF-3					1		1.82	
H. romeroi		SIF-61	3	2.91	2.94	3.00	4	1.85	1.91	1.99
H. romeroi		SIF-79	1		2.82		1		1.81	
H. cf. *adroveri*	m3	SIF-1	1		2.53		1		1.73	
H. cf. *adroveri*		SIF-3	2	2.45	2.57	2.68	2	1.46	1.55	1.63
H. romeroi		SIF-52					1		1.67	
R. cf. *lasallei*		SIF-413	1		2.52		1		1.59	

Table 4. Measurements (mm) of the teeth of *Occitanomys adroveri* from SIF-1 and SIF-3.

Element	Locality	Length				Width			
		N	Min	Mean	Max.	N	Min.	Mean	Max.
M1	SIF-1	8	2.00	2.07	2.15	12	1.26	1.39	1.47
	SIF-3	3	2.06	2.13	2.24	5	1.36	1.41	1.47
M2	SIF-1	9	1.35	1.45	1.55	9	1.23	1.37	1.44
	SIF-3	3	1.31	1.40	1.47	3	1.29	1.32	1.35
M3	SIF-1	12	0.88	1.00	1.09	13	0.90	0.99	1.08
	SIF-3	1		0.95		1		0.99	
m1	SIF-1	5	1.74	1.86	2.01	5	1.15	1.22	1.32
	SIF-3	5	1.80	1.92	2.11	5	1.16	1.22	1.30
m2	SIF-1	5	1.26	1.39	1.44	8	1.24	1.28	1.33
	SIF-3	3	1.42	1.43	1.43	6	1.24	1.28	1.35
m3	SIF-1	11	1.01	1.10	1.19	11	0.94	1.03	1.11
	SIF-3	2	1.02	1.06	1.09	3	0.95	1.04	1.10

Table 5. Measurements (mm) of the molars of *Occitanomys alcalai* from SIF-1, SIF-3, SIF-52, SIF-61, SIF-79 and SIF-413.

Element	Locality	Length				Width			
		N	Min	Mean	Max.	N	Min.	Mean	Max.
M1	SIF-1	1		1.73		1		1.25	
	SIF-3	1		1.74		1		1.27	
	SIF-52	1		1.97		2	1.33	1.37	1.41
	SIF-61	2	1.76	1.80	1.83	2	1.19	1.27	1.34
	SIF-79	1		1.80		1		1.20	
	SIF-413	1		1.70		1		1.18	
M2	SIF-3	6	1.21	1.28	1.36	5	1.21	1.24	1.28
	SIF-52	3	1.30	1.30	1.31	3	1.22	1.24	1.27
	SIF-61	2	1.27	1.29	1.30	2	1.25	1.27	1.29
	SIF-79	1		1.32		2	1.25	1.25	1.25
M3	SIF-52	1		0.89		1		0.81	
m1	SIF-3	2	1.66	1.70	1.73	3	0.99	1.05	1.12
	SIF-52					1		1.22	
	SIF-61	2	1.67	1.68	1.69	2	1.07	1.11	1.14
	SIF-79	1		1.62		2	1.05	1.09	1.13
	SIF-413	1		1.63		1		1.05	
m2	SIF-3	1		1.20		1		1.16	
	SIF-52	3	1.15	1.25	1.35	3	1.06	1.17	1.29
	SIF-61	1		1.33		1		1.21	
	SIF-79	2	1.21	1.29	1.37	1		1.19	
	SIF-413	2	1.15	1.16	1.18	1		1.06	
m3	SIF-3	1		0.99		1		1.03	
	SIF-52	2	0.90	0.95	1.00	2	0.89	0.85	0.96
	SIF-61	3	0.97	1.01	1.05	2	0.86	0.92	0.96
	SIF-413	1		0.90		1		0.86	

Table 6. Measurements (mm) of the teeth of *Occitanomys brailloni* from SIF-413 and SIF-P.

Element	Locality	Length				Width			
		N	Min	Mean	Max.	N	Min.	Mean	Max.
M1	SIF-413	2	2.05	2.15	2.25	3	1.42	1.46	1.55
	SIF-P	3	2.12	2.19	2.30	3	1.50	1.54	1.59
M2	SIF-413	1		1.67		1		1.48	
	SIF-P	1		1.45		1		1.45	
m2	SIF-413	1		1.34		2	1.22	1.28	1.33
	SIF-P	1		1.45		1		1.38	

Table 7. Measurements (mm) of the teeth of the genus *Stephanomys* from the Sifón de Librilla section.

Species	Element	Locality	Length				Width			
			N	Min	Mean	Max.	N	Min.	Mean	Max.
S. ramblensis	M1	SIF-1					2	1.49	1.54	1.59
		SIF-3	8	2.07	2.18	2.28	9	1.52	1.62	1.84
		SIF-52	2	2.32	2.41	2.49	4	1.51	1.64	1.76
		SIF-61	6	2.09	2.25	2.32	7	1.55	1.62	1.72
		SIF-79	1		2.17		1		1.57	
S. dubari		SIF-413	2	2.30	2.33	2.35	3	1.76	1.77	1.77
S. cordii		SIF-P	8	2.35	2.56	2.71	8	1.71	1.78	1.90
S. ramblensis	M2	SIF-1	1		1.62		1		1.55	
		SIF-3	5	1.46	1.54	1.64	6	1.42	1.47	1.52
		SIF-52	4	1.54	1.61	1.66	4	1.49	1.57	1.71
		SIF-61	7	1.56	1.64	1.74	7	1.51	1.59	1.66
S. dubari		SIF-413					1		1.65	
S. cordii		SIF-P	5	1.65	1.72	1.81	5	1.60	1.65	1.76
S. ramblensis	M3	SIF-1	3	1.11	1.12	1.15	3	1.00	1.05	1.08
		SIF-3	1		1.20		1		1.05	
		SIF-52	1		1.00		1		1.09	
		SIF-61	2	1.16	1.19	1.23	2	1.10	1.13	1.16
S. dubari		SIF-413	3	1.26	1.26	1.27	3	1.01	1.04	1.07
S. cordii		SIF-P	2	1.24	1.32	1.39	2	1.19	1.21	1.22
S. ramblensis	m1	SIF-1	1		2.00		1		1.23	
		SIF-3	2	1.90	1.98	2.06	5	1.27	1.32	1.43
		SIF-52	1		2.08		3	1.31	1.33	1.37
		SIF-61	3	2.04	2.08	2.14	4	1.29	1.31	1.34
S. dubari		SIF-413	5	2.06	2.12	2.20	6	1.22	1.29	1.40
S. cordii		SIF-P	5	2.12	2.18	2.25	5	1.34	1.42	1.52
S. ramblensis	m2	SIF-1					2	1.37	1.41	1.44
		SIF-3	1		1.47		3	1.32	1.42	1.54
		SIF-52	2	1.56	1.60	1.64	1		1.56	
		SIF-61	2	1.47	1.51	1.57	3	1.43	1.47	1.51
		SIF-79	1		1.55		1		1.41	
S. dubari		SIF-413	5	1.51	1.54	1.56	4	1.37	1.41	1.44

S. cordii		SIF-P	2	1.61	1.71	1.80	2	1.51	1.52	1.53
S. ramblensis	m3	SIF1					1		1.15	
		SIF3					2	1.13	1.17	1.21
		SIF52	2	1.22	1.25	1.28	3	1.12	1.23	1.36
		SIF61	4	1.12	1.20	1.28	4	1.08	1.13	1.22
S. dubari		SIF-413	2	1.20	1.26	1.32	3	1.22	1.26	1.31
S. cordii		SIF-P	3	1.34	1.43	1.51	5	1.21	1.32	1.44

Table 8. Frequency of the different development stages for the posterior connections on t1 and t3 of the M1 and M2 of *Stephanomys* from the SIF section.

Species	Element	Level	% on t1				% on t3			
			N	C	S	A	N	C	S	A
S. ramblensis	M1	SIF-1	4	25	75	0	4	25	75	0
		SIF-3	13	15.4	76.9	7.7	13	15.4	76.9	7.7
		SIF-52	6	15.1	66.7	15.1	7	71.4	28.6	0
		SIF-61	9	11.2	55.5	33.3	8	50	12.5	37.5
		SIF-79	1	0	100	0	1	0	100	0
S. dubari		SIF-413	4	75	25	0	4	75	25	0
		SIF-430	1	100						
S. cordii		SIF-P	8	100	0	0	8	100	0	0
S. ramblensis	M2	SIF-1	1	0	0	100	1	0	0	100
		SIF-3	6	0	66.7	33.3	6	0	33.3	66.7
		SIF-52	4	0	75	25	4	0	0	100
		SIF-61	8	12.5	50	37.5	8	12.5	25.3	62.2
S. dubari		SIF-413	2	50	50	0	2	100	0	0
S. cordii		SIF-P	5	100	0	0	5	100	0	0

Notes: C = crest; S = spur; A = absent; N = number of molars.

Table 9. Measurements (mm) of the molars of *Apodemus gudrunae* from SIF-1, SIF-3, SIF-61, and *Apodemus* cf. *gudrunae* from SIF-413.

Element	Locality	Length				Width			
		N	Min	Mean	Max.	N	Min.	Mean	Max.
M1	SIF-1	1		2.18		1		1.47	
	SIF-3	2	2.00	2.07	2.13	3	1.28	1.30	1.32
	SIF-413	2	2.03	2.04	2.05	3	1.25	1.27	1.30
M2	SIF-1	1		1.47		1		1.38	
	SIF-61	1		1.38				1.36	
	SIF-413	2	1.37	1.39	1.41	2	1.18	1.25	1.32
M3	SIF-1	1		0.97		1		0.97	
m1	SIF-1	2	1.94	1.96	1.98	3	1.17	1.20	1.23
	SIF-3	2	1.87	1.89	1.90	2	1.17	1.19	1.20
	SIF-61	1		2.02		1		1.21	
	SIF-413	1		1.75		3	1.09	1.17	1.22
m2	SIF-1	7	1.35	1.40	1.45	7	1.28	1.31	1.40
	SIF-3	1		1.40		2	1.33	1.34	1.35
	SIF-413	4	1.36	1.42	1.50	4	1.21	1.29	1.33
m3	SIF1	7	1.07	1.13	1.23	7	0.99	1.06	1.13
	SIF3	1		1.12		1		1.09	

Table 10. Measurements (mm) of the teeth of *Apodemus gorafensis* from SIF-3, SIF-52 and SIF-61.

Element	Locality	Length				Width			
		N	Min	Mean	Max.	N	Min.	Mean	Max.
M1	SIF-3	1		2.40		1		1.53	
	SIF-52					1		1.40	
	SIF-61	2	2.45	2.47	2.48	2	1.54	1.58	1.61
M2	SIF-3	1		1.68		1		1.54	
	SIF-61	3	1.67	1.70	1.71	3	1.50	1.55	1.60
M3	SIF-3	2	1.12	1.13	1.13	2	1.11	1.12	1.12
	SIF-61	1		1.20		2	1.19	1.21	1.22
m1	SIF-3	1		2.18		1		1.23	
	SIF-61	1		2.14		2	1.27	1.28	1.28
m2	SIF-52	1		1.56		1		1.40	
	SIF-61	3	1.59	1.60	1.61	3	1.40	1.42	1.44
m3	SIF-52	2	1.24	1.27	1.29	2	1.15	1.17	1.18
	SIF-61	4	1.25	1.29	1.32	2	1.19	1.20	1.20

Table 11. Measurements (mm) of the specimens of *Paraethomys meini* from SIF-61, SIF-79, SIF-413 and SIF-430.

Element	Locality	Length				Width			
		N	Min	Mean	Max.	N	Min.	Mean	Max.
M1	SIF-61	5	2.09	2.17	2.20	5	1.43	1.46	1.51
	SIF-79	2	2.12	2.13	2.13	3	1.38	1.44	1.48
	SIF-413	7	2.11	2.31	2.53	8	1.44	1.51	1.57
M2	SIF-61	7	1.50	1.56	1.63	3	1.36	1.44	1.50
	SIF-79	4	1.51	1.62	1.67	3	1.35	1.40	1.43
	SIF-413	16	1.50	1.59	1.68	14	1.34	1.42	1.51
	SIF-430	1		1.50		1		1.50	
M3	SIF-61	1		1.06		1		0.93	
	SIF-79	1		0.98		1		1.01	
	SIF-413	5	1.03	1.08	1.12	5	1.01	1.04	1.09
m1	SIF-61	5	1.96	2.02	2.16	5	1.17	1.23	1.31
	SIF-79	1		2.03		1		1.31	
	SIF-413	12	1.91	2.04	2.10	11	1.20	1.28	1.36
	SIF-430	1		1.95		1		1.27	
m2	SIF-61	9	1.39	1.47	1.61	9	1.24	1.32	1.40
	SIF-79	2	1.40	1.44	1.47	3	1.25	1.30	1.37
	SIF-413	15	1.43	1.50	1.57	14	1.28	1.36	1.41
m3	SIF-61	5	1.18	1.22	1.25	5	1.09	1.13	1.21
	SIF-413	3	1.19	1.26	1.33	4	1.14	1.18	1.22

Table 12. Measurements (mm) of the teeth of *Paraethomys* aff. *abaigari* from SIF-P.

Element	Length				Width			
	N	Min	Mean	Max.	N	Min.	Mean	Max.
M1	2	2.55	2.58	2.60	4	1.51	1.62	1.68
M2	6	1.61	1.74	1.87	3	1.49	1.60	1.73
M3	2	1.16	1.22	1.27	2	1.07	1.15	1.23
m1	2	2.30	2.33	2.35	5	1.37	1.47	1.55
m2	2	1.67	1.68	1.69	1		1.50	
m3	2	1.46	1.50	1.53	2	1.33	1.34	1.34

Table 13. Frequency of the different development stages for the longitudinal connections on the m1 and m2 of *Paraethomys* from the Sifón de Librilla section.

Species	Level	% Longitudinal spur on m1			% Longitudinal spur on m2			
		N	Reduced	Absent	N	Reduced	Absent	N
P. meini	SIF-61	8	50	50	12	66.6	33.3	4
P. meini	SIF-79	1	0	100	3	33.3	66.6	1
P. meini	SIF-413	17	70.59	19.41	18	44.44	55.56	16
P. meini	SIF-430	1	100	0				
P. aff. *abaigari*	SIF-P	6	100	0	3	66.6	33.3	5

Table 14. Frequency of the different development stages for the posterior spurs on t1 and t3 of the M1 and M2, and t9 of the M2 of *Paraethomys meini* from SIF-61, SIF-79, SIF-413 and SIF-430, and *Paraethomys* aff. *abaigari* from SIF-P.

Level	Spur on t1 (M1)			Spur on t3 (M1)			Spur on t1 (M2)			t9 (M2)		
	N	P	A	N	P	A	N	P	A	N	P	A
SIF-61	8	25	75	8	100	0	6	33.3	66.6	6	66.6	33.3
SIF-79	3	66.6	33.3	3	100	0	4	25	75	4	50	50
SIF-413	12	50	50	12	83.3	16.6	14	28.6	71.4	14	21.43	78.6
SIF-430							1	100	0	1	0	100
SIF-P	5	100	0	5	100	0	4	75	25	3	0	100

Notes: N = number of elements; P = present; A = absent.

Table 15. Measurements (mm) of the molars of *Debruijnimys* sp. from SIF-413.

Element	Length				Width			
	N	Min	Mean	Max.	N	Min.	Mean	Max.
M1					2	2.01	2.02	2.03
M2					1		1.86	
M3	1		1.21		1		1.01	
m1	1		2.94		3	1.83	1.85	1.87

Table 16. Measurements (mm) of the teeth of the genus *Eliomys* from the Sifón de Librilla section.

Species	Element	Locality	N	Length	N	Width
E. truci	P4	SIF-P	1	0.99	1	1.11
E. truci	M1	SIF-413	1	1.19	1	1.47
E. cf. *intermedius*	M1-2	SIF-P	1	1.34		
E. truci	M3	SIF-1	1	0.89	1	1.10
		SIF-61	1	0.96	1	1.30
E. truci	d4	SIF-P	1	1.15	1	0.97
E. truci	m1-2	SIF-1	1	1.22	1	1.16
		SIF-413	1	1.25	1	1.26
E. truci	m2	SIF-P	1	1.24		
E. truci	m3	SIF-P	1	1.18	1	1.35

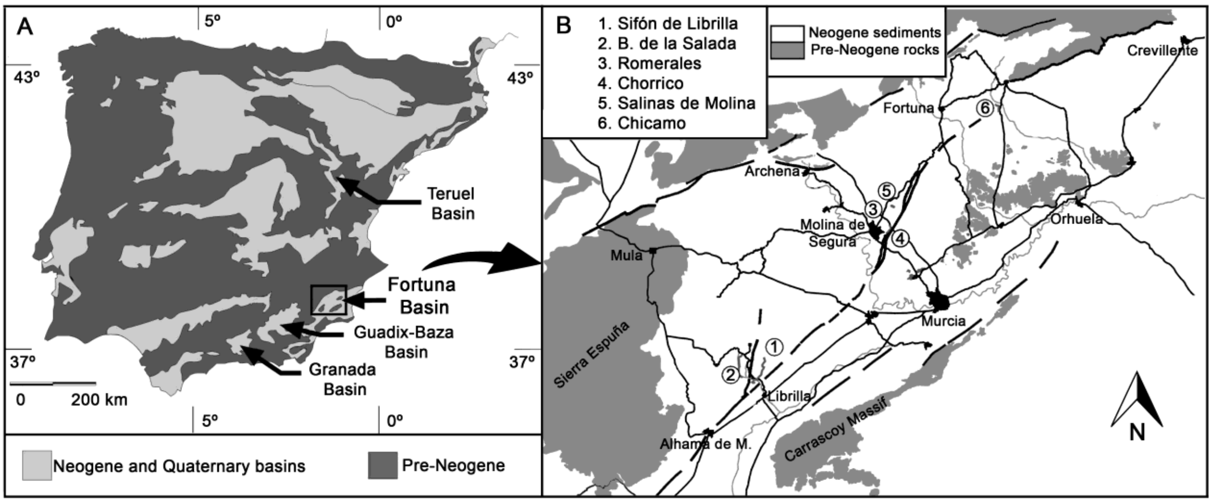

Figure 1. Geological and geographic setting of the Sifón de Librilla section. Notes: (A) Simplified map of the Iberian Peninsula, indicating the main Neogene and Quaternary basins referred to in the text. (B) Map of the Fortuna Basin indicating the location of Sifón de Librilla and other related sections.

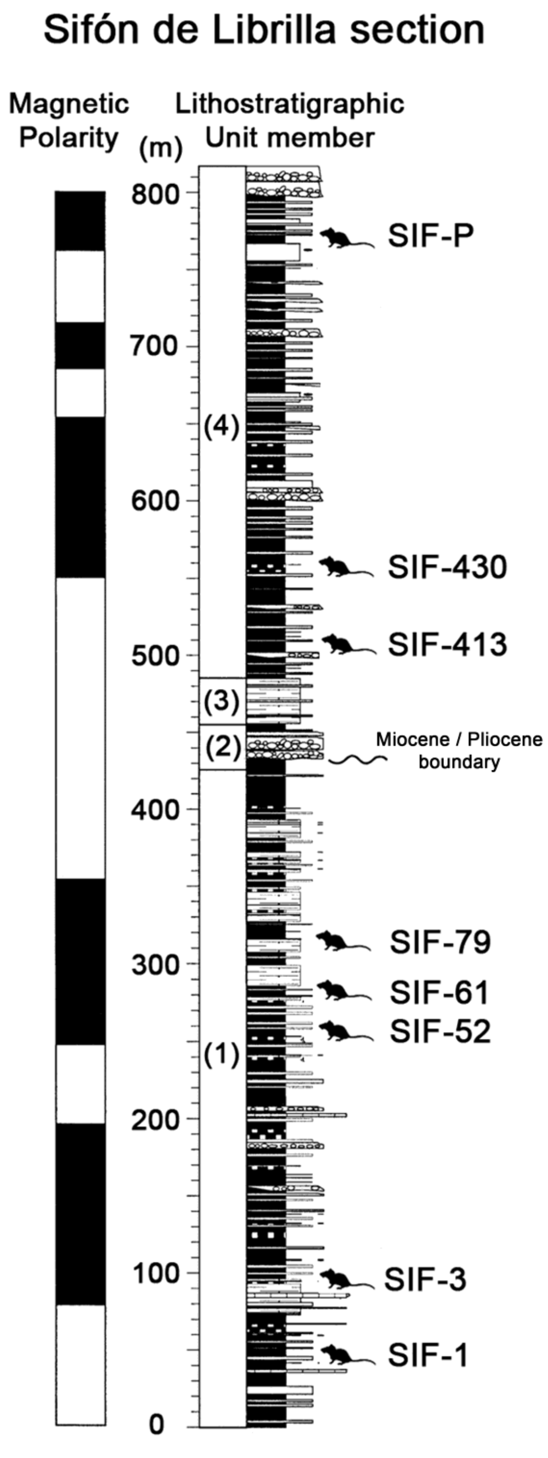

Figure 2. Lithostratigraphic column and magnetic polarity of the Sifón de Librilla section (Fortuna Basin), showing the position of the localities SIF-1, SIF-3, SIF-52, SIF-61, SIF-79, SIF-413, SIF-430 and SIF-P. Note: Modified from Garcés et al. (2001).

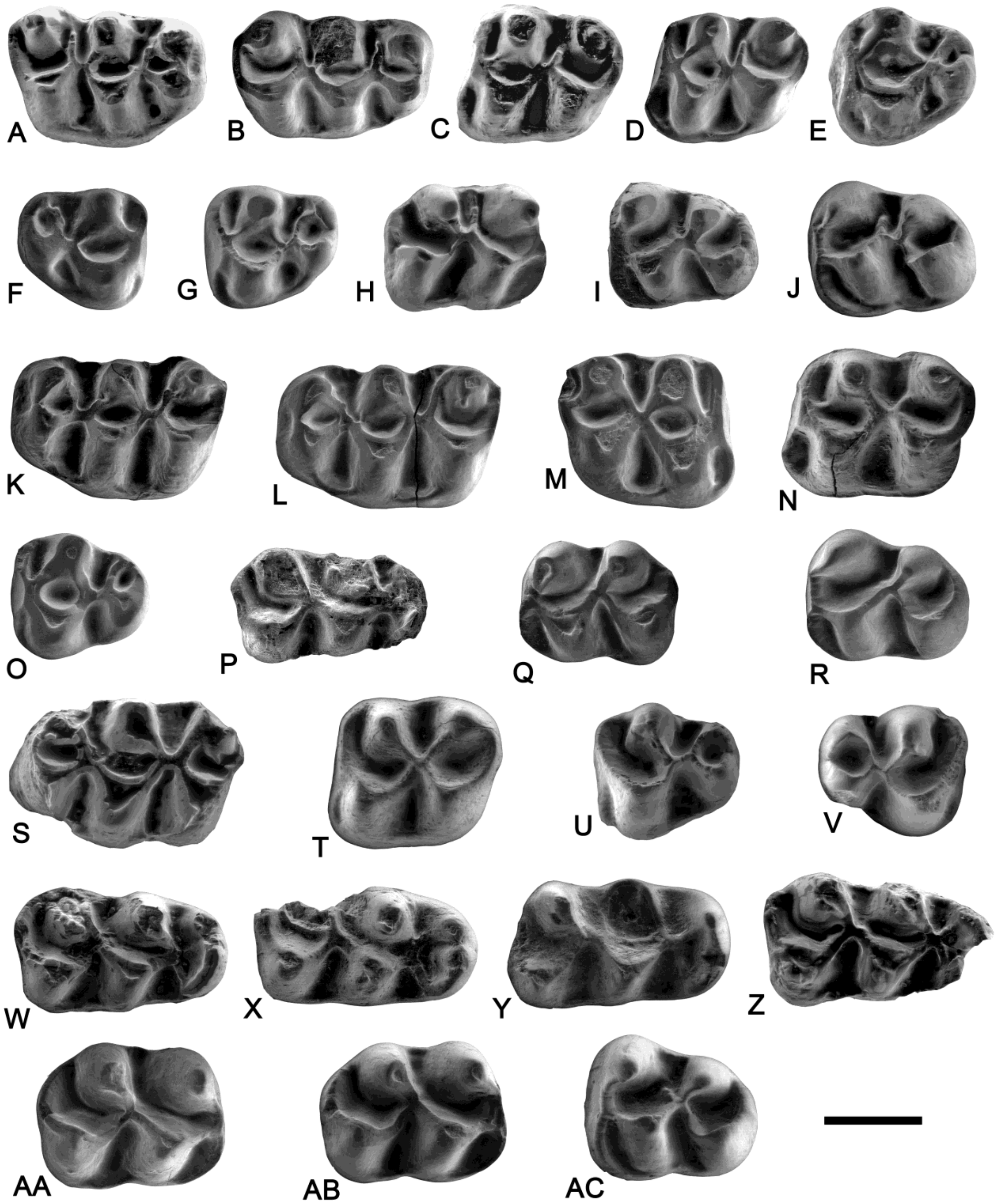

Figure 3. ESEM photographs of Cricetinae from the Sifón de Librilla section. *Necricetodon seseae*: (A) right M1, IPS-100772 (SIF-1); (B) right M1, IPS-100883 (SIF-3); (C) left M2, IPS-100774 (SIF-1); (D) left M2, IPS-100885 (SIF-3); (E) left M3, IPS-100778 (SIF-1); (F) right M3, IPS-100889 (SIF-3); (G) left M3, IPS-100886 (SIF-3); (H) right m2, IPS-100783 (SIF-1); (I) left m3, IPS-100788 (SIF-1); (J) left m3, IPS-100892 (SIF-3). *Apocricetus alberti*:

(K) left M1, IPS-101083 (SIF-61); (L) left M1, IPS-101085 (SIF-61); (M) right M2, IPS-101087 (SIF-61); (N) left M2, IPS-101137 (SIF-79); (O) left M3, IPS-101089 (SIF-61); (P) right m1, IPS-101092 (SIF-61); (Q) left m2, IPS-101097 (SIF-61); (R) left m3, IPS-101101 (SIF-61). *Apocricetus* aff. *barrierei*: (S) left M1, IPS-101376 (SIF-P); (T) left M2, IPS-101381 (SIF-P); (U) left M3, IPS-101390 (SIF-P); (V) right M3, IPS-101392 (SIF-P); (W) right m1, IPS-101276 (SIF-413); (X) right m1, IPS-101277 (SIF-413); (Y) right m1, IPS-101394 (SIF-P); (Z) right m1, IPS-101397 (SIF-P); (AA) right m2, IPS-101270 (SIF-413); (AB) right m2, IPS-101400 (SIF-P); (AC) left m3, IPS-101280 (SIF-413). Note: Scale bar equals 1mm.

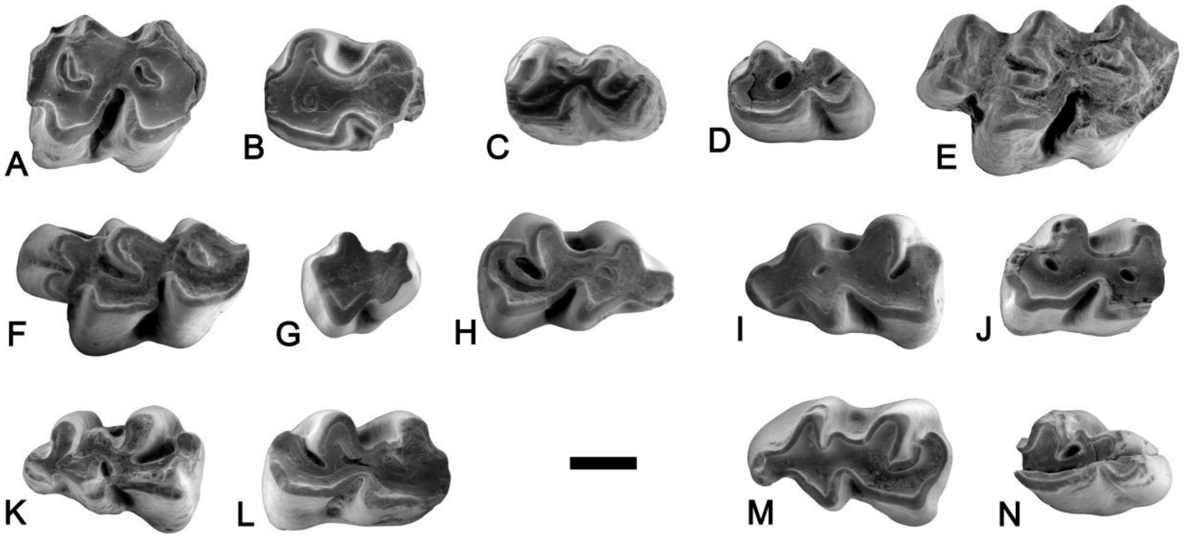

Figure 4. ESEM phographs of fossil Cricetodontinae from the Sifón de Librilla section *Hispanomys* cf. *adroveri*: (A) left M1, IPS-100893 (SIF-3); (B) left m2, IPS-100894 (SIF-3); (C) left m3, IPS-100791 (SIF-1); (D) right m3, IPS-100897 (SIF-3). *Hispanomys romeroi*: (E) left M1, IPS-100980 (SIF-61); (F) left M1, IPS-100982 (SIF-61); (G) left M3, IPS-101105 (SIF-61); (H) right m1, IPS-100984 (SIF-61); (I) left m1, IPS-100985 (SIF-61); (J) right m2, IPS-101110 (SIF-61); (K) right m2, IPS-101139 (SIF-79); (L) left m1, IPS-100949 (SIF-52). *Ruscinomys* cf. *lasallei*: (M) left m1, IPS-101284 (SIF-413); (N) left m3, IPS-101282 (SIF-413). Note: Scale bar equals 1mm.

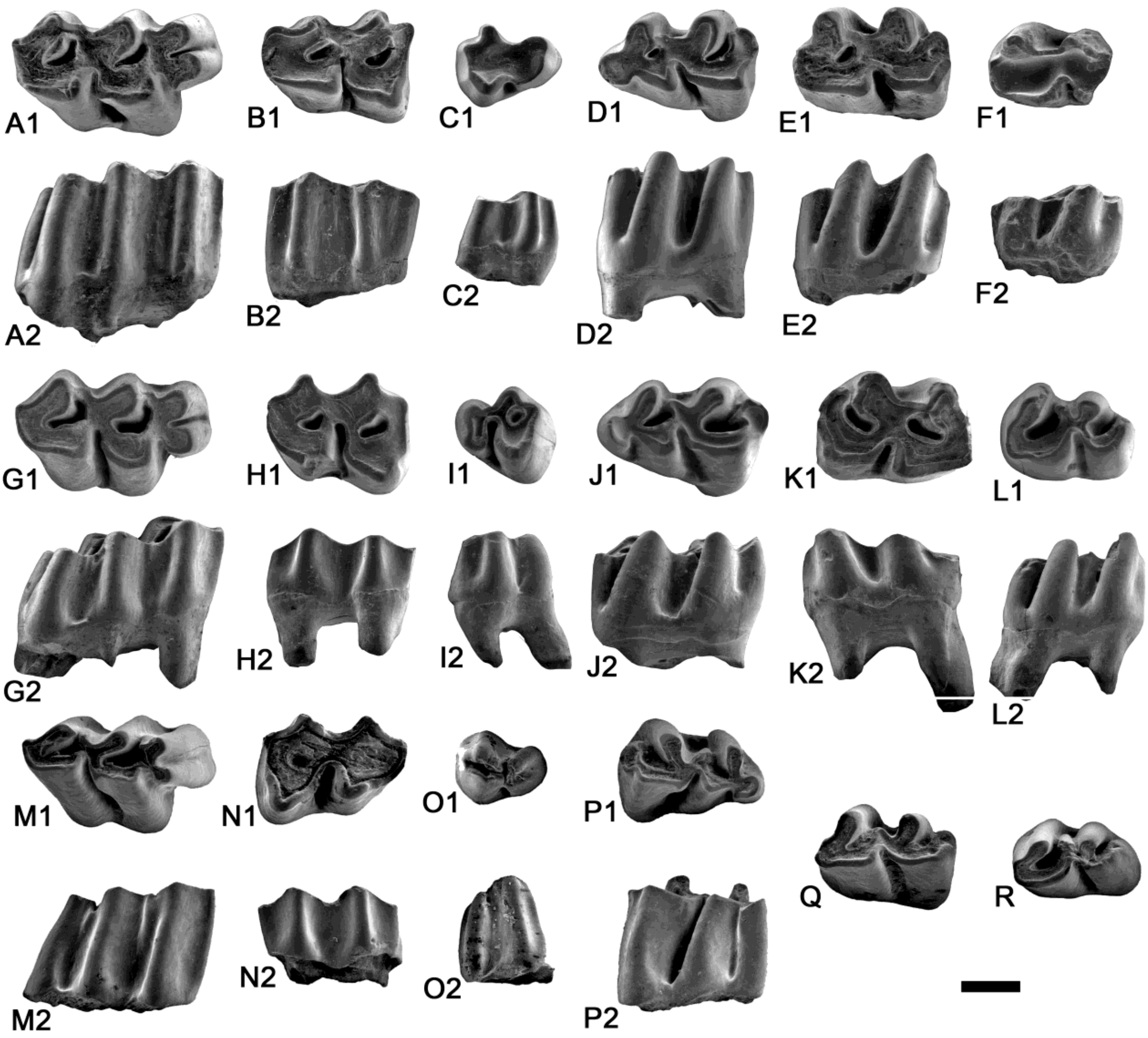

Figure 5. Fossil Cricetodontinae from the Sifón de Librilla, Casa del Acero, and Romerales. *Hispanomys romeroi*: (A) right M1 (Holotype), occlusal (1) and labial (2) views, IPS-101104 (SIF-61); (B) right M2, occlusal (1) and labial (2) views, IPS-100948 (SIF-52); (C) right M3, occlusal (1) and labial (2) views, IPS-101106 (SIF-61); (D) left m1, occlusal (1) and lingual (2) views, IPS-101107 (SIF-61); (E) left m2, occlusal (1) and lingual (2) views, IPS-100990 (SIF-61); (F) left m3, occlusal (1) and lingual (2) views, IPS-100953 (SIF-52). *Hispanomys adroveri* from Casa del Acero (unpublished material): (G) right M1, occlusal (1) and labial (2) views, IPHES-ACE/1-0; (H) right M2, occlusal (1) and labial (2) views, IPHES-ACE/1-10; (I) right M3, occlusal (1) and labial (2) views, IPHES-ACE/1-13; (J) left m1, occlusal (1) and lingual (2) views, IPHES-ACE/1-18; (K) right m2, occlusal (1) and lingual (2) views, IPHES-ACE/1-24; (L) left m3, occlusal (1) and lingual (2) views, IPHES-ACE/1-28. *Ruscinomys* aff. *gilvosi* from Romerales (modified from Piñero et al. 2017a): (M) right M1,

occlusal (1) and labial (2) views, IPS-91840; (N) left M2, occlusal (1) and labial (2) views, IPS-90625; (O) left M3, occlusal (1) and labial (2) views, IPS-90617; (P) right m1, occlusal (1) and labial (2) views, IPS-91862; (Q) left m2, IPS-91885; (R) left m3, IPS-91896. Note: Scale bar equals 1mm.

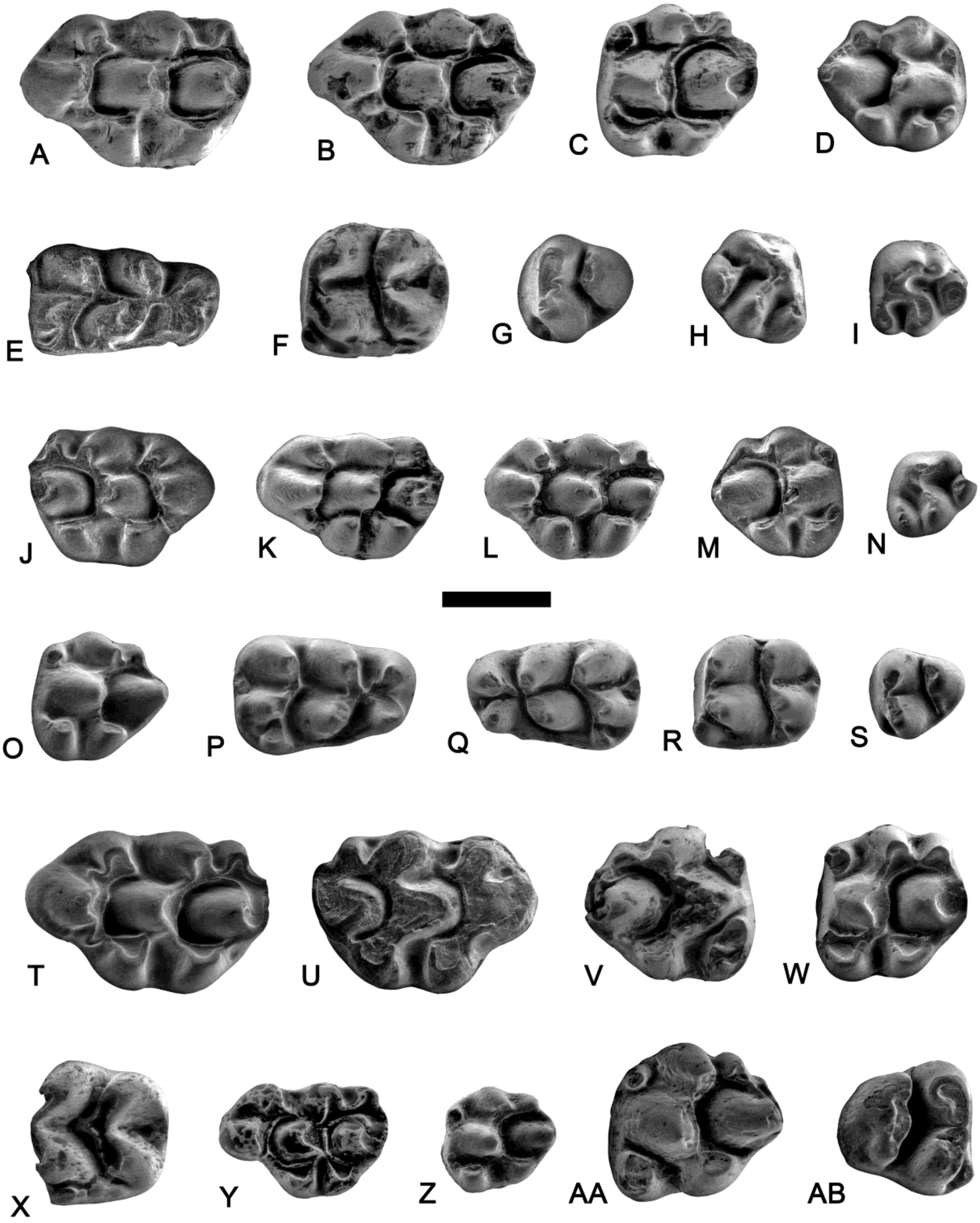

Figure 6. ESEM phographs of fossil murids from the Sifón de Librilla section. *Occitanomys adroveri*: (A) left M1, IPS-100695 (SIF-1); (B) left M1, IPS-100698 (SIF-1); (C) left M2, IPS-100720 (SIF-1); (D) right M2, IPS-100837 (SIF-3); (E) right m1, IPS-100737 (SIF-1); (F) left m2, IPS-100753 (SIF-1); (G) left m3, IPS-100764 (SIF-1); (H) right M3, IPS-100730 (SIF-1); (I) left M3, IPS-100728 (SIF-1). *Occitanomys alcalai*: (J) right M1, IPS-100855

(SIF-3); (K) left M1, IPS-101127 (SIF-79); (L) left M1, IPS-101162 (SIF-413); (M) right M2, IPS-100857 (SIF-3); (N) left M2, IPS-100928 (SIF-52); (O) left M3, IPS-100930 (SIF-52); (P) right m1, IPS-101030 (SIF-61); (Q) left m1, IPS-101163 (SIF-413); (R) left m2, IPS-101164 (SIF-413); (S) left m3, IPS-101166 (SIF-413). *Occitanomys brailloni*: (T) left M1, IPS-101167 (SIF-413); (U) right M1, IPS-101305 (SIF-P); (V) right M2, IPS-101170 (SIF-413); (W) left M2, IPS-101308 (SIF-P); (X) left m2, IPS-101171 (SIF-413). *Castillomys gracilis*: (Y) left M1, IPS-101310 (SIF-P); (Z) left M2, IPS-101311 (SIF-P). *Castromys* cf. *littoralis*: (AA) left M2, IPS-100962 (SIF-61); (AB) right m3, IPS-100963 (SIF-61). Note: Scale bar equals 1mm.

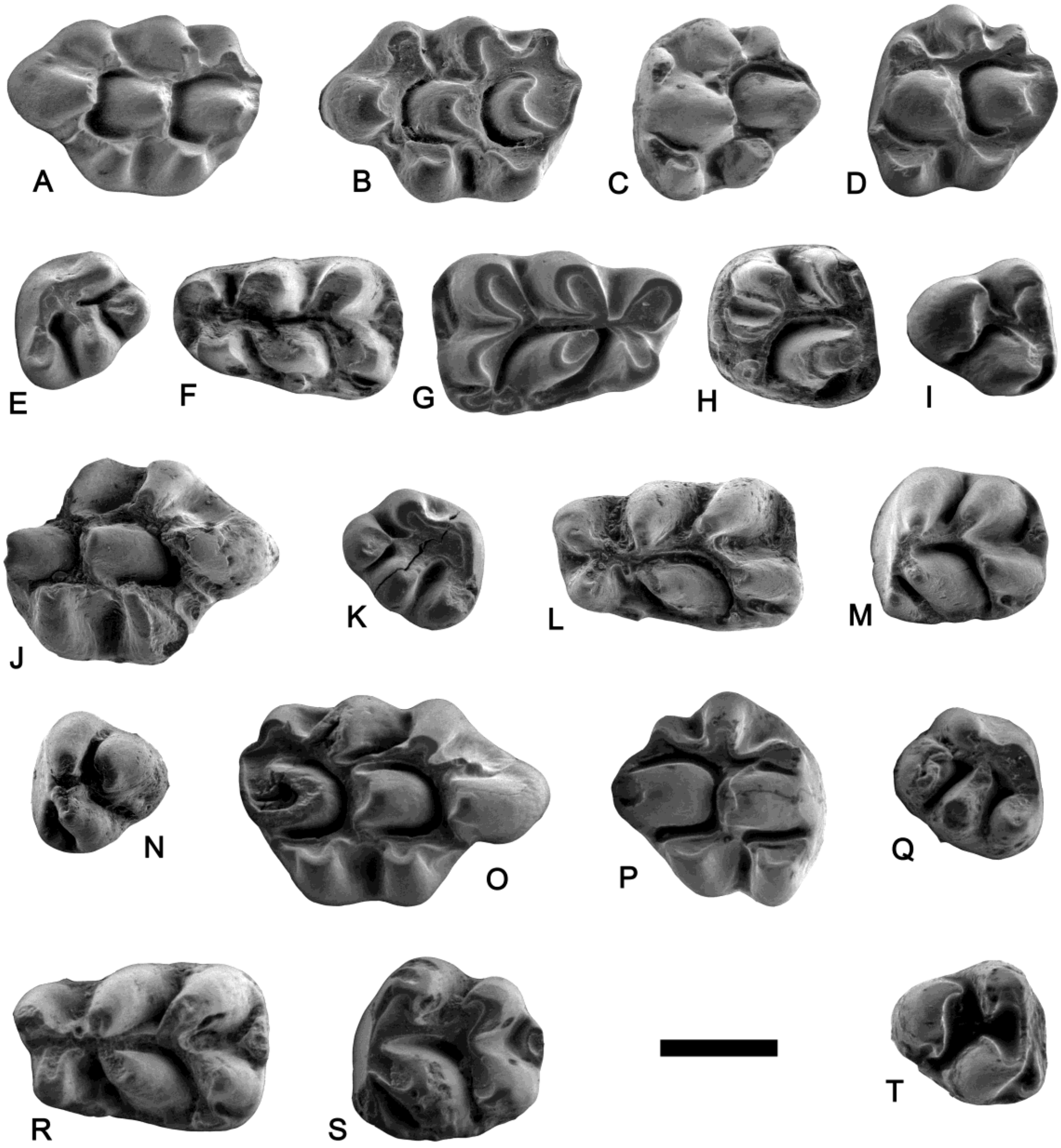

Figure 7. ESEM photographs of *Stephanomys* from the Sifón de Librilla section. *Stephanomys ramblensis*: (A) left M1, IPS-100805 (SIF-3); (B) left M1, IPS-100998 (SIF-61); (C) left M2, IPS-100687 (SIF-1); (D) left M2, IPS-101004 (SIF-61); (E) left M3, IPS-101011 (SIF-61); (F) left m1, IPS-100691 (SIF-1); (G) right m1, IPS-1010115 (SIF-61); (H) right m2, IPS-101126 (SIF-79); (I) right m3, IPS-101021 (SIF-61). *Stephanomys dubari*: (J) right M1, IPS-101140 (SIF-413); (K) right M3, IPS-101147 (SIF-413); (L) left m1, IPS-101153 (SIF-413); (M) left m2, IPS-101157 (SIF-413); (N) left m3, IPS-101161c (SIF-413). *Stephanomys cordii*: (O) right M1, IPS-101347 (SIF-P); (P) right M2, IPS-101354 (SIF-P); (Q) right M3, IPS-101359 (SIF-P); (R) left m1, IPS-101361 (SIF-P); (S) left m2, IPS-101367 (SIF-P); (T) right m3, IPS-101373 (SIF-P). Note: Scale bar equals 1mm.

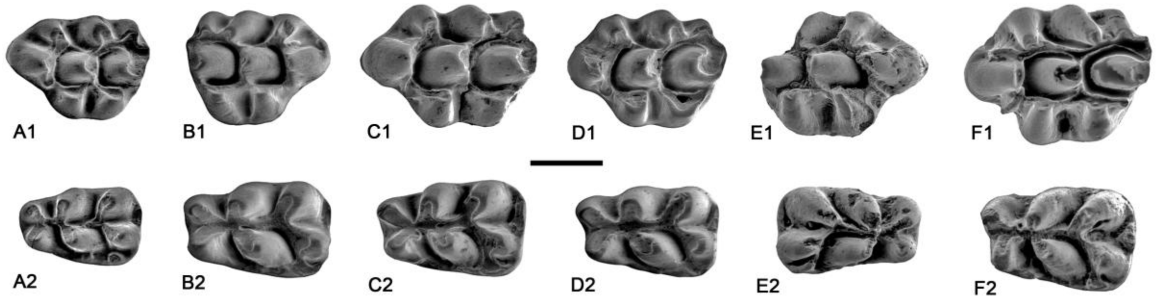

Figure 8. Evolution of the lineage *Occitanomys – Stephanomys* from the Fortuna Basin. (A) *O. adroveri* from Casa del Acero (unpublished material); (1) left M1, IPHES-ACE/2-51; (2) left m1 IPHES-ACE/2-64. (B) *S. ramblensis* from SIF-3; (1) right M1, IPS-100796; (2) left m1, IPS-100815; (C) *S. ramblensis* from SIF-52; (1) left M1, IPS-100899; (2) left m1, IPS-100912; (D) *S. ramblensis* from SIF-61; (1) left M1, IPS-100954; (2) left m1, IPS-100958; (E) *S. dubari* from SIF-413; (1) right M1, IPS-101140; (2) right m1, IPS-101149; (F) *S. cordii* from SIF-Pista; (1) left M1, IPS-101341; (2) left m1, IPS-101361. Scale bar equals 1 mm.

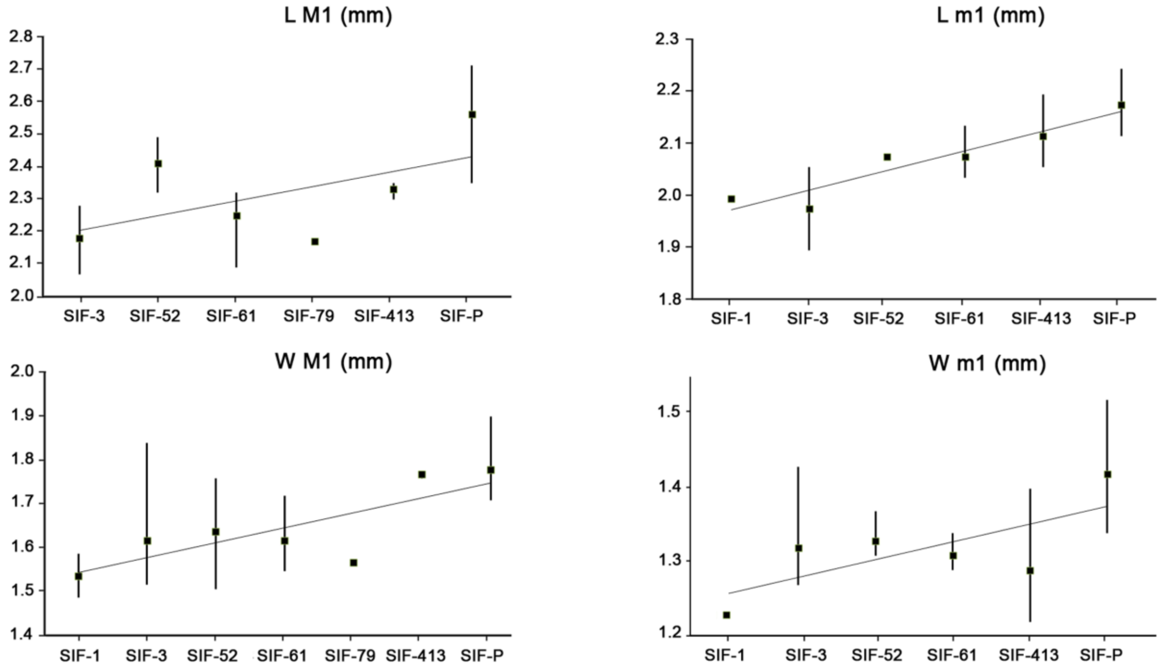

Figure 9. Ranges of variation and tendency lines of length and width of the upper and lower first molars of *Stephanomys ramblensis* from SIF-1, SIF-3, SIF-52, SIF-61 and SIF-79, *Stephanomys dubari* from SIF-413, and *Stephanomys cordii* from SIF-P. The squares represent the mean values.

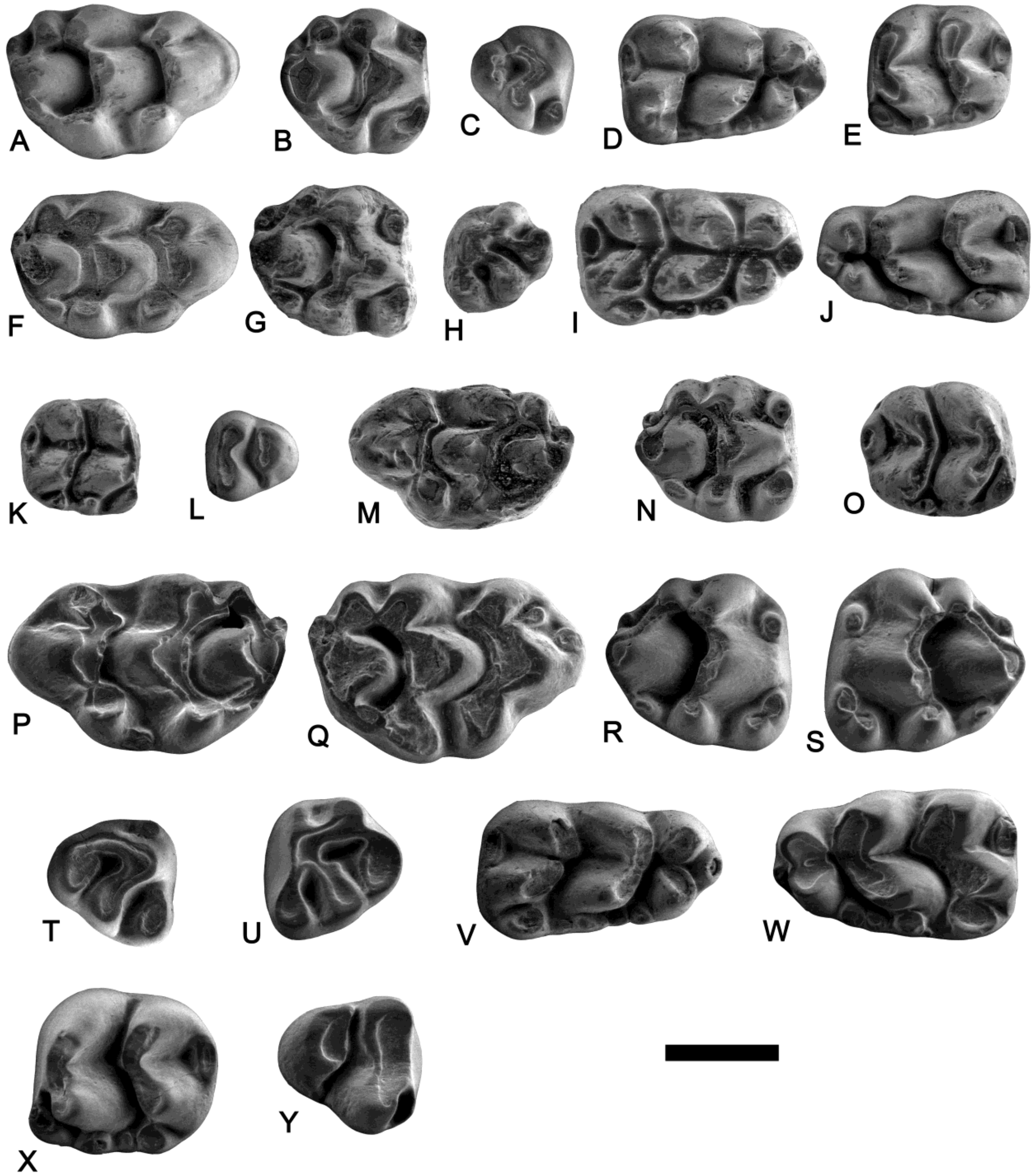

Figure 10. ESEM photographs of *Apodemus* from Casa del Acero (unpublished material) and Sifón de Librilla section. *Apodemus barbarae*: (A) right M1, IPHES-ACE/2-8; (B) right M2, IPHES-ACE/2-13; (C) right M3, IPHES-ACE/2-17; (D) right m1, IPHES-ACE/2-27; (E) left m2, IPHES-ACE/2-64. *Apodemus gudrunae*: (F) right M1, IPS-100875 (SIF-3); (G) right M2, IPS-94706 (SIF-1); (H) left M3, IPS-94707 (SIF-1); (I) right m1, IPS-94711 (SIF-1); (J) left m1, IPS-100878 (SIF-3); (K) right m2, IPS-100670 (SIF-1); (L) left m3, IPS-100675 (SIF-1). *Apodemus* cf. *gudrunae*: (M) left M1, IPS-101256 (SIF-413); (N) right M2, IPS-101259 (SIF-

413); (O) right m2, IPS-101266 (SIF-413). *Apodemus gorafensis*: (P) left M1, IPS-101036 (SIF-61); (Q) right M1, IPS-101037 (SIF-61); (R) right M2, IPS-100870 (SIF-3); (S) left M2, IPS-101039 (SIF-61); (T) right M3, IPS-100871 (SIF-3); (U) left M3, IPS-101041 (SIF-61); (V) right m1, IPS-100873 (SIF-3); (W) left m1, IPS-101043 (SIF-61); (X) left m2, IPS-101046 (SIF-61); (Y) right m3, IPS-101051 (SIF-61). Note: Scale bar equals 1mm.

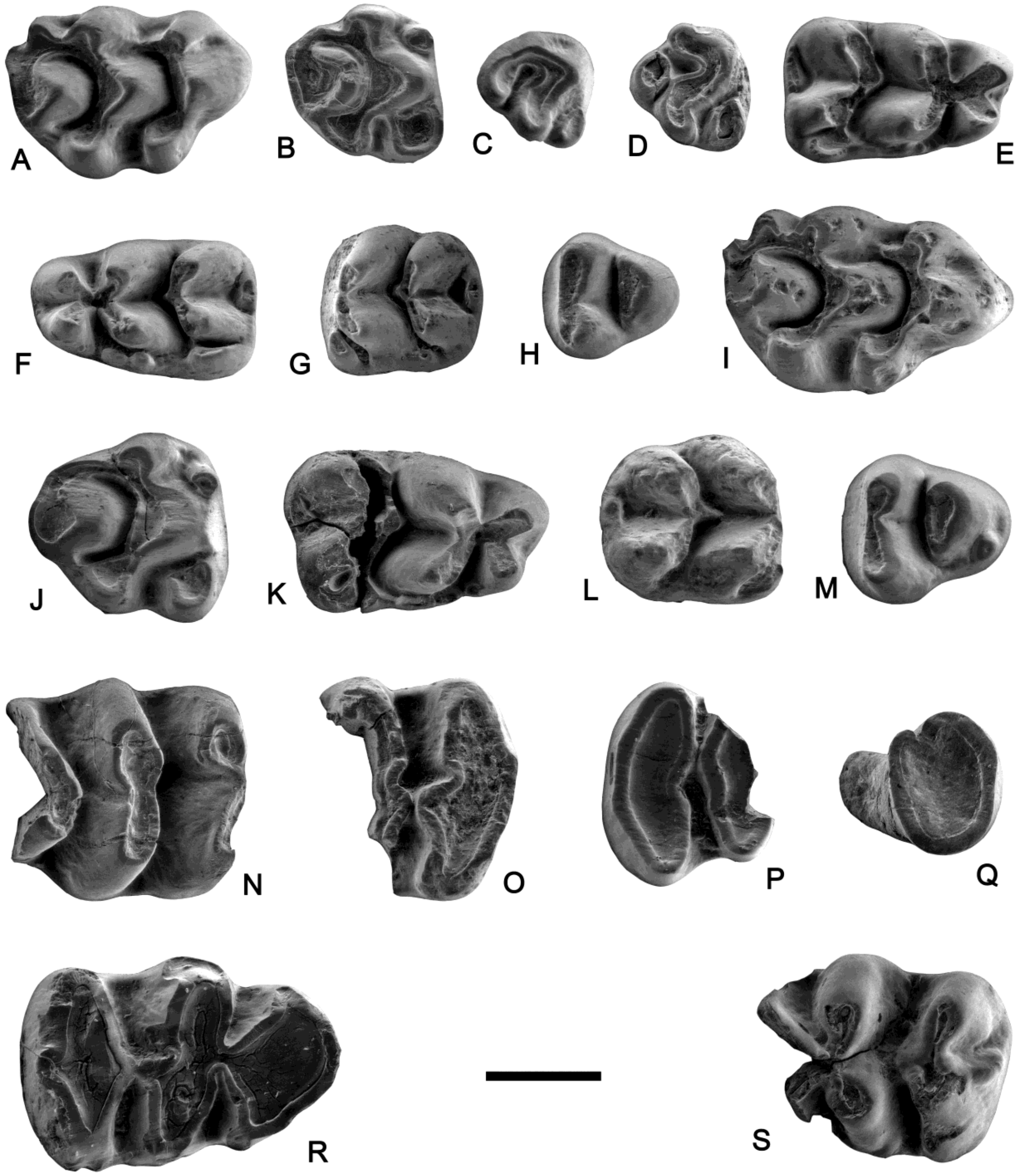

Figure 11. ESEM phographs of fossil murids from the Sifón de Librilla section. *Paraethomys meini*: (A) right M1, IPS-101058 (SIF-61); (B) right M2, IPS-101295 (SIF-430); (C) right M3, IPS-101069 (SIF-61); (D) right M3, IPS-101210 (SIF-413); (E) right m1, IPS-101064 (SIF-61); (F) left m1, IPS-101225 (SIF-413); (G) left m2, IPS-101240 (SIF-413); (H) left m3, IPS-101080 (SIF-61). *Paraethomys* aff. *abaigari*: (I) right M1, IPS-101312 (SIF-P); (J) right

M2, IPS-101317 (SIF-P); (K) right m1, IPS-101327 (SIF-P); (L) right m2, IPS-101336 (SIF-P); (M) left m3, IPS-101338 (SIF-P). *Debruijnimys* sp: (N) left M1, IPS-101286 (SIF-413); (O) left M1, IPS-101290 (SIF-413); (P) left M2, IPS-101291 (SIF-413); (Q) right M3, IPS-101289 (SIF-413); (R) right m1, IPS-101292 (SIF-413); (S) left m1, IPS-101287 (SIF-413). Note: Scale bar equals 1mm.

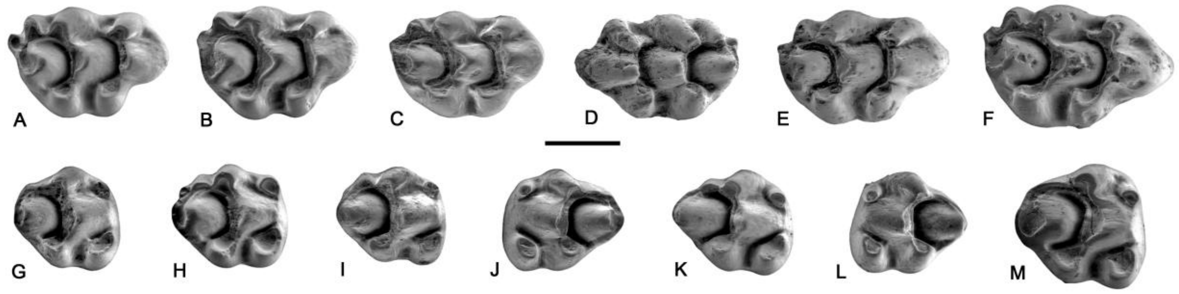

Figure 12. Morphological variability and evolution of M1 and M2 of the genus *Paraethomys* from the Sifón de Librilla section. *Paraethomys meini*: (A) right M1, IPS-101059 (SIF-61); (B) right M1, IPS-101058 (SIF-61); (C) right M1, IPS-101112 (SIF-79); (D) left M1, IPS-101184 (SIF-413); (E) right M1, IPS-101180 (SIF-413); (G) right M2, IPS-100968 (SIF-61); (H) right M2, IPS-101062 (SIF-61); (I) right M2, IPS-101116 (SIF-79); (J) left M2, IPS-101118 (SIF-79); (K) right M2, IPS-101208 (SIF-413); (L) left M2, IPS-101197 (SIF-413). *Paraethomys* aff. *abaigari*: (F) right M1, IPS-101312 (SIF-P); (M) right M2, IPS-101317 (SIF-P). Note: Scale bar equals 1mm.

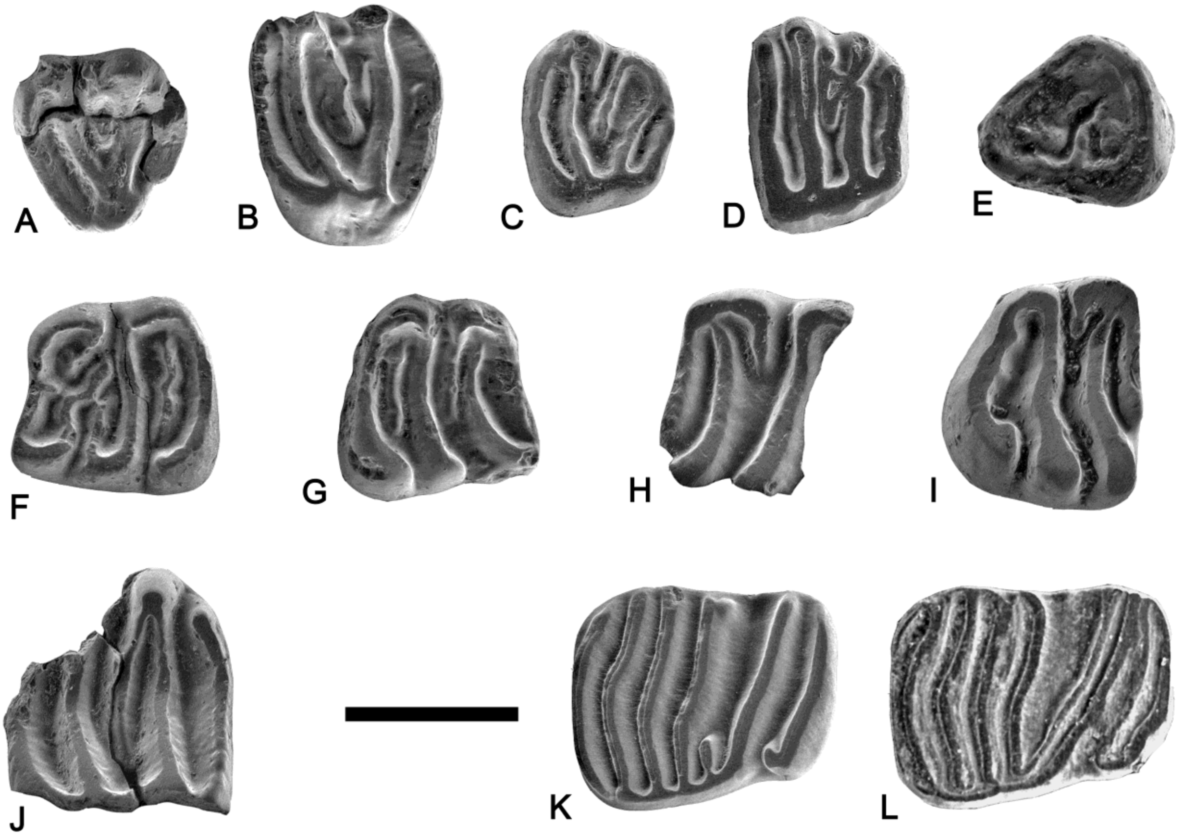

Figure 13. ESEM photographs of glirids from the Sifón de Librilla section. *Eliomys truci*: (A) left P4, IPS-101418 (SIF-P); (B) left M1, IPS-101293 (SIF-413); (C) left M3, IPS-100793 (SIF-1); (D) left M3, IPS-101111 (SIF-61); (E) left d4, IPS-101419 (SIF-P); (F) left m1-2, IPS-100794 (SIF-1); (G) right m1-2, IPS-101294 (SIF-413); (H) left m2, IPS-101416 (SIF-P); (I) right m3, IPS-101417 (SIF-P). *Eliomys* cf. *intermedius*: (J) right M1-2, IPS-101415 (SIF-P). *Muscardinus vireti*: (K) right M1, IPS-100882 (SIF-3); (L) right M1 (La Hornera). Note: Scale bar equals 1 mm.

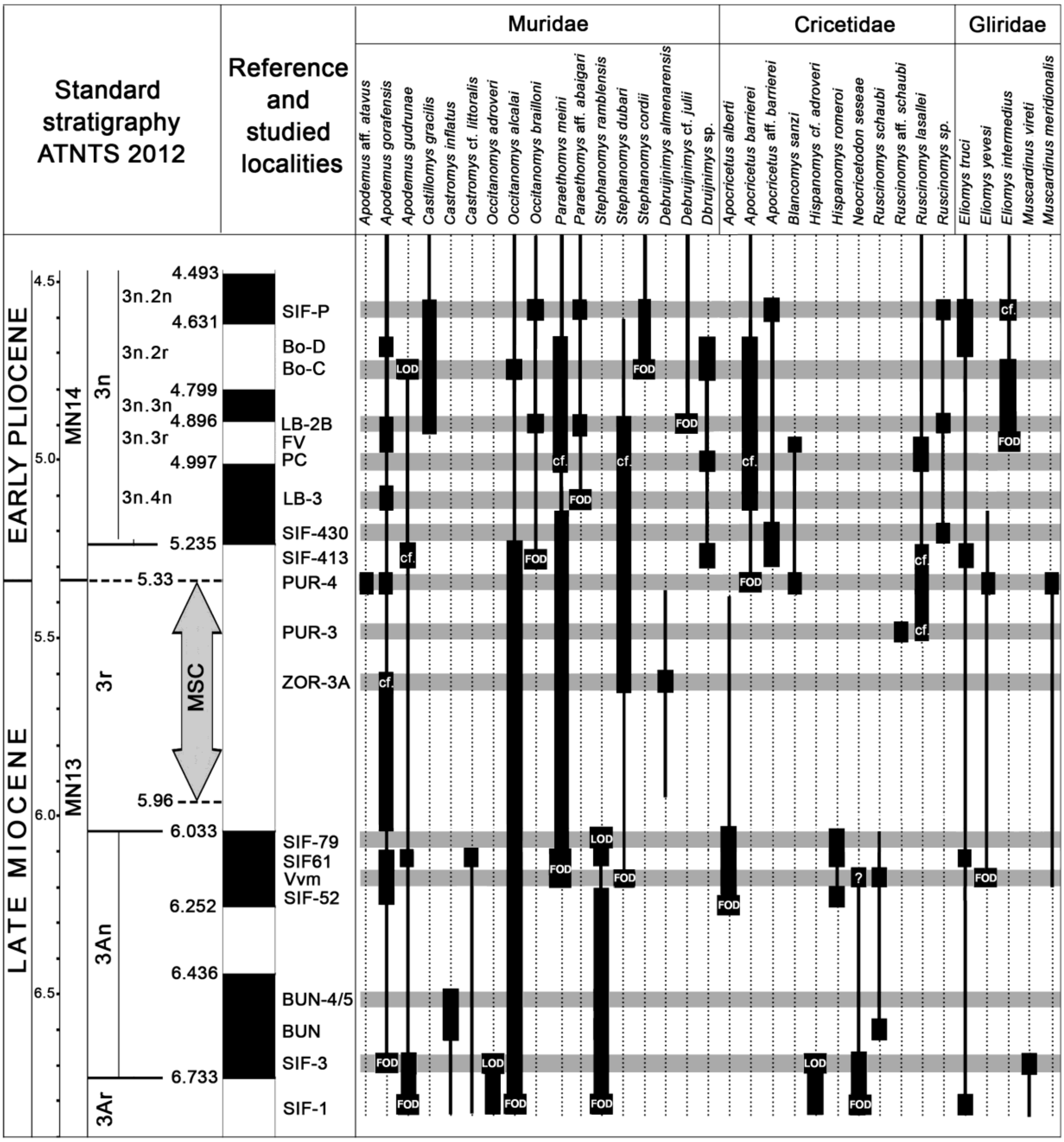

Figure 14. Chronostratigraphic framework of the record of different rodent species from the Sifón de Librilla section, showing their distribution supported by other magnetostratigraphically dated sites. Abbreviations: BUN, Búnker de Valdecebro (Van Dam et al. 2001); PUR, Purcal (García-Alix et al. 2008c; Martín Suárez et al. 1998); ZOR, Zorreras (Martín Suárez et al. 2000); Vvm, Venta del Moro (Montoya et al. 2006; Gibert et al. 2013; Mansino et al. 2014, 2017a); PC, Puerto de la Cadena (Piñero et al. 2017b); FV, Fuente del Viso (Opdyke et al. 1997); LB, La Bullana (Mansino et al. 2015b).

VII. LA FAUNA DE VERTEBRADOS CONTINENTALES DEL PLIOCENO INFERIOR DEL PUERTO DE LA CADENA (SE ESPAÑA) Y SU RELACIÓN CON LA CORRELACIÓN MARINO-CONTINENTAL DEL NEÓGENO SUPERIOR DE LAS BÉTICAS ORIENTALES

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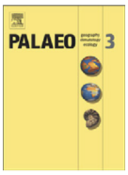

Early Pliocene continental vertebrate Fauna at Puerto de la Cadena (SE Spain) and its bearing on the marine-continental correlation of the Late Neogene of Eastern Betics

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ABSTRACT

In this paper, we synthesize sedimentological, magnetostratigraphic and paleontological data from the continental vertebrate site of Puerto de la Cadena (Murcia, SE Spain), in order to clarify its age. The study site is located on the northern edge of the Carrascoy mountain range, in the upper part of the Cigarrón Unit. The end-Messinian discontinuity has been detected at the base of this unit, which indicates it has an early Pliocene age. Abundant remains of small and large vertebrates, including rodents, lagomorphs, primates, carnivorans, perissodactyls, artiodactyls, proboscideans, testudines, squamats, and crocodiles, have been found in this area. Some of these elements are of African origin, such as *Debruijnimys* sp., *Macaca* sp., and *Sivatherium* cf. *hendeyi*, and their presence is related to the Messinian Salinity Crisis. In addition, remains found at this site verify the persistence of Crocodylia in the European record beyond the late Miocene. The association includes typical elements of the early Ruscinian terrestrial record (MN14), like *Apocricetus* cf. *barrierei*, *Sivatherium*, *Gazella* aff. *baturra*, and *Hipparion fissurae*. The Puerto de la Cadena site is located in a reversed geomagnetic chron that has been correlated with C3n.3r (from 4.997 to 4.896 Ma). According to this correlation, the MN13/MN14 boundary has a minimum age of 4.9 Ma.

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1. Introduction

The importance of the newly discovered site of Puerto de la Cadena lies in its great abundance and diversity of fossil vertebrate remains, as the large mammal association is novel for the Spanish fossil record of the Miocene/Pliocene boundary. In fact, contemporary large-vertebrate sites are scarce in the Iberian Peninsula, which makes Puerto de la Cadena a reference locality.

The area of Puerto de la Cadena has a rich paleontological record, known since the early 1970s (Montenat and Crusafont, 1970; Montenat, 1973; Mein et al., 1973). The sites of La Alberca and La Paloma stand out among the sites with continental vertebrate remains as they were identified during the first geological study in the area (Montenat and Crusafont, 1970). Aguirre et al. (1974) and de Bruijn et al. (1975) established a late Miocene age for these localities by correlating them to the site of El Arquillo (Teruel, Spain). La Alberca yielded an important fossil assemblage, being Montenat (1973) the first to report its faunal list, which has been subsequently revised and updated (Morales, 1984; López Martínez, 1989; Freudenthal et al., 1998; Pérez-García et al., 2011): *Cricetus kormosi* (=*Apocricetus alberti*), *Stephanomys medius* (=*Stephanomys dubari*, *Stephanomys cordii*), *Ruscinomys lasallei*, *Paraethomys miocaenicus* (=*Paraethomys meini*), *Castillomys* sp., *Eliomys* sp., *Hispanolagus crusafonti* (=*Trischizolagus crusafonti*), *Prolagus michauxi*, *Percrocuta minor*, *Plioviverrops guerini*, *Hipparion concudense*, *Dicerorhinus schleiermacheri*, *Birgerbohlinia* sp., Cervidae indet., Bovidae indet., *Titanochelon* cf. *bolivari*, and Trionychinae indet. The La Paloma site has only yielded two taxa (Montenat and Crusafont, 1970): Cervidae indet., and *Decennatherium pachecoi*. Based on the faunal assemblage, these localities were correlated with the MN13 unit (Aguirre et al., 1976; Morales, 1984), and more recently with the Ventian land mammal age (latest Miocene/earliest Pliocene; Morales et al., 2013).

Besides the giant tortoise shell from the locality of La Alberca (here reassigned to *Titanochelon* sp.), additional specimens have been recovered from the vicinity of Puerto de la Cadena. This is the case of the unpublished, more-incomplete shell remains found at the Autovía site (Murelaga et al., 2007), which could belong to the same taxon. Another example is the carapace of an adult specimen from Barranco del Cigarrón (located to the west of the Puerto de la Cadena site), which Mancheño et al. (2001) reported and preliminary assigned to '*Testudo*' *bolivari*. This taxonomic ascription is not supported here, thus we consider the presence of a second synchronous testudinid from Barranco del Cigarrón (see Supplementary information).

From the stratigraphical and sedimentological points of view, the fossil remains recovered from the Puerto de la Cadena area come from roughly equivalent levels to those of Autovía and Barranco del Cigarrón, and were deposited under similar depositional environments (Murelaga et al., 2007; Romero and Fierro, 2010). Even though the area of Puerto de la Cadena is very rich in continental vertebrate remains, none of these outcrops has been hitherto accurately dated. The aim of the present paper is to provide taxonomic attributions for the vertebrate fauna recovered from Puerto de la Cadena, as well as to accurately date this site based on a synthesis of geological, magnetostratigraphic and paleontological data.

2. Geological setting

The Neogene outcrop of Puerto de la Cadena (Murcia Region, SE Spain) is located 8 km SSW of the town of Murcia, and 2.5 km south of El Palmar, on the northern flank of the Carrascoy range mountain (Fig. 1). The location coordinates are 37° 55′ 9″ N, 1° 9′ 41″ W, with an altitude of 160 m AMSL. This site was discovered in 2008 as a result of the construction of the MU-31 motorway in the vicinity of Puerto de la Cadena, which is an open natural pass between the mountains of Carrascoy and Cresta del Gallo, connecting the cities of Murcia and Cartagena.

Some geological units with great lateral continuity are located in Puerto de la Cadena area, and their position is influenced by the neotectonic activity. In 2008, the construction works of the MU-31 motorway began to affect some of these units, which led to the recovery of large vertebrate remains.

2.1. Regional context

One of the best sites for describing the Neogene stratigraphic record on the northern side of the Carrascoy mountain range is Barranco del Cigarrón, where we have documented a stratigraphic succession that includes at least five lithostratigraphic units (Figs. 1–2). The lower three units are clearly recognizable and equivalent to those described in the Bajo Segura Basin: Columbares Formation, Torremendo Formation and La Virgen Formation (Montenat, 1990; Soria et al., 2008). The two uppermost units, identified here as Cigarrón Unit and La Paloma Unit, have not been previously described.

The fossiliferous outcrop of Puerto de la Cadena is located on the upper part of the Cigarrón Unit, which might be the lateral equivalent to the Rojales and Variegated Marl formations of Montenat (1977), both early Pliocene in age (Soria et al., 2008). On the north side of the Carrascoy range, Montenat (1977) described these units as composed of marls and gray calcareous sands, with conglomeratic levels, cross stratification and reactivation surfaces. He further reported the presence of bone debris in yellow sandy outcrops (such as at the La Alberca and La Paloma paleontological sites).

The lower stratigraphic boundary of the Cigarrón Unit, which hosts the Puerto de la Cadena site in the upper part, corresponds to a surface of marked erosion. This surface is present in both the La Virgen Fm. and Torremendo Fm. (see geological map in Fig. 1). This stratigraphic discontinuity is immediately overlain with sands and sandy marls, which include large-sized clasts bored by lithobiont bivalves and abundant shells of small ostreids similar to those of the genus *Pycnodonte*. The marls are finely laminated and contain a diversified microfossil assemblage, represented by foraminiferans, ostracodes bryozoans, bivalves, carbonate sponge spicules, and sea urchin spicules. All the macro and micropaleontological data indicate that sedimentation of the Cigarrón Unit began under normal salinity marine conditions in a shallow water depositional environment, and a subsequent transgressive event can be recognized at the top of La Virgen Fm. This transgressive event is recorded in the same way in numerous places in the Bajo Segura Basin, coinciding with the beginning of the Pliocene (Corbí and Soria, 2016). This implies that the erosive surface documented at the base of the Cigarrón Unit corresponds to the end-Messinian discontinuity (Soria et al., 2005, 2008).

2.2. Sedimentary record at the fossil site

The Cigarrón Unit at the Puerto de la Cadena site is represented by a sand and lutite alternating succession (Fig. 2). The sandy facies association is characterized by coarse sediments (mainly sands, but also microconglomerates and conglomerates), that are mainly organized in sets of trough and planar cross-stratification. These sets have a thickness of between a few centimeters and a meter, and most of them have an erosive base that exhibits a basal lag with intraformational mud clasts, fragmentary bones and plant fossil remains. They fine upwards, with frequent reactivation surfaces.

The macrovertebrate fossil remains are mainly located in the conglomeratic layers of the sands or in the basal lag of the sedimentary sets. The sand components are medium-sized to coarse siliciclastic grains with very little matrix and no cement. Cross-bedding in the sedimentary sets exhibits internal lamina that are variably inclined, from quasi-horizontal to 30°, and in most cases points towards N55°E.

The lutitic intercalations display different features. Some of them are thick lutitic intercalations (metric scale) with a concave base and a planar top. Bioturbation frequently occurs at the top of these bodies,

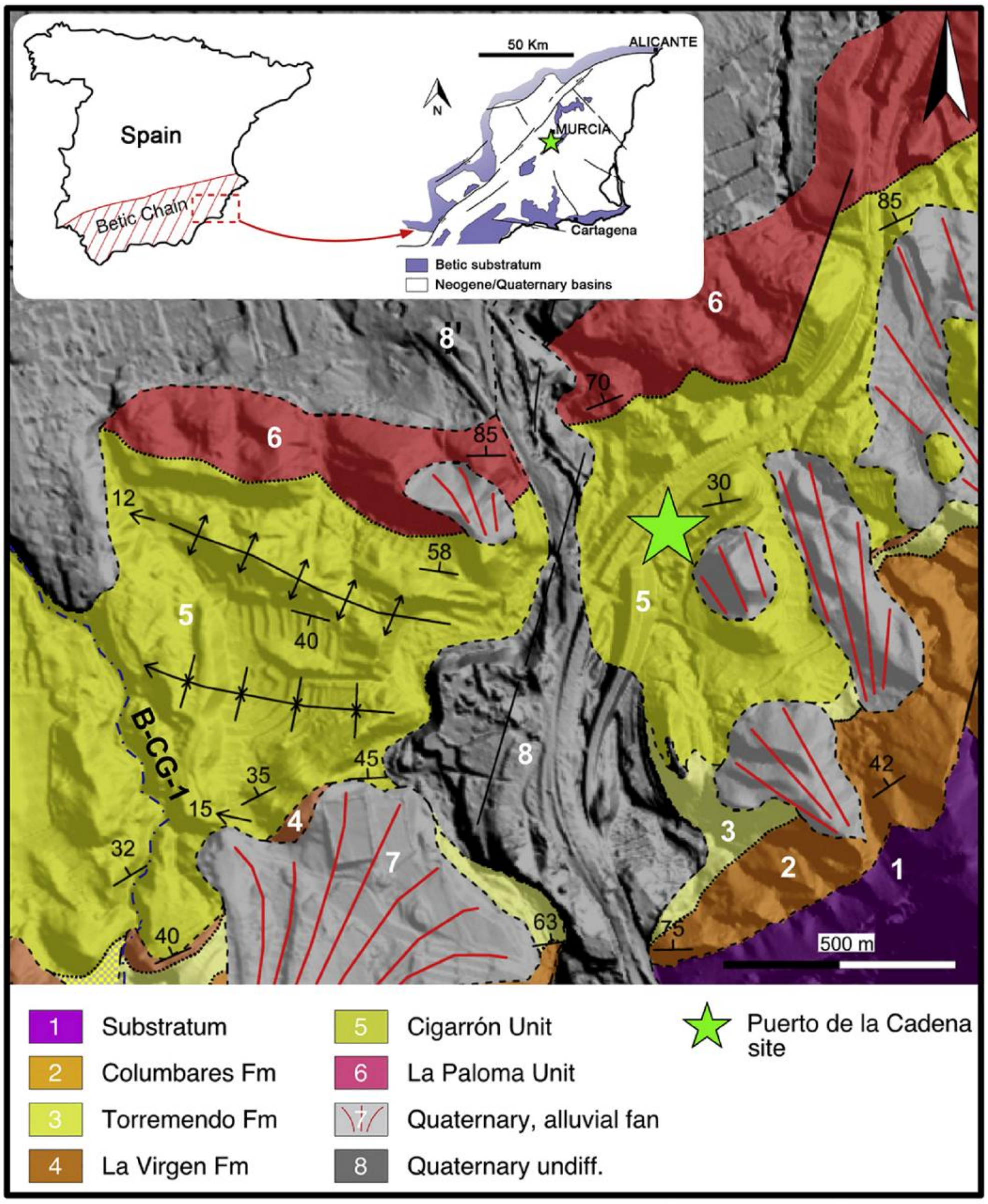

Fig. 1. Geographical and geological setting of the Puerto de la Cadena site.

consisting of 5–7 cm long (vertical development) traces with a characteristic U-shape and circular cross-section of about 0.5 cm (*Arenicolites* isp.; Simo and Olsavsky, 2007). In contrast, other thinner (centimetric to metric) lutitic intercalations have an irregular morphology. Most of the micromammal remains (about 5% of the total fossil remains) were obtained from the latter lutitic levels.

2.3. Geological interpretation

Mancheño et al. (2001) provided an interpretation of the depositional context for a tortoise carapace found in geological units similar to those described above, and concluded that fluvial transport would have brought the carapace to the sea. However, stratigraphical and sedimentological information from the different subunits at the top of the Cigarrón Unit leads us to favor a continental depositional context related to fluvial systems near the coast.

We agree with Mancheño et al. (2001) about the fluvial context for the upper part of the Cigarron Unit, where the Puerto de la Cadena site is located. Sand and gravel beds with unidirectional cross-stratification correspond to channels through which dunes and megaripples migrate. The fluctuating flow regime causes the frequent reactivation of surfaces that separate the sets of cross-stratification. The lutitic interbeds between sandy bodies represent floodplain deposits of the fluvial system, dominated by channel overbank processes. The presence of micromammal fossils in the lutites indicates that there were episodes of vegetation development. The inferred depositional context for the

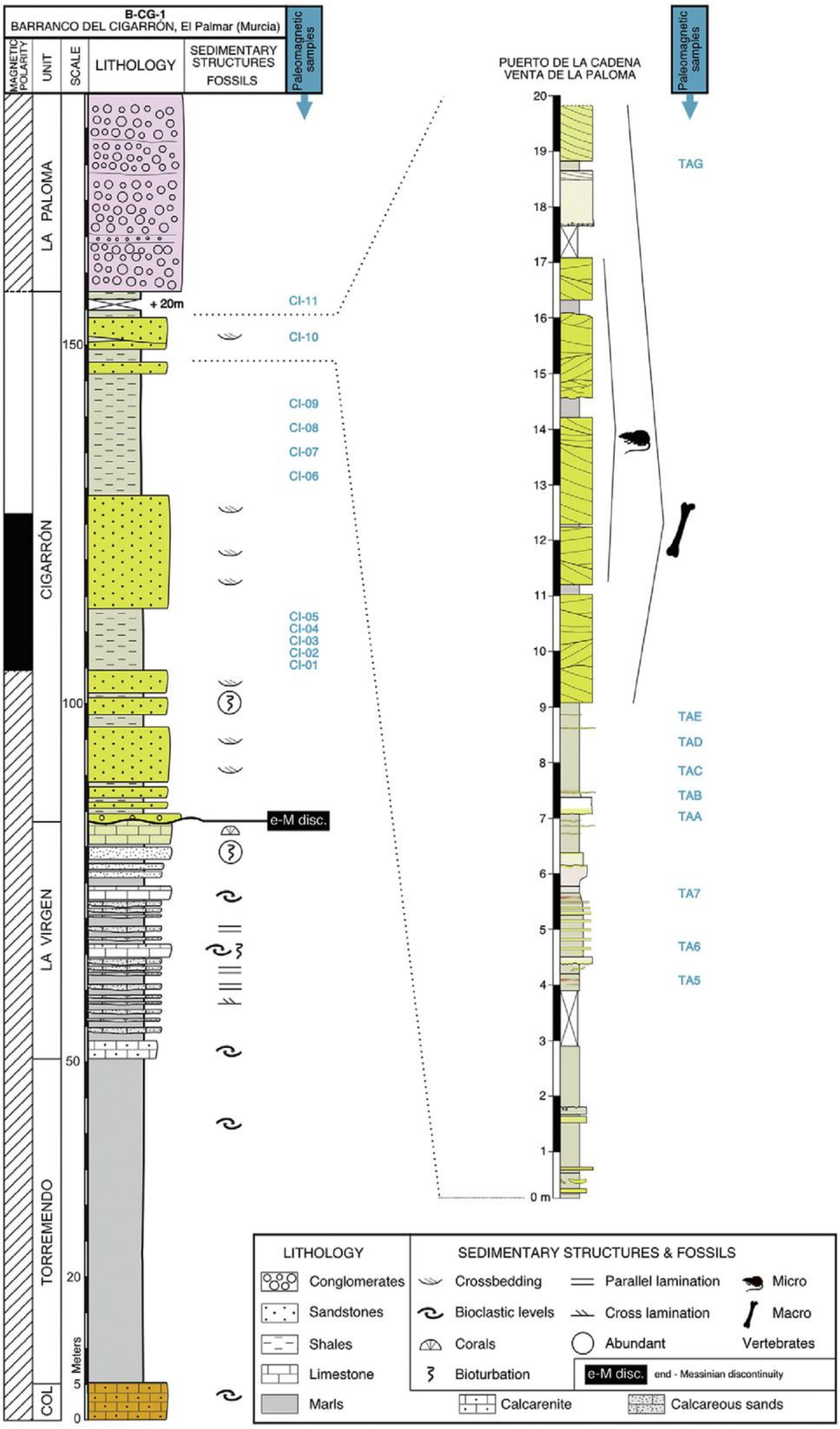

Fig. 2. Stratigraphic log on Barranco del Cigarrón with detailed of the Puerto de la Cadena paleontological site.

Puerto de la Cadena site shows certain similarities to the fluvial system described for the Rojales micromammal site (early Pliocene) located in the Bajo Segura Basin (Soria et al., 1996). In this case, as in the Puerto de la Cadena, microfossils are concentrated in vegetated areas of the floodplain.

2.4. The age of the Cigarrón Unit

The basal marine sediments of the Cigarrón Unit contain a varied assemblage of foraminifera in which benthic forms dominate (ca. 80%) over planktonic forms. The benthic foraminifera association includes the genera *Ammonia*, *Amphicoryna*, *Biasterigerina*, *Bigenerina*, *Bolivina*, *Bulimina*, *Cibicides*, *Elphidium*, *Fursenkoina*, *Globulina*, *Nonion*, *Pullenia*, *Reussella*, *Siphonina*, *Textularia*, and *Trifarina*. The dominant planktonic association includes *Globigerinoides extremus*, *Globigerinoides obliquus*, *Globigerinoides trilobus*, *Neogloboquadrina* spp., *Globorotalia scitula*, *Globigerina bulloides*, *Globoturborotalita* spp., and *Orbulina universa*. This marine microfossil biofacies is similar to that of the transgressive deposits at the base of the Pliocene Unit (P Unit; Soria et al., 2005) in the Bajo Segura Basin. This implies that the two units are correlative and that the underlying erosive surface corresponds to the end-Messinian discontinuity described by Soria et al. (2005). More specifically, there are four significant features at the beginning of the Pliocene Unit from the Bajo Segura Basin that coincide with those in the Cigarrón Unit: (a) abundant ostreids (*Pycnodonte* sp.) and clasts bored by lithobionts (Montenat, 1990; Soria et al., 2005; Caracuel et al., 2011); (b) prevalence of benthic foraminiferans (70–90%) over planktonic ones (Corbí, 2010); (c) abundant and diversified content of benthic foraminiferans, most of them represented by the genera *Ammonia*, *Bolivina*, *Bulimina*, *Cibicides*, *Elphidium*, *Nonion*, and *Textularia* (Corbí et al., 2016); and (d) an association of normal-sized planktonic foraminiferans, typical of oligotrophic warm water, dominated by *Globigerinoides* (mainly *G. trilobus* and *G. obliquus/extremus*; Corbí et al., 2016).

Assigning the Cigarrón Unit to the Pliocene implies a post-MSC (Messinian Salinity Crisis) sedimentation, i.e., it occurred after the Mediterranean flooded with normal marine water from the Atlantic Ocean. In this basin, under high-level sea conditions, the Mediterranean margins were progressively filled with sediments, leading to regressive or shallowing sequences (Caracuel et al., 2004, 2009; Soria et al., 2005). The Cigarrón Unit represents one of these sequences, and displays an evolution from shallow marine to continental environments over time. The latter are represented by fluvial systems with channels and floodplain development, which is the depositional context in which the sediments of the Puerto de la Cadena site were accumulated.

3. Material and methods

Systematic excavations were carried out at the Puerto de la Cadena site in 2009, 2010 and 2011. They yielded about 2000 well-preserved fossil remains of a diverse fauna of continental vertebrates (Figs. 5–9). Large amounts of sediment were also screen-washed using superimposed 4.0, 1.0 and 0.5 mm mesh screens. The recovered fossils represent at least 26 species and are currently housed at the Museo Arqueológico de Murcia (MAM; Murcia, Spain).

In this work, we update the systematic of the vertebrate taxa found so far in the early Pliocene levels of the Puerto de la Cadena area. We both review previously found remains and analyze and discuss recently found material (see Supplementary information and Table 1).

Measurements of the small mammal teeth were taken on the occlusal plane of the molars with the software DinoCapture 2.0, using photographs from the Digital Microscope AM4115TL Dino-Lite Edge. Micromammal teeth are illustrated by means of micrographs taken with Environmental Scanning Electron Microscopy (ESEM) at the Servei de Recursos Científics i Tècnics de la Universitat Rovira i Virgili (Tarragona). Upper and lower teeth are denoted by capital letters ('P' for premolars and 'M' for molars) followed by superscripts and subscripts

Table 1
Vertebrate faunal list of the site of Puerto de la Cadena.

Order	Family	Species
Rodentia	Muridae	*Stephanomys* cf. *dubari*
		Paraethomys cf. *meini*
		Debruijnimys sp.
	Cricetidae	*Apocricetus* cf. *barrierei*
		Ruscinomys lasallei
Lagomorpha	Leporidae	*Trischizolagus maritsae*
	Prolagidae	*Prolagus* cf. *michauxi*
Primates	Cercopithecidae	*Macaca* sp.
Carnivora	Canidae	*Eucyon monticinensis*
Proboscidea	Gomphotheriidae	*Anancus arvernensis*
Perissodactyla	Equidae	*Hipparion* aff. *fissurae*
	Rhinocerotidae	*Dihoplus schleiermacheri* vel *Dihoplus megarhinus*
Artiodactyla	Cervidae	Cervidae indet.
	Giraffidae	*Sivatherium* cf. *hendeyi*
	Bovidae	*Gazella* aff. *baturra*
		Gazella aff. *lydekkeri*
		Bovidae indet. sp. 1
		Bovidae indet. sp. 2
		Bovidae indet. sp. 3
		Parabos sp.
Crocodilya		Crocodilya indet.
Testudines	Testudinidae	*Titanochelon* sp.
		Testudinidae indet.
	Trionychidae	Trionychidae indet.
Squamata	Viperidae	*Vipera* sp.
	Colubridae	*Malpolon* gr. *monspessulanus-mlynarski*

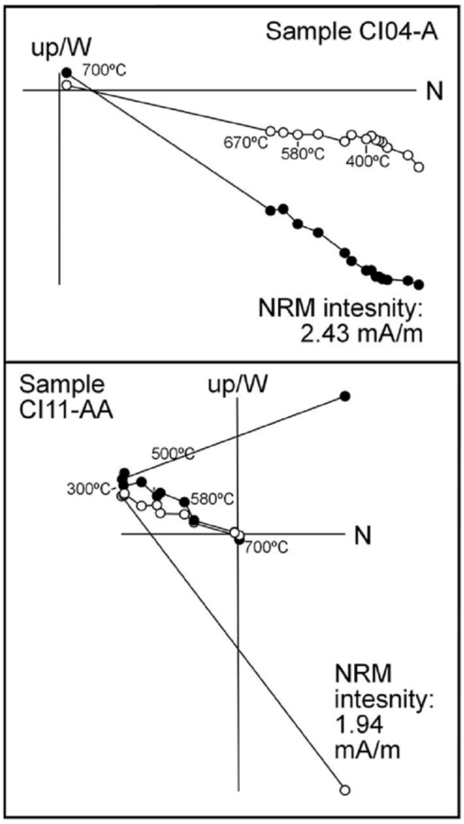

Fig. 3. Demagnetization plots of the Barranco del Cigarrón section. Top: sample with normal polarity zone from the La Virgen formation. Bottom: sample with reversed polarity from the Cigarrón Unit.

respectively, whereas deciduous premolars are denoted with the letter 'D'.

The descriptions and measurements of murid molars follow van de Weerd (1976) and Martín Suárez and Freudenthal (1993) respectively. The terminology used to describe gerbillid teeth is that of Wood and Wilson (1936), and length and width were measured as defined by Minwer-Barakat (2005). Mein and Freudenthal (1971) were followed when we described and measured cricetid teeth. The term "prelophid" is taken from Freudenthal (1985). The terms used to describe prolagid teeth follow Angelone and Sesé (2009). The descriptions and measurements of leporid remains follow the nomenclature and methods proposed by López-Martínez et al. (2007) and Angelone and Sesé (2009) respectively.

A magnetostratigraphic study was performed based on 22 paleomagnetism stations distributed along a 60 m-thick composite series of the Puerto de la Cadena. Rock samples were extracted both with a portable drilling machine and by hand shaping of oriented blocs. Analytics were carried out at the Paleomagnetism Laboratory of SCT-Universitat de Barcelona-CSIC. A minimum of one sample per paleomagnetism station underwent a stepwise thermal demagnetization. The

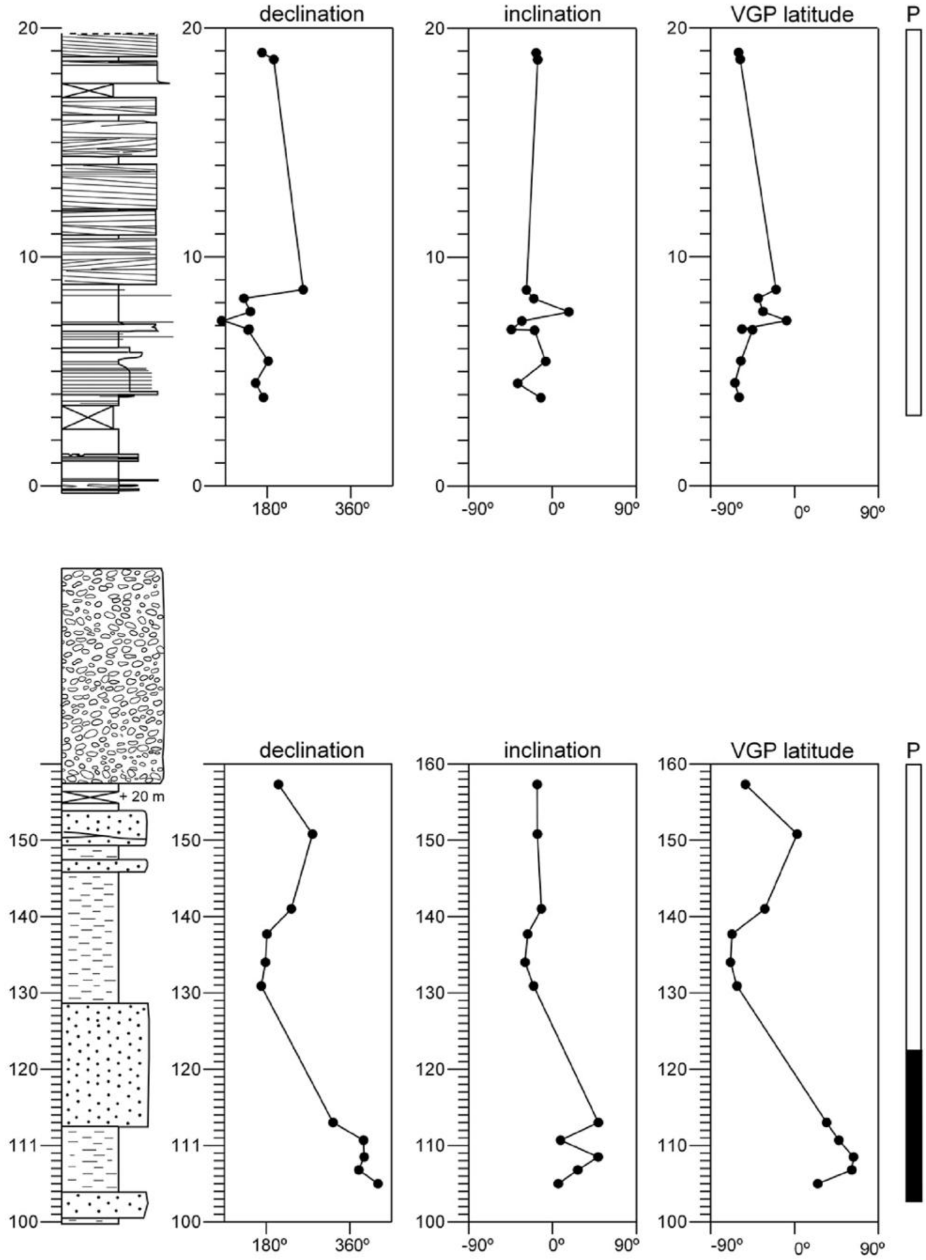

Fig. 4. Magnetostratigraphic results from the studied sections. Top: Isleta section, encompassing the Puerto de la Cadena site. Bottom: Upper part of Barranco del Cigarrón section. P indicates polarity (normal in black and reversed in white).

demagnetization included up to 15 steps, from room temperature to 700 °C. A few alternating field demagnetizations were also carried out, and bulk susceptibility was measured during the whole process to detect any mineralogical changes. The results were correlated to the latest Astronomical Tuned Neogene Time Scale (ATNTS; Hilgen et al., 2012).

4. Magnetostratigraphy

A magnetostratigraphic survey was carried out in order to date the Puerto de la Cadena site based on the correlation with both the magnetostratigraphy-calibrated mammal scale for the Iberian Peninsula (Agustí et al., 2001) and the magnetostratigraphically dated successions of nearby sections with the same age and stratigraphic units (Krijgsman et al., 2006; Soria et al., 2008). The limited stratigraphic context of the Puerto de la Cadena site (relatively thin Isleta section) made it necessary to also include the thicker Barranco del Cigarrón section in the magnetostratigraphic study. Thus, a first sampling was focused on the Cigarrón Unit in the two sections, and a second sampling was focused on the uppermost part of the La Virgen Units.

Thermally demagnetized samples displayed a stable demagnetization plot (see examples in Fig. 3) with high magnetization intensity values. A high temperature interval from around 300 °C to full demagnetization was considered to calculate a primary component. At lower temperatures, a normal polarity component was observed, and is considered to be a recent overprint of the geomagnetic field. The high temperature component provided both normal and reversed polarities (Fig. 4). In the Cigarrón Unit, normal polarities are recorded from meter 100 to 120, while in the upper remaining section only reversed polarities have been found. In the Isleta section only reversed polarities are observed. Samples from the La Virgen Unit provided unreliable results due to the low intensities and the instability of the magnetization.

5. Biostratigraphic correlations

5.1. Small mammals

The micromammal list of Puerto de la Cadena includes *Stephanomys* cf. *dubari*, *Paraethomys* cf. *meini*, *Apocricetus* cf. *barrierei*, *Ruscinomys lasallei*, *Debruijnimys* sp., *Prolagus* cf. *michauxi*, and *Trischizolagus*

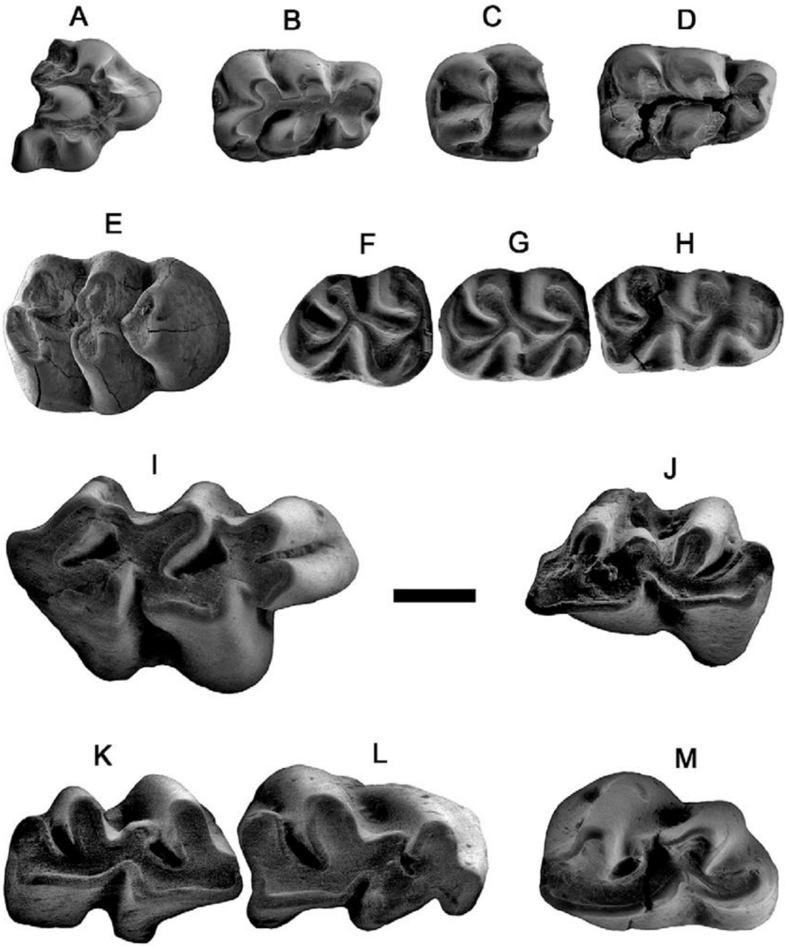

Fig. 5. Rodent teeth collection from Puerto de la Cadena. *Stephanomys* cf. *dubari*: A. partial right M^1, MAM/DA/2012-0019/A5-2; B. right M$_1$, MAM/DA/2012-0019/A5-1. *Paraethomys* cf. *meini*: C. right M$_2$, MAM/DA/2012-0019/A27′06-9; D. right M$_1$, MAM/DA/2012-0019/A26-2; *Debruijnimys* sp.: E. right M^1, MAM/DA/2012-0019/A5′06-1. *Apocricetus* cf. *barrierei*: F. left M$_3$, MAM/DA/2012-0019/VLP2-831a; G. left M$_2$, MAM/DA/2012-0019/VLP2-831b; H. left M$_1$, MAM/DA/2012-0019/VLP2-831c. *Ruscinomys lasallei*: I) right M^1, MAM/DA/2012-0019/VLP2-799; J. left M$_2$, MAM/DA/2012-0019/A5′06-4; K. right M$_2$, MAM/DA/2012-0019/VLP2-869b; L. right M$_1$, MAM/DA/2012-0019/VLP2-869a; M. left M$_3$, MAM/DA/2012-0019/Puerto-de-la-Cadena. Scale bar equals 1 mm.

maritsae (see Figs. 5–6, Table 1, and Supplementary information), and can be assigned to the base of MN14 (earliest Ruscinian).

Mein et al. (1990) defined the base of MN14 in the Teruel Basin as the entry of *Celadensia*. However, Agustí et al. (2001) considered the base of MN14 to be the first appearance of the arvicolid *Promimomys* due to the occurrence of *Celadensia* in Baccinello (Italy), a MN13 locality (Rook and Torre, 1995). The range of *Promimomys* within the Iberian Peninsula is limited to the Teruel region (Mein et al., 1990), so correlations with southern Iberian basins are difficult to establish. In the absence of arvicolids, Agustí et al. (2001) proposed differentiating MN13 and MN14 based on the evolutionary stages of *Apodemus*, *Stephanomys*, *Paraethomys*, *Ruscinomys* and *Apocricetus*. In agreement with Morales et al. (2013), the appearance of a large-sized *Paraethomys* (*P.* aff. *abaigari*, *P. abaigari*) with a smaller one (*P. meini*) marks the beginning of the subzone N2. Mansino et al. (in press) considered this subzone to be early Ruscinian (MN14). The remains of *Stephanomys* from Puerto de la Cadena display a more derived evolutionary stage than those of *S. ramblensis*, the most characteristic late Turolian taxon in Spanish basins (Agustí and Llenas, 1996). In contrast, its descendant, *Stephanomys dubari*, is common in latest Turolian and earliest Ruscinian assemblages (García-Alix et al., 2008; Mansino et al., 2015). *Apocricetus barrierei* is a typical taxon of early Rusinian or MN14 unit (Mein, 1975; Mein et al., 1990; Freudenthal et al., 1998; Kälin, 1999; García-Alix et al., 2008). Therefore, the joint occurrence of *Apocricetus* cf. *barrierei* and *Stephanomys* cf. *dubari*, leads us to assign Puerto de la Cadena to the base of the MN14 unit.

We can compare the small mammal record of Puerto de la Cadena with that of some nearby late Turolian localities. Librilla 1, Molina de Segura 9, Sifón 61, and Sifón 79, located in the Fortuna Basin (Agustí et al., 1983, 2006), and Crevillente 6, situated in the Crevillente Basin (Martín Suárez and Freudenthal, 1998), share with Puerto de la Cadena the presence of *Paraethomys meini* as well as a Cricetodontinae like *Ruscinomys* sp. In addition, *Prolagus michauxi* is present in the Fortuna Basin levels. However, these localities differ from Puerto de la Cadena due to the presence of *Stephanomys ramblensis* and *Apocricetus alberti*, suggesting that they have an older age. In spite of the great faunal similarity, the absence of the gerbil *Debruijnimys* in Molina de Segura 9, Sifón 61, Sifón 79, and Crevillente 6 has a biostratigraphic interest. Following Agustí et al. (2006), the so named "Gerbil Event" (third Messinian Mammalian Event, MME 3) took place between 5.96 and 5.33 Ma, when rodents of African affinities came into the Western Mediterranean, such as members of the genera *Myocricetodon* and *Debruijnimys*. This dispersal event clearly occurred after the arrival of *Paraethomys*, and is directly related to the MSC. Therefore, all the cited localities were deposited before the onset of MME 3, as they have a lower stratigraphical position than Puerto de la Cadena. In contrast, the studied small mammal assemblage is very similar to that of the Sifón 413 locality (Agustí et al., 2006). Similar taxa have been recognized in this level: *Debruijnimys* sp., *Paraethomys miocaenicus* (=*P. meini*), *Stephanomys medius* (=*S. dubari*, *S. cordii*), *Ruscinomys lasallei* and *Prolagus michauxi*.

The nearby site of La Alberca has also yielded a similar small mammal association, with the occurrence of *Stephanomys medius* (=*S. dubari*, *S. cordii*), *Ruscinomys lasallei*, *Paraethomys meini*, *Prolagus michauxi*, and the genus *Trischizolagus* (Montenat, 1973; López Martínez, 1989; Freudenthal et al., 1998). Following de Bruijn et al. (1975), the La Alberca site is late Miocene in age. They based their dating on the association of planktonic foraminiferan association found in higher and lower marine sediments, between which the continental site is intercalated. If this dating is correct, then La Alberca would be older than Puerto de la Cadena. This is consistent with the absence of gerbils in La Alberca and the presence of *Apocricetus alberti*.

The joint presence of *Stephanomys* cf. *dubari*, *Paraethomys* cf. *meini*, *Ruscinomys lasallei*, *Apocricetus* cf. *barrierei* and *Debruijnimys* sp. leads us to correlate the Puerto de la Cadena site with the subzone N1 of the Ventian proposed by Morales et al. (2013), in further agreement with the large-mammal association.

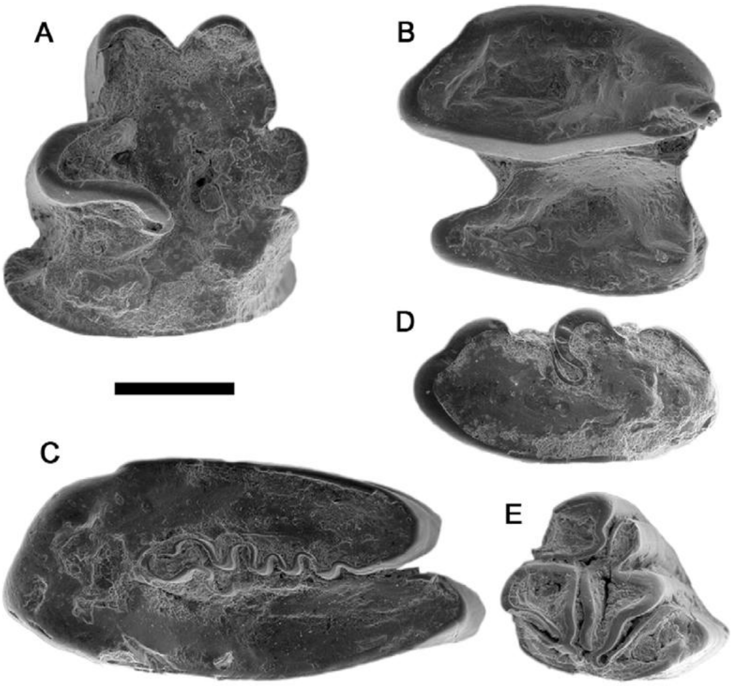

Fig. 6. Lagomorph teeth from Puerto de la Cadena. *Trischizolagus maritsae*: A. left P_3, MAM/DA/2012-0019/VLP2-593; B. left lower molariform, MAM/DA/2012-0019/VLP2-626; C. left P^2, MAM/DA/2012-0019/A-27; D. right upper molariform, MAM/DA/2012-0019/VLP2-656. *Prolagus* cf. *michauxi*: E. left P_3, MAM/DA/2012-0019/A-26. Scale bar equals 1 mm.

5.2. Large mammals

The large mammal assemblage from Puerto de la Cadena (Fig. 7 and Table 1) includes taxa that, in Spain, either (a) first appear in MN13 (*Eucyon*, *Macaca*, *Parabos*); (b) are as yet only known from MN14 (*Sivatherium*, *Gazella* aff. *baturra*, *Hipparion fissurae*); (c) are recorded for the first time (*Gazella* aff. *lydekkeri*); or (d) occur in both MN13 and MN14 (see Supplementary information). Taken as a whole, the large mammal association from Puerto de la Cadena suggests an age close to the MN13–MN14 transition, which is another important novelty for the Spanish fossil record of the Miocene/Pliocene boundary. In fact, in the Iberian Peninsula there are nearly no fossil localities with ages comprised between those of Venta del Moro (Valencia; local biozone M3; Morales, 1984; Montoya et al., 2006) and La Gloria 4 (Teruel; biozone O; Alcalá, 1994). The very few localities in between have yielded a small number of large mammal fossils: Arenas del Rey (Granada; Aguirre, 1963; Alberdi and Boné, 1978), Almenara-Casablanca M (Castellon; Agustí et al., 1989, 2011; Köhler et al., 2000), La Alberca (Murcia; Montenat and Crusafont, 1970) and Baza-1 (Granada; Piñero et al., in press; Ros-Montoya et al., in press). In contrast, the micromammal record is abundant, although it is difficult to interpret (Morales et al., 2013). Therefore, it is not surprising that Puerto de la Cadena contains so many taxa not previously recorded in this geographical area: *Eucyon monticinensis*, *Hipparion* aff. *fissurae*, *Sivatherium* cf. *hendeyi*, *Gazella* aff. *baturra*, *Gazella* aff. *lydekkeri*, and the possible presence of the caprine *Norbertia hellenica*. *Macaca* sp. which was already known from Almenara-M (Köhler et al., 2000), although the new record from Puerto de La Cadena confirms its presence in the early Pliocene of Spain (see Supplementary information). The remaining large mammal remains from Puerto de la Cadena either cannot be assigned to a species

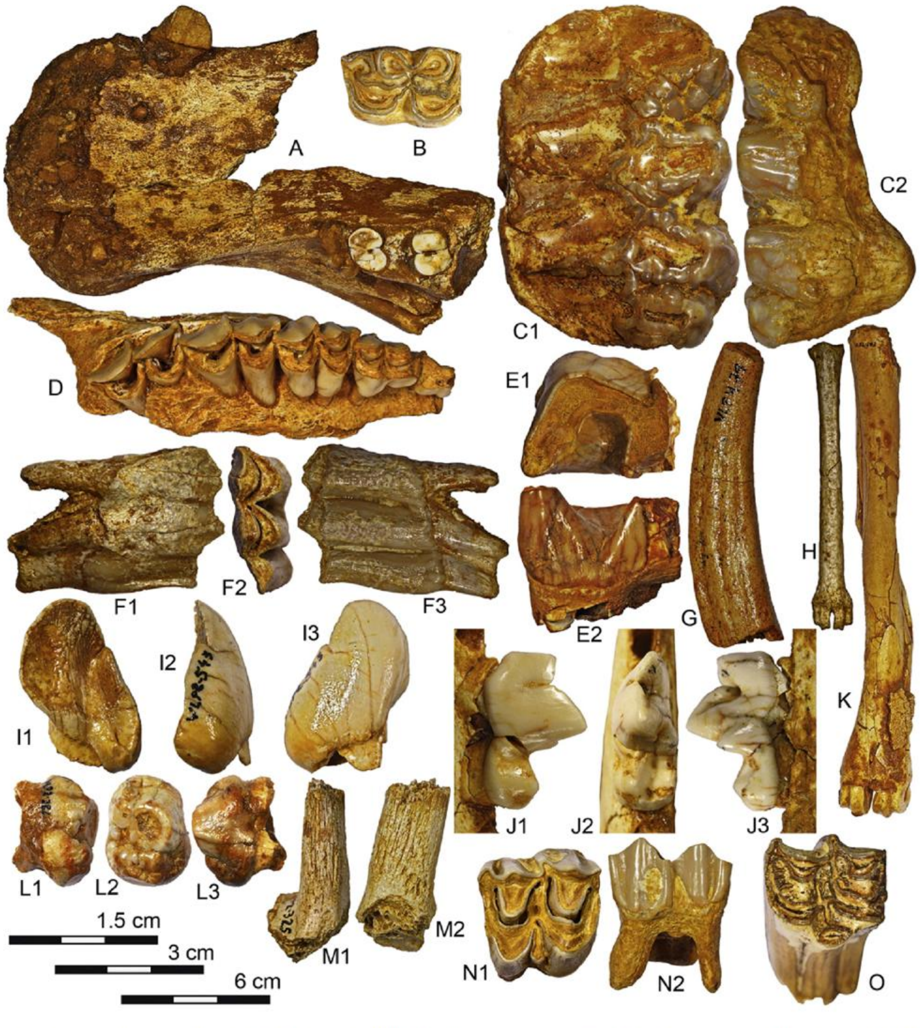

Fig. 7. Large mammals from the early Pliocene locality of Puerto de la Cadena. *Dihoplus schleiermacheri/megarhinus*: A. anterior part of mandible, MAM/DA/2012/VLP3-682; E. left $D_{3/4}$, occlusal (1) and lingual (2) views, MAM/DA/2012/VLP2-507. *Hipparion* aff. *fissurae*: B. right $P_{3/4}$, occlusal view, MAM/DA/2012/VLP2-446; O. left $M^{1/2}$, occlusal view, MAM/DA/2012/VLP3-579. *Anancus arvernensis*: C. left $D^{3/4}$, occlusal (1) and buccal (2) views, MAM/DA/2012/VLP2-234; L. left D^2, lingual (1), occlusal (2) and buccal (3) views, MAM/DA/2012/VLP2-282. Bovidae indet. sp. 3: D. maxilla with D^2-M^2, occlusal view, MAM/DA/2012/VLP2-212. Bovidae indet. sp. 2: F. right M_3, lingual (1), occlusal (2) and buccal (3) views, MAM/DA/2012/VLP2-563. Cervidae indet.: G. antler fragment, MAM/DA/2012/VLP4-79. Bovidae indet. sp. 1: H. right metatarsus, anterior view, MAM/DA/2012/VLP2-272. *Sivatherium* cf. *hendeyi*: I. right lower canine, lingual (1), distal (2) and labial (3) views, MAM/DA/2012/VLP2-543. *Eucyon monticinensis*: J. left M_1, buccal (1), occlusal (2) and lingual (3) views, MAM/DA/2012/VLP2-51. *Gazella* aff. *lydekkeri*: K. right metacarpus, anterior view, MAM/DA/2012/VLP2-103. *Gazella* aff. *baturra*: M. left female horn core, anterior (1) and lateral (2) views, MAM/DA/2012/VLP2-325. *Parabos* sp.: N. right M^2, occlusal (1) and buccal (2) views, MAM/DA/2012/VLP2-464. The 1.5 cm scale bar goes with figure J, the 6 cm scale bar goes with figures H and K, and the 3 cm scale bar goes with the remaining figures.

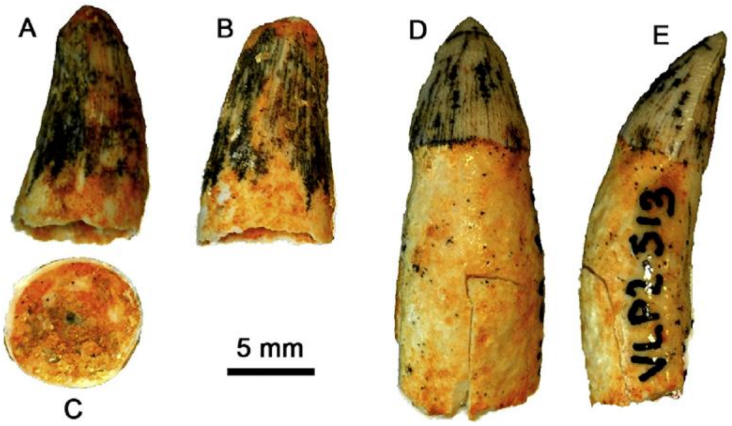

Fig. 8. Crocodylia indet. from the early Pliocene of Puerto de la Cadena. A–C. Anterior maxillary tooth (MAM/DA/2012/VLP2-63) in lateral, posterior and dorsal views; D–E. posterior maxillary tooth (MAM/DA/2012/VLP2-513) in anterior and lateral views.

(as is the case with the sole remain of a deer antler and the rhinoceros *Dihoplus*). The proboscidean *Anancus* appears in MN12 and the bovine *Parabos* at the end of MN13 (in local zone M3). These new appearances are framed within the major faunal turnover that took place at the end of the Miocene, which in part is related to the Messinian Salinity Crisis (Agustí et al., 2006; Van der Made et al., 2006; Gibert et al., 2013; Morales et al., 2013). The appearance of several of these species is also recorded in other Mediterranean localities, namely: *Eucyon monticinesis*, which was described from Brisighela, Italy (Rook, 1992); *Sivatherium*, which in Macedonia was described as *Sivatherium garevskii* (see Geraads, 2009) and in Turkish Thrace (Edirne = Adrianopolis) as *Sivatherium giganteum* (see Abel, 1904); *Gazella* aff. *lydekkeri* and likely the possible caprine dentition, which could correspond to the *Gazella* sp. and *Norbertia hellenica* from Maramena (Köhler et al., 1995).

6. Magnetobiostratigraphic correlation

The correlation of the obtained polarities with the Geomagnetic Polarity Time Scale (Fig. 10) is based on the available geological and biostratigraphic data. First, the regional geological and magnetostratigraphic context of Krijgsman et al. (2006) and Soria et al. (2008) indicates that the Cigarrón Unit is equivalent to the Pliocene Unit in Soria et al. (2005). Both units correspond to the infilling of the post end-Messinian erosion by transitional environments in which the Puerto de la Cadena paleontological remains accumulated.

The entire Puerto de la Cadena section records a reversed polarity chron, whereas the Cigarrón Unit, whose upper part includes the Puerto de la Cadena site, records a normal-reversed polarity sequence (Fig. 4). According to the above-mentioned end-Messinian discontinuity at the base of the Cigarrón Unit, correlation with the reversed chron C3r is discounted because it covers the Mio-Pliocene boundary. Therefore, the normal polarity interval at the base of the Cigarrón section must be correlated with chron C3n.4n (or younger).

In turn, the correlation among Iberian micromammal sites that have been magnostratigraphically dated and the Puerto de la Cadena site supports that the correlation of the latter must be older than C3.2n. This is the case of Sifón P (correlated to C3.2n by Garcés et al., 2001), a site which has a more derived *Stephanomys* than that from Puerto de la Cadena. Such constraints indicate that the reversed polarity span at Puerto de la Cadena is likely correlated to C3n.3r or C3n.2r. A correlation to C3n.3r is preferred based on the large similarity in the small mammal association with Fuente del Viso (see Supplementary information), which is correlated with that chron (Opdyke et al., 1997; Freudenthal et al., 1998). Therefore, we correlate the normal interval at the Cigarrón section with chron C3n.4n, and the upper reverse span at the upper part with C3n.3r. The Puerto de la Cadena site is therefore dated between 4.997 and 4.896 Ma (Fig. 10).

Our interpretation is consistent with other well-dated sites. The older age indicated for Venta del Moro and Sifón 79 is in line with their assignment to the normal chron C3An.1n (6.252–6.033 Ma; Garcés et al., 2001; Agustí et al., 2006; Gibert et al., 2013). Similarly, the somewhat older Purcal 3, 4, and Zorreras 3A were correlated to chron C3r, ranging from 5.235 to 6.033 Ma (Martín-Suárez et al., 1998, 2000). Finally, the Sifón 413 level was situated in the Pliocene span of chron C3r (5.330–5.235 Ma; Garcés et al., 2001), and although its small mammal association resembles that of Puerto de la Cadena,

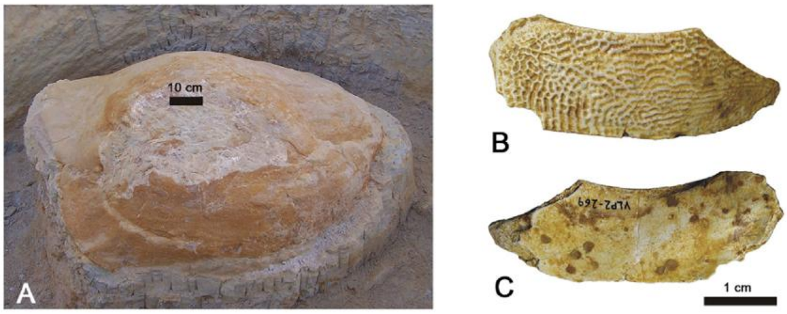

Fig. 9. The two clades of turtles identified in the early Pliocene site of Puerto de la Cadena (Murcia). A. Carapace of *Titanochelon* sp. "in situ"; B–C. VLP2-269, nuchal plate of Trionychidae indet. (Cryptodira), in dorsal (B) and ventral (C) views.

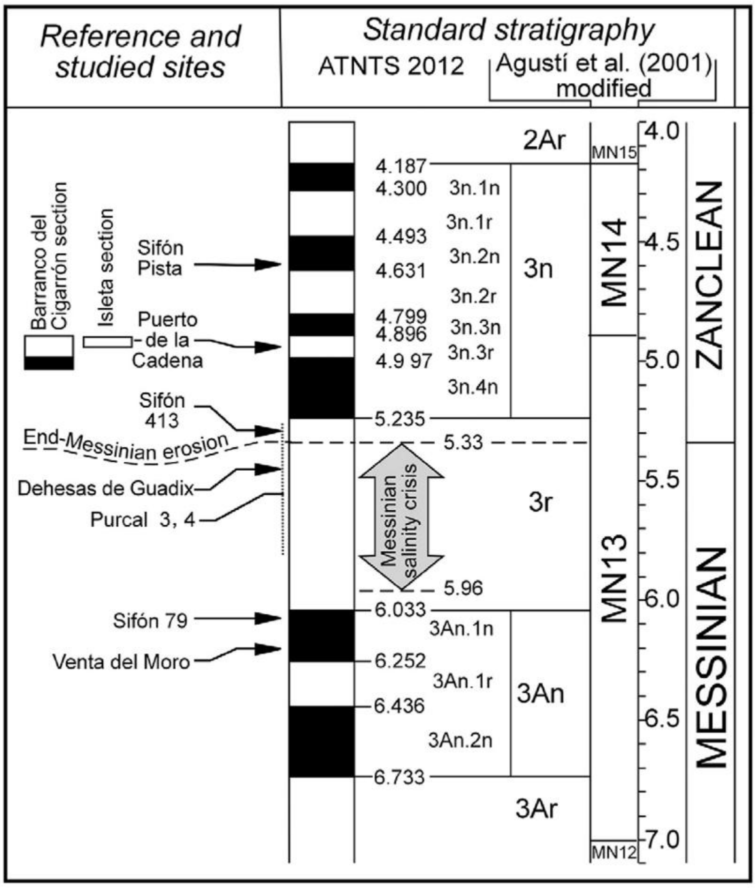

Fig. 10. Magnetobiostratigraphic correlation of the studied locality and other reference sites, with the magnetic polarity time scale.

considering the chronostratigraphic information, Sifón 413 is at least 200 kyr older.

Martín-Suárez et al. (2000) and Agustí et al. (2001) considered the Fuente del Viso faunal association as MN14, instead of latest MN13 as indicated by Opdyke et al. (1997). The faunal assemblage of Puerto de la Cadena has been interpreted in this work as earliest MN14. Considering these data, a minimum age for the base of MN14 is established within the chron C3n.3r. This permits bracketing the MN13/MN14 boundary between 4.997 and 4.896 Ma. This correlation is consistent with that of Opdyke et al. (1997) and Agustí et al. (2001), who supported an MN13/MN14 limit younger than its traditional position at the marine Miocene/Pliocene boundary.

Therefore, according to this correlation, Puerto de la Cadena is closely coeval of the Tomea Eksi 3 level, at the other edge of the Mediterranean Basin, in the Pliocene lacustrine deposits of the Florina-Ptolemais-Servia Basin (Greece; Hordijk and de Bruijn, 2009), also placed within chron C3n.3r. However, when we compare the two small mammal assemblages, striking differences are evident. The rodent fauna from Tomea Eksi 3 is composed of a diversified fauna of murids related to *Apodemus* (*Micromys bendai*, *Rhagapodemus primaevus*, *Apodemus atavus*, *Apodemus dominans*?) together with an archaic arvicolid (*Mimomys* aff. *davakosi*). This association suggests a forested environment, with predominant humid conditions, which is confirmed by the other rodent associations present in closer levels of the basin, including, among others, flying squirrels of the species *Pliopetaurista dehneli* (Vorio 3/3a; Hordijk and de Bruijn, 2009).

In contrast, Puerto de la Cadena has a very different small mammal association, with most of the rodent species indicating open-dry conditions. This is the case of the hamsters *Apocricetus* cf. *barrierei* and *Ruscinomys lasallei* (a selenodont/hypsodont cricetid), the gerbil *Debruijnimys* sp. and the stephanodont murid *Stephanomys* cf. *dubari*. These evidences point to the existence of very different environmental conditions at the two extremes of the Mediterranean. In the Western Mediterranean there is the persistence of an open landscape, with prevalent dry conditions, which most possibly are reminiscent of the Messinian Salinity Crisis (as indicated by the persistence of gerbils of African origin). In contrast, the conditions in South Eastern Europe suggest a forested environment in a humid context. This difference can be explained by the influence of the neighboring Black Sea, which possibly increased precipitation due to lake effect.

7. Conclusions

The Puerto de la Cadena site, in the upper part of the Cigarrón Unit, at the northern flank of the Carrascoy range mountain (Murcia, Spain), has yielded diverse vertebrate continental fauna, and up to 26 different species were recorded. The recovered assemblage can be correlated to the base of MN14 (earliest Ruscinian of the early Pliocene). The small mammal association consists of *Stephanomys* cf. *dubari*, *Paraethomys* cf. *meini*, *Debruijnimys* sp., *Apocricetus* cf. *barrierei*, *Ruscinomys lasallei*, *Trischizolagus maritsae*, and *Prolagus* cf. *michauxi*. The large mammal record comprises *Macaca* sp., *Eucyon monticinensis*, *Anancus arvernensis*, *Hipparion* aff. *fissurae*, *Dihoplus schleiermacheri* vel *Dihoplus megarhinus*, Cervidae indet., *Sivatherium* cf. *hendeyi*, *Gazella* aff. *baturra*, *Gazella* aff. *lydekkeri*, *Parabos* sp., and three additional indeterminate bovids. Among the reptiles, Puerto de la Cadena records Crocodylia indet., *Malpolon* gr. *monspessulanus*-*mlynarski*, *Vipera* sp., Trionychidae indet., *Titanochelon* sp., and one indeterminate testudinid. This fauna includes a number of elements of African origin, such as *Debruijnimys* sp., *Macaca* sp., and *Sivatherium* cf. *hendeyi*, which most likely settled on the Iberian Peninsula during the Messinian Salinity Crisis (as has been reported in previous studies).

Puerto de la Cadena is one of the youngest localities of the MN14 (early Pliocene), with the joint presence of typical elements of this unit, like *Apocricetus* cf. *barrierei Sivatherium*, *Gazella* aff. *baturra*, and *Hipparion fissurae*. According to the magnetostratigraphic correlation proposed in this work, the faunal association from Puerto de la Cadena is dated to the early Pliocene. Our results allow us to establish the boundary between MN13 and MN14 within the reversed polarity interval C3n.3r (4.997–4.896 Ma). In addition, this study confirms the persistence of crocodiles in the early Pliocene of Europe.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.palaeo.2017.04.020.

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SUPPLEMENTARY INFORMATION

1. The vertebrate paleontological record

A preliminary faunal list of the vertebrate remains yielded by the Puerto de la Cadena site was published by Mancheño et al. (2013). However, in the present work we provide the results of a more thorough study of the faunal remains, including some measurements and photographs that led to minor amendments and additions to the previously reported faunal list (Table 1).

1.1. Mammals

1.1.1. Small mammals

Among the small mammals, rodents are represented by the families Muridae and Cricetidae, while lagomorphs include representatives of the families Prolagidae and Leporidae. The murid association comprises the species *Stephanomys* cf. *dubari*, *Paraethomys* cf. *meini*, and *Debruijnimys* sp., represented by four, three and two teeth, respectively.

The two M^1 of *Stephanomys* cf. *dubari* (2.58 x — mm; — x 1.73 mm) display the t1 displaced backwards, the labial crest is well developed, and the lingual crest is low in one specimen and high in the other one. They have both t1bis and t2bis (Fig. 5A). The two M_1 (2.25 x 1.47 mm; 2.05 x — mm) have a well-developed longitudinal crest connecting the hypoconid-entoconid to the protoconid-metaconid. The labial cingulum is moderate, with a low oval c1 attached to the hypoconid, and accessory cusps are absent. The tma is very weak and low, and the posterior heel is oval and of medium size (Fig. 5B). These teeth show the typical features of *Stephanomys*, such as a high crown, longitudinal crest in the lower teeth, and posterior crests and spurs on t1 and t3 in the upper teeth. The studied material shows morphological and biometrical differences with respect to the older representatives of the genus, *Stephanomys stadii* and *Stephanomys ramblensis*. The late Pliocene species of *Stephanomys* have a higher crown, larger size, and greater development of the stephanodonty than the studied molars (Minwer-Barakat et al., 2011). In contrast, the described specimens are similar to those of *Stephanomys dubari* and *Stephanomys cordii*. The moderate size and rather poorly developed longitudinal connections agree better with *S. dubari* than with *S. cordii*, although given the restricted sample we prefer to be cautious and use open nmenclature. *Stephanomys dubari* is present in late Miocene to Early Pliocene assemblages of the Iberian Peninsula (García-Alix et al., 2008a; Mansino et al., 2015a).

With regard to the teeth from Puerto de la Cadena assigned to *Paraethomys* cf. *meini* (Fig. 5C, 5D), there is an M_1 (2.24 x 1.50 mm) with a slightly asymmetrical anteroconid and no tma. It displays a poorly developed longitudinal spur. The labial cingulum is moderate, and the c1 is large and round. There is a small elongated posterior heel. The two M_2 (1.53 x 1.48 mm; 1.65 x 1.5 mm) have a weak labial cingulum. The c1 is small, low and separated from the hypoconid. The anterolabial cusp is poorly preserved. The posterior heel is weak and laminar. The teeth of *Paraethomys* from Puerto de la Cadena are clearly smaller than those of *Paraethomys jaegeri*, and also slightly smaller than those of *Paraethomys abaigari* (see Adrover et al., 1988) and *Paraethomys belmezensis* (Castillo Ruiz, 1992), more closely resembling the maximum values reported for *Paraethomys meini* from Sète (type locality; Adrover, 1986). The morphology of the described specimens also agrees with that of *Paraethomys meini*, given the presence of a weak labial cingulum and the lack of tma. However, we use open nomenclature due to the scarcity of remains. According to Agustí et al. (2006), the first occurrence of *Paraethomys* in the Iberian Peninsula is recorded in the neighboring Fortuna Basin (Southern Spain; few kilometers north of our site) prior to the MSC (ca. 6.2 Ma), although this taxon further persisted during the Ruscinian (Mein et al., 1990; Adrover et al., 1993; García-Alix et al., 2008a; Minwer-Barakat et al., 2012; Mansino et al., 2015a; Piñero et al., in press.). Agustí et al. (2006) associated the *Paraethomys* dispersal with the entry of camels of the genus *Paracamelus* into southern Spain, being likely part of the same dispersal event from northern Africa. Similarly, Gibert et al. (2013) indicated the first entry of *Paraethomys* and *Paracamelus* in the Iberian Peninsula in Venta del Moro (Spain) at 6.23 Ma.

Gerbils are represented by *Debruijnimys* sp. (Fig. 5E). The sample consists of two M^1, one of them fragmentary (2.88 x 2.07 mm; 2.76 x — mm). The anterocone is composed of two lobes, which are widely confluent. There is a spur on the posterior side of the anterocone, which does not reach the paracone. Protocone and paracone are connected by a transverse ridge, the paracone being larger than the protocone. The posterior wall of the paracone is projected towards the metacone without reaching this cusp. The hypocone and the metacone are connected. The metacone is much smaller than the hypocone and it is connected to the anterolabial wall of this cusp. *Debruijnimys* sp. from Puerto de la Cadena agrees in size and occlusal morphology with the molars ascribed to *Debruijnimys* sp. from the early Pliocene localities of Sifón 413 (Agustí et al., 2006), Alcoy 4B (Agustí, 1991), Botardo C (Martín Suárez, 1988), Gorafe 1 and Caravaca (Bruijn, 1974), and La Gloria 4 (Adrover et al., 1993). According to Agustí and Casanovas-Vilar (2003), the genus *Debruijnimys* settled on the Iberian Peninsula at least two times during the Miocene-Pliocene transition, migrating in two different waves from North Africa. The first one corresponds to *Debruijnimys almenarensis*, recorded in some late Miocene localities, like Almenara-Casablanca M (Agustí, 1990; Agustí et al., 2011), Negratín-1 (Minwer-Barakat et al., 2009a), Salobreña (Aguilar et al., 1984), Zorreras-3A (Martín-Suárez et al., 2000), and Gafares 2B (García-Alix et al., 2016), while the second one comprises *Debruijnimys* sp. from the previously mentioned early Pliocene localities (Castillo and Agustí, 1996; Agustí and Casanovas-Vilar, 2003), which might be the ancestors of *Debruijnimys julii* (see Agustí and Casanovas-Vilar, 2003).

Cricetids are represented at Puerto de la Cadena by *Apocricetus* cf. *barrierei* and *Ruscinomys lasallei*. The remains of *Apocricetus* cf. *barrierei* consist of a single mandible with the M_1 (2.53 x 1.40 mm), M_2 (2.12 x 1.54 mm) and M_3 (2.10 x 1.59 mm; Fig. 5F, 5G, 5H), all these teeth being very worn. In the M_1, the anteroconid is crest-like and simple, with a double anterolophulid and very short prelophid. The protolophid and metalophid are anterior and there is no evidence of mesolophid. The M_2 and M_3 display the same occlusal pattern as the M_1, with a well-developed labial cingulum, no lingual cingulum, anterior protolophid and metalophid, and no mesolophid. The crest-like anteroconid and the presence of a short prelophid are common traits in both *A. barrierei* and *A. alberti* (see Ruiz Sánchez et al., 2014; Mansino et al., 2014). In addition, the size fit well with this species, enabling to distinguish the described specimen from *Apocricetus plinii*, *Apocricetus alberti* and *Apocricetus angustidens*. We tentatively attribute the studied teeth to *Apocricetus* cf. *barrierei*. The presence of a single mandible leads us to use open nomenclature. *Apocricetus barrierei* was originally identified in the early Pliocene of Southern France (Hautimagne, Chabrier, Celleneuve, Vendargues; Mein and Michaux, 1970), but later recognized in many sites from Spain (Freudenthal et al., 1988). This species is considered a key element of MN14 by several authors (Mein et al., 1990; Freudenthal et al., 1998; Kälin, 1999; García-Alix et al., 2008a).

Ruscinomys lasallei is represented by one M_1 (3.08 x 2.01 mm), two M_2 (3.03 x 2.15 mm; 2.91 x 1.90 mm), one M_3 (2.92 x 1.96 mm), and two M^1 (one fragmentary; 4.28 x 2.61 mm;

— x 2.28 mm). In the M^1, an anterior groove separates the two lobes of the anterocone (Fig. 5I). There are well-developed ectolophs, and the anterior one reaches the anterior wall of the paracone, being placed in a lower position with respect to this cusp. The posterior ectoloph is connected to the anterior wall of the metacone, and it is placed at the same level than this cusp. The M_1 has a very simple dental pattern, with a small and rounded anteroconid, and lacking the anterolophid (Fig. 5L). There is a short mesolophid that does not reach the posterior wall of the metaconid. The posterolophid does not close the posterosenid. The M_2 follows the same pattern as the M_1, with no anterolophid and a short mesolophid (Fig. 5J, 5K). In one specimen, this mesolophid does not reach the posterior wall of the metaconid, while it does in the other one, closing the mesosinusid. In the M_3, the anterolophid is also absent, and there is a short mesolophid that reaches the posterior wall of the metaconid, closing the mesosinusid (Fig. 5M). An alternate assignment to *Ruscinomys schaubi*, *Ruscinomys gilvosi*, or *Ruscinomys bravoi* is ruled out because of their smaller size, whereas an attribution to *Ruscinomys europaeus* is discounted by the larger dimensions of the latter. The great crown height of the studied molars, their large size, and some morphological traits (such as the lingual lobe of the M^1 anterocone directed forward with a sharp lingual angle, and the rounded M_1 anteroconid lacking the anterolophid) allows us to ascribe these teeth to *Ruscinomys lasallei* (see García-Alix et al., 2008b).

Two lagomorph species are represented at Puerto de la Cadena: the leporid *Trischizolagus maritsae* and the prolagid *Prolagus* cf. *michauxi*. The former is the most abundant small mammal species at the site. It is represented by nearly a hundred of upper and lower isolated teeth. Most of them are damaged, probably due to transport prior to the deposition of the sandy sediments in which they are included, as it is shown by the frequent abraded or polished surfaces of these teeth. The sample includes several P_3 and P^2, which are the most diagnostic elements from a taxonomic perspective in lagomorphs. The P_3 display a typical archaeolagine structure, with five reentrant folds, although the development of the mesoflexid is variable (Fig. 6A). None of the specimens exhibit crenulations on the enamel of the posterior wall of the hypoflexid. The P^2 show a simple structure (Fig. 6C). The paraflexus is the deepest reentrant fold, followed by the mesoflexus, whereas the hypoflexus appears in all the specimens as a very shallow enamel invagination. No specimen exhibits crenulations on the enamel of the lingual wall of the paraflexus. All of the upper molariform teeth (Fig. 6D) display crenulations on the enamel of the anterior wall of the hypoflexus. In some of them, crenulations are also visible on the enamel of the posterior wall, although they are usually smoother than those of the anterior wall. All these features agree with the morphology of *T. martisae* from Maritsa (Greece), the type locality of the species (Bruijn et al., 1970). The size of the teeth from Puerto de la Cadena (length of P_3 ranges from 2.25 to 2.99 mm) is slightly larger than in those from Maritsa. This slight difference might be due to the fact that most specimens from Maritsa correspond to juvenile teeth, whereas within the Puerto de la Cadena sample there are both juvenile and adult specimens.

In the nearby La Alberca site, *Hispanolagus crusafonti* was originally described by Janvier and Montenat (1971), being later transferred to *Trischizolagus* by López Martínez (1989). The material from Puerto de la Cadena differs from *T. crusafonti* in the presence of a mesoflexid and the lack of crenulations on the enamel of the posterior wall of the hypoflexid of the P_3, as well as in having a simple paraflexus (instead of double as in *T. crusafonti*, at least judging from the illustrations) without crenulations on the enamel of its lingual wall. La Alberca is currently considered to be slightly older (latest Miocene; Mein et al., 1973; Bruijn et al., 1975) than Puerto de la Cadena (earliest Pliocene). Therefore, the record of two different species of the genus *Trischizolagus* in two sites so geographically close might be due to the slight differences in age. However, their close chronological proximity suggests that this fact might also stem from a misinterpretation of the material from La Alberca, as it was yet suggested by López Martínez (1989).

In Puerto de la Cadena, the prolagid *Prolagus* cf. *michauxi* is much less abundant than *T. maritsae*, and only a few teeth can be ascribed to the former species. For the same reasons as in the case of *T. maritsae* (see above), in general these teeth are poorly preserved. The only available P_3 (Fig. 6E) displays a large and rounded anteroconid, similar in size to the metaconid, protoconid and hypoconid. The metaconid is connected to the entoconid by a narrow metaisthmus. The protoconid shows an elongated protonoculid projected forward. The protoconid is connected to the entoconid-hpoconid complex by a narrow protoisthmus. The crochet is absent. These characteristics agree with those of *Prolagus michauxi*. However, taking into account the scarcity of the sample and the lack of more diagnostic material, we provide a species identification with open nomenclature. *Prolagus michauxi* was also identified in the nearby La Alberca site (López Martínez, 1989). According to Sesé (2006), in Spain *T. maritsae* and *P. michauxi* occur around the Mio-Pliocene boundary, from MN13 to MN15.

1.1.2. Large mammals

The large mammal assemblage from Puerto de la Cadena comprises primates (family Cercopithecidae), carnivorans (Canidae), proboscideans (Gomphotheriidae), perissodactyls (Equidae and Rhinocerotidae), and artiodactyls (Cervidae, Giraffidae, and Bovidae).

The primate remains from Puerto de la Cadena consist of two isolated cercopithecid teeth (a damaged and partial male upper canine, and a well preserved and only slightly worn upper molar crown) attributable to genus *Macaca*. They come from distinct outcrops and therefore belong to different individuals. The canine is dagger-like and labiolingually compressed, and displays a conspicuous mesiolingual sulcus extending from the crown onto the root. The upper molar is an M^3, as indicated by its distally-tapering contour, the lack of distal contact facet, and the presence of a distal accessory cuspule. It displays a bilophodont and generalized papionin occlusal pattern, which is characteristic of the dentally-conservative cercopithecid genus *Macaca* (Delson, 1973, 1975). The moderate occlusal relief and shallow median notches rule out an alternate attribution to the papionin *Theropithecus* and the colobine *Mesopithecus*. An assignment to the latter is further discounted by the restricted mesial fovea and the moderately developed median lingual cleft, among other features. In turn, a referral to the larger papionin *Paradolichopithecus* is discounted by the dimensions of the M^3, which only minimally exceed those of living Barbary macaques from North Africa (*Macaca sylvanus sylvanus*), and fit well with those of the early Pliocene *Macaca sylvanus prisca* and the younger *Macaca sylvanus florentina* (see Alba et al., 2011). Although cercopithecid canines are less informative from a taxonomic viewpoint (Delson, 1973), the specimen from Puerto de la Cadena similarly resembles in size and shape those of living and fossil *Macaca sylvanus* subspp. (Alba et al., 2011). Given current uncertainties about the distinctiveness of European macaque subspecies and the taxonomic identity of latest Miocene macaques from Europe, as well as the scarcity of the sample, pending more detailed comparisons we attribute the material from Puerto de la Cadena to *Macaca* sp. Macaques have also been recorded from the late Miocene of North Africa (Delson, 1973, 1975, 1980; Szalay and Delson, 1979) and the latest Miocene of Spain (Almenara-Casablanca M; Köhler et al., 2000) and Italy (Moncucco Torinese; Alba et al., 2014), undoubtedly representing an immigrant element of African origin.

The canid *Eucyon monticinensis* (Fig. 7J) is represented by three mandibular fragments (with P_4-M_1, M_2, and the talonid of the M_1 and M_2, respectively), as well as by two isolated

M^1, one of them with the lingual wall broken. The morphology and size are identical to those of *Eucyon monticinensis* from Brisighella, Italy (Rook, 1992), which mainly differs from *Eucyon debonisi* of Venta del Moro, Spain, in the larger size of its dentition (Montoya et al., 2009).

Proboscidean remains include a D^2 (Fig. 7L) and a molariform tooth (Fig. 7C) with at least four lobes. The latter has crenulated enamel, it is worn flat, and there is no lophodonty, unlike in *Mammuthus* or *Zygolophodon* and the lobes are not anteroposteriorly compressed as the plates of the Elephantidae. An assingment to *Gomphotherium* or *Tetralophodon* can be discounted because these tend to have molariform teeth with three and four lobes, respectively and relatively large D^2. It seems more likely the material belongs to *Anancus*. The only European species of this genus is *A. arvernensis*. The size of the molariform tooth suggests a D^3 or D^4, and considering the small size of the D^2 compared to this tooth it might be a D^4. In the Iberian Peninsula, *Anancus* appeared not later than MN12 and lasted at least until the beginning of the Pleistocene (Mazo and Van der Made, 2012). In central Europe it is recorded since MN11 (Göhlich, 1999).

The large mammal assemblage of Puerto de la Cadena includes two perissodactyls: the equid *Hipparion* aff. *fissurae*, and the rhinocerotid *Dihoplus schleiermacheri* vel *Dihoplus megarhinus*. *Hipparion* aff. *fissurae* is represented by a fragment of right $D^{3/4}$, three right P^2, two right and one left $M^{1/2}$ (Fig. 7O), two right M^3, one left D_2, one right P_2, two right and one left $P_{3/4}$, one right (Fig. 7B) and a fragment of a left $M_{1/2}$, two left M_3, a partial humerus, a tuber calcis fragment of calcaneum, two left astragali, a right third metacarpal and a diaphyseal fragment of a third metacarpal, a fragment of a third metatarsal, and a proximal central phalanx. The dentition is of intermediate size and fairly hypsodont. The occlusal pattern is moderately complex, the caballine fold is of type 1, the protocone varies between square-oval and elongate-oval, and the fossettes do not have many folds. The lower teeth have a simple morphology, with the double knot (metaconid and metastylid) displaying an elongate oval shape, a wide linguaflexid, and a deep ectoflexid with a fold in the premolars. The ectoflexid may reach the lingualflexid. The protostylid is usually present and isolated on the occlusal surface, depending on the degree of wear. The postcranial skeleton is gracile. The third metacarpal is very similar to those from Layna (the type locality of *H. fissurae*), but a little shorter, and therefore closer in morphology, like the proximal phalanx, to the remains from Orrios 1, assigned by Alberdi and Alcalá (1999) to *Hipparion* aff. *fissurae*.

Rhinocerotidae are represented by a carpal bone, some fragments of deciduous teeth (Fig. 7E), and a mandibular symphysis (Fig. 7A), which has two rounded and not very large alveoli for the incisors. The latest Miocene and Pliocene rhinoceroses from Europe belong to *Stephanorhinus*, *Ceratotherium, Chilotherium*, as well as *Dihoplus scheleiermacheri* and *Dihoplus megarhinus* (Heissig, 1996, 1999). Although a discussion on the generic affinities of *Dihoplus megarhinus* is outside the scope of this paper, it should be noted that it has been classified in different genera (Guérin, 1980; Fortelius et al., 1993; Heissig, 1999; Lacombat, 2007): *Dicerorhinus*, *Dihoplus*, *Stephanorhinus* and *Lartetotherium*. *Ceratotherium* and *Stephanorhinus* reduced the incisors (Heissig, 1999), whereas *Chilotherium* is characterized by large incisors. *Dihoplus schleiermacheri* and *Dihoplus megarhinus* might belong to a single lineage and have relatively small incisors (Heissig, 1999, p. 184, fig. 16.18). Most probably the material from Puerto de la Cadena belongs to this lineage, but it is not possible to conclusively discern, whether it belongs to *D. schleiermacheri* or to *D. megarhinus*. The former species ranged MN9–MN12/13 and the latter MN 14-15 (Heissig, 1996; Guérin, 1980), though recently material from MN 12 was been assigned to *D. megarhinus* (Pandolfi et al., 2015, 2016).

The artiodactyls of Puerto de la Cadena include a cervid (Cervidae indet.), a giraffid (*Sivatherium* cf. *hendeyi*), and six bovids (Bovidae indet. sp. 1, *Gazella* aff. *baturra*, *Gazella* aff. *lydekkeri*, Bovidae indet. sp. 2, Bovidae indet. sp. 3, and *Parabos* sp. The only indication of the presence of a deer in this locality is an antler fragment of an indeterminate cervid (Fig. 7G). The giraffids remains are assigned to *Sivatherium* cf. *hendeyi*. The taxonomically most significant specimens are a complete metacarpal III-IV and some isolated dental remains (Fig. 7I). The great degree of robustness of the metacarpal is remarkable, as well as the large size of the dentition, compared to the giraffids known from the late Miocene of the Iberian Peninsula, which include the genera *Decennatherium* and *Birgerbohlinia* (Crusafont, 1952; Morales and Soria, 1981; Montoya and Morales, 1991; Alcalá and Montoya, 1994; Montoya 1994; Ríos et al., 2016). Morphologically and morphometrically, the specimens from Puerto de la Cadena compares very well with *Sivatherium hendeyi* from the early Pliocene of Langebaanweg, South Africa (Harris, 1976). Other giraffid bones from this locality have a smaller size, either indicating the presence of a second taxon or the existence of very wide range of intraspecific variation. It is possible that two astragali from other nearby localities might belong to *Sivatherium* cf. *hendeyi*: IPS34709 (housed at the Institut Català de

Paleontologia Miquel Crusafont, in Sabadell) is from La Alberca and was previously identified by Montenat and Crusafont (1970) as belonging to a sivatheriine of large size. The other one is from the early Pliocene of La Gloria 4 (Teruel), and was reported as cf. *Birgerbohlinia* sp. by Alcalá and Montoya (1994).

The Puerto de La Cadena fauna has a great bovid diversity, with as much as six different species. Bovidae indet. sp. 1 is represented by a nearly complete metatarsal (Fig. 7H). This bone is robust for a gazelle, and more robust but smaller than another metatarsal, which we attribute to *Gazella* aff. *baturra*. The proximal articular surface is damaged, but it seems to have been relatively wider than in *Gazella*.

The small antelope *Gazella* aff. *baturra* is represented by numerous specimens, which include postcranial remains, dentition, a cranial fragment, and a horn core (Fig. 7M). All remains are of small size, clearly smaller than those attributed to *Gazella* aff. *lydekkeri*, and even smaller than *Gazella baturra* from the locality Gloria 4 (Alcalá and Morales, 2006).

A second *Gazella* species, *Gazella* aff. *lydekkeri,* is represented by three fragments of male horn core (two of which are of the same individual) and a fragment of frontal with a female horn core. Of the two fragments of horn core from the same male individual, one includes the upper part of the orbit and the lower part of the horn core, in which there is no sinus, but spongious bone. A little postcornual fossa is present. The frontal is thick. The basal section of the horn core is ca. 28 x 27 mm, nearly circular. The other fragment is the part of the horn core above the pedicle, but the two specimens do not fit together, because a small part is lacking. The surface is ornamented with wide and deep vertical grooves. There is an anterior faint keel and a wide and deep posterior groove. There is a gentle “anti-clock screw torsion”. The other male horn core has a similar morphology. The grooves are less marked and discontinuous on the anterior side and absent posteriorly. There is a slight indication of an anterior keel. The most common late Miocene gazelle is *Gazella deperdita*, but its horn cores are more flattened and the females do not have horn cores. The shape and morphology of the horn cores from Puerto de la Cadena are close to those of *Gazella lydekkeri* described by Pilgrim (1937) from the Dhok Pathan stage of the Middle Siwaliks. Another similar form is *Gazella* sp. from Maramena, Greece (Köhler et al., 1995). The frontal with horn core, attributed to a female, is short and has a circular section, and resembles the females of *Gazella borbonica* (see Heintz, 1975), and the specimen from the Baynunah Formation (Abu Dhabi), attributed by Gentry (1999) to *Gazella* aff. *lydekkeri*. It is difficult to relate these specimens to teeth or postcranial remains, though possibly a nearly complete but crushed metacarpal (Fig. 7K) and an intermediate phalanx may belong to this species. The shape of the articular surfaces of the second phalanx resembles those of *Gazella*. The metapodial is large and relatively short (robust) for a gazelle. In recent species, the metapodials tend to be much more elongated.

Bovidae indet. sp. 2 from Puerto de la Cadena is larger than *Gazella* aff. *lydekkeri*. It is represented by dental material (Fig. 7F) and postcranial bones. The teeth are moderately high crowned and the third molars are large and the premolars are reduced in size. These teeth are morphologically similar to those from the locality of La Gloria 4 (Teruel, Spain), described as *Tragoreas oryxoides* by Alcalá (1994), although the former are a little larger. The latter species is again similar to *Norbertia hellenica* described on the basis of material from Maramena (Köhler et al., 1995). However, both species appear to have P_4 with a more derived morphology than in Puerto de La Cadena. Postcranial remains larger than those assigned to *Gazella* aff. *lydekkeri* include metapodial fragments and a second phalanx. This phalanx is morphologically clearly different from the specimen assigned to the large gazelle. Its morphology lacks derived features seen in *Gazella* and Caprinae. Notably, it differs from the phalanx of *Norbertia*, which is clearly caprine (Köhler et al., 1995, Pl.6, fig. 2). Either the teeth and bones belong to a single species, which is not *Norbertia*, or the teeth represent that genus and the bones still another taxon.

A maxilla with three deciduous teeth and the first molars (Fig. 7D) as well as a P^2 represent a still larger species identified as Bovidae indet. sp. 3. It is a little smaller than *Parabos*, which is represented by the same deciduous teeth. The anterior parts of the D^2 and P^2 are very reduced.

The remains of *Parabos* sp. consist of deciduous and adult dentition: a maxilla with D^2-M^1 and a mandible with D_2-M_1, M^2 (Fig. 7N), P^3 and postcranial bones. They can be attributed to a primitive Bovini, close to *Parabos soriae* from Venta del Moro (Morales, 1984), or to *Parabos cordieri* from Montpellier (Gromolard and Guérin, 1980). The absence of a horn core impedes a precise attribution.

1.2. Reptiles

The reptile record of Puerto de la Cadena includes representatives of Crocodylia, Testudines, and Ophidia. The crocodilians represented at Puerto de la Cadena are indeterminate (Crocodylia indet.). The sample consists of two well-preserved teeth (Fig. 8) and a few fragments of osteoderms (not available for study). One tooth is somewhat robust and pointed, with a rather short crown (8.1 mm tall and 7.6 mm wide at the base; these proportiosn are indicative of a posterior tooth) that displays an average crocodylian morphology: classic conical shape with a mesiodistal, non-serrated carina separating the slightly swollen labial surface from the smaller lingual surface. Both surfaces are rather smooth, devoid of evident wrinkles, and the boundary between the crown and the root is marked by a small constriction. In contrast to the former tooth, which suggests that the crocodile died, the other corresponds to a shed tooth, so that only the tooth crown is preserved. The crown was at least 13 mm tall (it is slightly worn apically) and 8.3 mm wide at the base (mesiodistal diameter). It seems to be more elongated and curved, and rather slender, than the other tooth (indicative of an anterior maxillary tooth). The preserved morphology does not enable the precise taxonomic allocation of these specimens even to family rank, although it must be noted that they fit the typical tooth shape displayed by crocodyloids, only represented at that time in Europe by genus *Crocodylus* (Delfino and Rossi, 2013; Georgalis et al., 2016). Given that Puerto de la Cadena is here considered to be early Pliocene in age, the crocodilian bones described here (and attributed Crocodylia indet.) would represent, together with the fossils from Gargano (latest Messinian or early Zanclean; Apulia, Italy) attributed to *Crocodylus* sp. (Delfino et al., 2007), the youngest report of crocodilians in Europe. The oldest possible evidence of the presence of *Crocodylus* in Europe is from the early Tortonian Scrontone site (Abruzzo, Southern Italy; Delfino and Rossi, 2013), thus indicating that this taxon might have already reached Europe during the Tortonian, well before the MSC, which has been traditionally considered as the event that caused several trans-Mediterranean dispersals during the latest Miocene.

All the turtle remains identified in Puerto de la Cadena belong to the Cryptodira. The most abundant lineage is the family Testudinidae (i.e., tortoises or terrestrial turtles). It is relatively diverse, with three different forms being identified. In addition, a trionychid (softshell turtle) is also recognized.

One of the testudinids recognized in the area of study is *Titanochelon* sp. (Fig. 9A). The presence of a large testudinid was already recognized by Montenat (1973) in La Alberca, based on fragmentary material. He interpreted that this taxon had a similar size to ‘*Testudo*’ *perpiniana*, a French species recently reassigned to the genus *Titanochelon* (Pérez-García and

Vlachos, 2014). New remains from La Alberca, corresponding to fragments of plates and to a phalanx, were also identified as assignable to a large testudinid, having been attributed to '*Cheirogaster*' cf. *bolivari* (Pérez-García et al., 2011). In turn, a carapace found in another locality westward from Puerto de la Cadena, Barranco del Cigarrón, was preliminarily attributed to '*Cheirogaster*' *bolivari* (Mancheño et al., 2001). All the large species of Testudinidae (i.e., whose shell length is greater than 1 m) recorded in the European Neogene record, including the Iberian species '*Cheirogaster*' *bolivari*, have recently been reassigned to *Titanochelon* by Pérez-García and Vlachos (2014). The currently confirmed stratigraphic distribution of the species *Titanochelon bolivari* is from the Aragonian to the lower Vallesian (Langhian to early Tortonian, MN5 to MN10), of both Spain and Portugal (Pérez-García and Vlachos, 2014; Pérez-García et al., 2016). The preparation and study of the specimen preliminarily presented by Mancheño et al. (2001), and the preliminary analysis of other specimens found both in that locality and in other outcrops of Puerto de la Cadena (including well-preserved and relatively complete shells, partial shells, isolated plates, vertebrae and appendicular elements), do not allow us to support this specific attribution. Therefore, this taxon is here recognized as *Titanochelon* sp. The detailed study of these specimens, currently in progress, will allow a specific determination. This genus is known from the early Miocene to the Pleistocene (Pérez-García and Vlachos, 2014; Pérez-García et al., 2017). This is the most abundant turtle so far found in Puerto de la Cadena.

Apart from *Titanochelon* sp., Barranco del Cigarrón has yielded a partial shell that probably corresponds to a new taxon of Testudinidae. This shell, attributable to an adult individual, has an estimated length of less than one meter. The general morphology of its carapace, as well as characters such as the morphology and proportions of the nuchal plate and the epiplastra, allow us to exclude its attribution to the genus *Titanochelon*. This putative new taxon is larger in size than the members of the lineage of *Chersine hermanni,* but smaller than the representatives of *Titanochelon*.

Several disjointed elements corresponding to carapace plates of a relatively small form of Testudinidae (i.e., whose shell is less than 30 cm in length) are recognized in Puerto de la Cadena. As in the other testudinids, these plates are relatively thick, and the pleuro-marginal sulci overlap or are very close to the costo-peripheral sutures. The degree of development of the ossification of these plates enables their attribution to adult specimens. This relatively small taxon probably corresponds to a member of the lineage of *Chersine hermanni*, a well-represented clade in the Iberian record, known from the early Miocene and being part of the current diversity (Llorente et al., 2002; Pérez-García, 2017). In this paper we leave these specimens unassigned to genus as Testudinidae indet.

The presence of Trionychidae indet. has been previously recognized both in La Alberca and in other outcrops of Puerto de la Cadena area (see Pérez-García et al., 2011). The plates of this taxon lack sulci due to the absence of scutes. The external surface of the plates attributed to this clade is decorated by circular to elongated depressions, with a maximum length between 2 and 4 mm, separated by narrower crests (Fig. 9B, 9C). The material published so far is very scarce, so a more precise determination cannot be proposed. The recent identification of Trionychinae in Puerto de la Cadena represents the youngest reference in Spain, where this clade was known the Eocene to the early Miocene (see Pérez-García et al., 2011 and references therein). In addition, so far it corresponds to the only published reference to Trionychinae in the southern half of Spain.

Testudinids are terrestrial, whereas trionychids are aquatic turtles, with modifications in their appendicular skeleton which facilitated their dispersal both by continental freshwater environments and following the coasts (see Pérez-García et al., in press and references therein). The depositional environmental conditions interpreted for the top of Cigarrón Unit (where Puerto de la Cadena is placed), which is considered a continental setting related to fluvial systems near to the coast, is consistent with the environmental requirements of the turtles identified here.

At Puerto de la Cadena, ophidians are represented by the colubrine *Malpolon* gr. *monspessulanus-mlynarski* and the viperid *Vipera* sp. The former is represented by three large-sized trunk vertebrae with a centrum length (CL) longer than 6 mm and up to 7.2 mm. The trunk fossil vertebrae possess an elongated morphology of the neural arch wings in dorsal view as well as of the centrum in ventral view (CL/NAW > 1.3), a usually thin and sharp haemal keel, and straight posterior margins of the neural arch, which are characteristic of the representatives of the genus *Malpolon* (Szyndlar, 1988; Blain, 2005, 2009; Blain et al., 2007). The distinction between the extant *M. monspessulanus* and the extinct *Malpolon mlynarski* from the Pliocene (MN15) of Layna (Soria, Spain) is based on cranial elements (Szyndlar, 1988), thus precluding a species attribution within genus *Malpolon* for the material from Puerto de la Cadena.

The viperid is recorded by three large vertebrae (CL comprised between 8 mm and 11.8 mm) attributed to *Vipera* sp. "Oriental viper complex" sensu Szyndlar (1991). These isolated vertebrae can be referred to the genus *Vipera* on the basis of several characters (Rage, 1984; Szyndlar, 1991; Szyndlar and Rage, 2002): presence of a hypapophysis, depressed neural arch in posterior view, anteroventrally oriented parapophyseal processes, and slightly tilted prezygapophyseal facets. The large size of the vertebrae clearly suggest a referral to the representatives of the 'Oriental vipers' group, which hosts the largest representatives of the genus. Although reaching a similar size to the extinct *Daboia maxima* from the Pliocene (MN15) of Layna, the material from Puerto de la Cadena differs from the latter in lacking the depressed cotyle and condyle and the rectangular shape of the prezygapophyseal articular facets. 'Oriental vipers' have been identified in the Iberian fossil record in various Miocene localities of the Vallès-Penedès Basin (Delfino et al., 2015), in the early Pliocene of Caló d'en Rafelino (Manacor, Mallorca), in the Pliocene of Zújar (Bailon, 1991), and in the early Pleistocene of Medes Islands and Cova Bonica (Bailon, 1991; Blain, 2005, 2009; Bailon and Blain, 2007; Blain et al., 2016). Interestingly, the largest vertebra is very similar in size and shape to the trunk vertebra from Caló d'en Rafelino (CL = 12.7 mm – thus far the largest-sized European specimen of belonging to the "Oriental vipers complex"; Bailon et al., 2010) with a similar chronology ("very early Pliocene"). This fact suggests that they may belong to the same species, which would have dispersed across the Western Mediterranean Basin probably during the MSC.

2. Extended small mammal biostratigraphy

Zorreras 3A (Martín Suárez et al., 2000), in the Sorbas Basin, has in common with the Puerto de la Cadena the presence of *Paraethomys meini* and *Stephanomys dubari*. However, the former site records a different species of *Debruijnimys* (*D. almenarensis*). Similarly, the localities of Negratín 1 (Guadix Basin; Minwer-Barakat et al., 2009a) and Almenara-Casablanca M (Eastern Spain; Agustí, 1990; Agustí et al., 2011) share with Puerto de la Cadena the presence of *Paraethomys meini* and *Stephanomys dubari*. Moreover, *Ruscinomys lasallei* has been recognized in Almenara-Casablanca M, and *Ruscinomys* sp. in Negratín 1. However, these localities also record *Debruijnimys almenarensis* and *Apocricetus alberti*. The same applies to Gafares 2B, in the Almería-Níjar Basin, which has yielded remains of

Stephanomys dubari, *Paraethomys meini*, and *Debruijnimys almenarensis* (García-Alix et al., 2016).

The arrival of *Debruijnimys* sp. is related to a second immigration wave after to that of *Debruijnimys almenarensis* (see Agustí and Casanovas-Vilar, 2003). Whereas *Debruijnimys* sp. has been reported from early Pliocene localities, *Debruijnimys almenarensis* has been found in sites assigned to the late Miocene (Castillo and Agustí, 1996; Agustí and Casanovas-Vilar, 2003). This fact suggests an older age for Almenara-Casablanca M, Negratín 1, Gafares 2B, Salobreña, and Zorreras 3A.

The Puerto de la Cadena site can be compared with the *Apodemus gudrunae* zone of the Guadix Basin, in which the reference locality is Negratín 1 (Minwer-Barakat et al., 2012). Other localities assigned to this biozone are Rambla Chimeneas 3 (Minwer-Barakat et al., 2009b), which has in common the occurrence of *Stephanomys dubari* and *Paraethomys meini*, and Bacochas 1 (Sesé, 1989) in which *Paraethomys meini* and probably *Debruijnimys* (see Minwer-Barakat et al., 2009a) have been identified. However, the presence of *Apocricetus alberti* suggests a somewhat older age than Puerto de la Cadena.

The locality of Purcal 4, in the Granada Basin, resembles Puerto de la Cadena in recording *Paraethomys meini*, *Stephanomys dubari, Apocricetus barrierei* and *Ruscinomys lasallei* (García Alix et al., 2008c). This assemblage suggests a similar age to Puerto de la Cadena. In this way, the latter site may be correlated with the lower part of the *Apocricetus barrierei* zone in the Granada Basin (García-Alix et al., 2008c). The cricetid *Ruscinomys* aff. *schaubi* has been found in la Dehesa 16, suggesting a slightly older age. On the contrary, the appearance of a large-sized *Paraethomys* (*P.* aff. *abaigari*) in Purcal 13 (García-Alix et al., 2008a) indicates a younger age than for Puerto de la Cadena. *Paraethomys* aff. *abaigari* and *Paraethomys abaigari* are common elements in numerous localities assigned to the early Ruscinian (MN14; e.g., Mein et al., 1990; Adrover et al., 1993; García-Alix et al., 2008a; Mansino et al., 2013, 2015a; Piñero et al., in press).

Puerto de la Cadena may be correlated with other sites from the Iberian Peninsula. The Cabriel Basin has yielded a number of late Miocene/early Pliocene localities such as Venta del Moro (Montoya et al., 2006; Mansino et al., 2014, 2016a, 2016b), Fuente del Viso (Opdyke et al., 1997), and La Bullana 2B (Mansino et al., 2015b). The Puerto de la Cadena site has in common with Venta del Moro some rodent species, such as *Stephanomys dubari*, and *Paraethomys meini* (Mansino et al., 2014, 2016a). However, the record of *Apocricetus alberti*, and the ancestor of *Ruscinomys lasallei* (*Ruscinomys schaubi*) in Venta del Moro indicates an older age. In addition, this site was deposited before the start of the "Gerbil Event" (Agustí et al., 2006), unlike Puerto de la Cadena.

The presence of *Paraethomys* aff. *abaigari*, and *Debruijnimys* cf. *julii* in La Bullana 2B (Mansino et al., 2015b) indicates a younger age than Puerto de la Cadena. In contrast, Fuente del Viso may have a similar age, given the record of *Prolagus michauxi*, *Ruscinomys lasallei*, *Stephanomys medius* (=*S. dubari, S. cordii*), *Paraethomys anomalus* (=*P. meini*) and *Cricetus barrierei* (=*Apocricetus barrierei*) (Opdyke et al., 1997; Freudenthal et al., 1998), thereby suggesting a very close age to Puerto de la Cadena.

The small mammal association from Puerto de la Cadena may also be correlated with the *Apocricetus barrierei* zone proposed by Mansino et al. (in press) for the Alcoy Basin. The level of Alcoi Forn 1'07 resemble to Puerto de la Cadena in the occurrence of *Paraethomys meini*, *Stephanomys dubari* and *Apocricetus barrierei* (Mansino et al., 2015c).

Regarding the Teruel Basin, Puerto de la Cadena can be partly correlated with the upper part of the *Stephanomys ramblensis* Zone (Mein et al., 1990), in which the Arquillo 4 locality (Adrover et al., 1993) shares with Puerto de la Cadena the presence of *Paraethomys anomalus* (=*P. meini*), *Ruscinomys* cf. *lasallei*, and *Prolagus michauxi*, although the identification of *Stephanomys ramblensis* in Arquillo 4 suggests an older age. Similarly, Celadas 2 (Adrover et al., 1993) shares with Puerto de la Cadena the presence of *Ruscinomys lasallei* and *Prolagus michauxi*, but the occurrence of *Stephanomys ramblensis* and *Apocricetus* cf. *alberti* indicates a somewhat older age for the former. On the contrary, the presence of *Apocricetus barrierei* in Peralejos E (Adrover et al., 1988) indicates a close age to Puerto de la Cadena.

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VIII. LOS ROEDORES DE BAZA-1 (CUENCA DE GUADIX-BAZA, SE ESPAÑA): COMPLETANDO LA SUCESIÓN DEL PLIOCENO INFERIOR DE LAS BÉTICAS

Rodents from Baza-1 (Guadix-Baza Basin, SE Spain). Filling the gap of the early Pliocene succession in the Betics

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ABSTRACT

ABSTRACT—The Guadix-Baza Basin (Granada, southern Spain) represents one of the best continental records from the late Miocene to the middle Pleistocene in Western Europe, but stratigraphic gaps are present in the early Pliocene due to the scarcity of sites from this age. In this paper, rodent fossils from the locality of Baza-1 are described, providing new information on a time interval that was previously poorly known. The assemblage includes representatives of the genera *Ruscinomys*, *Apocritetus*, *Stephanomys*, *Apodemus*, *Castillomys*, *Paraethomys*, *Occitanomys*, *Eliomys*, *Debruijnimys* and *Trilophomys*, an association that indicates an early Ruscinian age (MN14). A paleoecological analysis indicates the Guadix-Baza Basin landscape during the early Pliocene was dominated by open herbaceous habitat under warm and dry climatic conditions. Our results contribute to the continuity of the stratigraphical record from the Betic Mountain range.

INTRODUCTION

The Pliocene (ca. 5.33–2.58 Ma) saw global climate shift from an early Pliocene warm period (5–3 Ma) to the intensification of Northern Hemisphere glaciation (~2.75 Ma) (Ravelo et al., 2004). Since it represents a kind of 'climatic optimum' before the onset of Pleistocene glacial-interglacial dynamics, the Pliocene can help us to understand climatic change patterns and climate sensivitiy (Pagani et al., 2010). The Pliocene marine record is well-known from several sections and cores, but continuous Neogene continental sections are scarce in the Western Mediterranean. In this sense, the Guadix-Baza Basin (southern Spain) represents one of the best continental records from the late Miocene to the middle Pleistocene in Western Europe,with localities providing a fairly complete stratigraphical sequence of micromammals. In fact, a basic tool for the identification of biochronologic units in the Neogene and Quaternary continental beds are small mammals, especially rodents (Fahlbusch, 1991; Minwer-Barakat et al., 2012). Most of the biozones from the Guadix-Baza Basin are defined on the basis of studies of micromammals from several sites (Agustí, 1986, 1990a; Martín Suárez, 1988; Ruiz

Bustos, 1990; Agustí and Martín Suárez, 1994; Oms et al., 2000; Gibert et al., 2007; Minwer-Barakat et al., 2012; Agustí et al., 2014; Piñero and Agustí, 2015).

Despite the excellent continental record in the Guadix-Baza Basin, a stratigraphic gap is present in the early Pliocene due to the scarcity of sites and material from this age. Some of early Pliocene localities in this basin are Yeguas, Gorafe A, 1 and 4. However, these sites have yielded scarce material, making it difficult to complete the biostratigraphic information of this period in the Guadix-Baza Basin. Guerra Merchán et al. (1991) provided a rodent list from other early Pliocene localities such as Aljibe 2, Aljibe 3 and Colorado 2. These sites are located in the same ravine as Baza-1 and their rodent associations are very similar to that of this locality. Aljibe 2 and Aljibe 3 are settled at levels above Baza-1 whereas Colorado 2 falls below on the opposite side (A. Guerra-Merchán, pers. comm., October, 2015). Unfortunately, no measurements, descriptions or discussion of the taxa was presented, making it difficult to confirm the biostratigraphical and chronostratigraphical position of these localities. Here we provide a complete discussion and description of the rodents from Baza-1 to better fill this gap in the Guadix-Baza sequence. The large number of fossils recovered from this locality helps complete the biostratigraphic succession of the early Pliocene of the Betics.

The site of Baza-1 is located near the town of Baza, in the ravine known as Seguidillas-Cuesta del Francés (Las Arrodeas), about 50 meters from a water reservoir (Ros-Montoya, 2010; Martínez-Navarro et al., 2015; Piñero et al., 2016a). The coordinates correspond to 37° 29′ 00″ N, 2° 47′ 05″ W. Baza-1 has provided a rich vertebrate assemblage making it of great interest given the scarce record of localities from early Pliocene in southern Spain. The following large mammals have been identified (Ros-Montoya, 2010; Martínez-Navarro et al., 2015): two proboscideans (*Mammut borsoni* and *Anancus arvernensis*, first record of the coexistence of both these species in the Iberian Peninsula); two bovids, a large-sized form (*Alephis* sp.) and a medium-sized form (under study); a rhinocerotid (*Stephanorhinus* sp. cf. *S. jeanvireti*); a cervid (Cervidae indet.) and an equid (*Hipparion* sp.). The herpetofaunal association comprises an anuran (Anura indet.), an anguid (Anguidae indet.), a lacertid (Lacertidae indet.), a blind snake (Scolecophidia indet.), a cobra (*Naja* sp.), and tortoises (Testudinae indet.). The site has also yielded several teeth and vertebrae of fishes belonging to the family Cyprinidae. Among the micromammals, besides the ten rodent taxa described in this article, two lagomorphs and four insectivores have been recognized: *Trischizolagus maritsae*, synonymous with *Trischizolagus crusafonti* (34 molars + premolars), *Prolagus michauxi* (five specimens), and Desmaninae indet. (one left P4), cf. *Sorex* sp. (two trigonids of right m1 and one left m2), cf. *Sorex minutus* (one right m2), and cf. Erinaceinae indet. (one premolar), respectively. Finally, a single tooth represents a bat (Chiroptera indet., one right m1).

GEOLOGICAL SETTING

The Baza-1 site is found within the sedimentary succession that infills the Guadix-Baza Basin (Granada Province, Southern Spain). This basin was located in the depression developed at the contact area between the Paleozoic basement and Mesozoic cover of the Betic chain (also known as External and Internal areas, respectively). During part of the Miocene the basin was infilled by marine rocks deposited in a corridor connecting the Atlantic Ocean with the Mediterranean Sea. The basin was uplifted around 8 Ma (see Hüsing et al., 2010) isolated it from the sea. This isolation led to the sedimentation of continuous terrestrial endorheic sedimentation (see main units in Fernández et al., 1996; Soria et al., 1998). The basin accumulated sediments until being completely filled up with the sedimentation of a stratigraphic unit known as ‘topmost level’ (Vera, 1970). This level provides the present day flat morphology of the center of the basin and is connected with the colluvial slopes of the basin margin. This level started to be eroded when the Guadix-Baza area became the catchment of the Guadalquivir River (Calvache and Viseras, 1997). This fluvial capture took place just before 205.000 years ago (Díaz-Hernández and Julià, 2006; see discussion in Oms et al., 2011).

The Guadix-Baza Basin, in fact, contains the Guadix and the Baza sub-basins, which are separated by the Baza fault (Alfaro et al., 2008). The Baza fault is a key feature of the structure of the Guadix-Baza Basin and is extended below the basin infill and south of Baza branches in several splays. It has been active since late Miocene (Alfaro et al., 2008) and at present day has a moderate level of seismic activity, and has likely been responsible for the earthquake that happened in 1531 at Baza town (Sanz de

Galdeano et al., 2012). At present, this fault has vertical slip rates between 0.17 and 0.49 mm/year (Sanz de Galdeano et al., 2012) and has an active control in the geomorphologic evolution of the study area by a displacing the glacis and modifying hill slopes (García-Tortosa et al., 2011, see also Goy et al., 1989).

The sedimentary infill of the Guadix-Baza Basin is dominated by two main formations: the alluvial Guadix Formation (Viseras, 1991) and the lacustrine Baza Formation (Vera, 1970). In the basin margins, where the Guadix Fm evolves laterally to the Baza Fm, the sucessive lake transgressions-regressions lead to the development of palustrine environments. These palustrine subenvironments within Baza Fm are generally built up by a succession of limestones and dark mudstones, being the latter rich in micromammals sites (Oms et al., 2000). This is the case of the Baza-1 site. In detail, this locality is build up of brown-to-black claystones and siltstones, with some thin stretches of sandstones. This distinctive level is found in a thicker succession of limestones and marly limestones displaying abundant structures typical of the palustrine environments such as calcrete nodules and root marks. The mechanical contrast between dark mudstones and limestones (ductile and fragile, respectively), together with the geomorphologic dynamics of the area, enhance local hillslope processes including the limited sliding of the studied rocks. That is the reason why the Baza-1 site and the adjacent strata appear so deformed. At the other side of the creek where the Baza-1 site is found, such processes are absent, so an unaltered succesion is observed. The careful study of the stratigraphy of the outcrop (Fig. 1D) and the fact that all paleontological material exactly cames from the excavated sediments permits to state that paleontological material belongs only to the ca. 1m dark mudstones.

MATERIALS AND METHODS

The microfaunal remains were recovered from the sediment collected at Baza-1 during the excavation campaign of 2001. The sediment was water-screened using superimposed 4, 1 and 0.5 mm mesh screens. Fossils are owned by the Junta de Andalucia but currently part of the collection (248 specimens) is kept at the Institut de Paleoecologia Humana i Evolució Social (IPHES; Tarragona, Spain), whereas the other part (157) is stored at the Institut Català de Paleontologia Miquel Crusafont (ICP; Sabadell, Barcelona, Spain).

Baza-1 assemblage includes 402 identified rodent teeth, representing at least 11 taxa. All the measurements (L x W) are expressed in millimeters and were taken on the occlusal plane of the molars with the software DinoCapture 2.0, using photographs from the Digital Microscope AM4115TL Dino-Lite Edge. Tooth images shown in the illustrations were made with the Environmental Scanning Electron Microscopy (ESEM) of the Servei de Recursos Científics i Tècnics de la Universitat Rovira i Virgili (Tarragona). The upper premolars and molars are indicated as P4, M1, M2 and M3, the lower premolars and molars as p4, m1, m2 and m3 and the deciduous specimens as D4.

In describing and measuring the teeth of Murinae, we have followed Van de Weerd (1976) and Martín Suárez and Freudenthal (1993), respectively. Wood and Wilson (1936) have been used for the nomenclature of Taterillinae and Minwer-Barakat (2005) for the measurements. The terminology employed for the description and method of measuring of the teeth of Gliridae are those defined by Freudenthal (2004). The nomenclature and method of measuring used in the descriptions of the Cricetidae teeth are those defined by Mein and Freudenthal (1971). The terms “preloph” and “prelophid” are taken from Freudenthal (1985). For the case of *Trilophomys*, we have followed Brandy (1979a).

The quantitative composition of the micromammal assemblage has been calculated on the basis of the relative abundance of each taxon (following Martín Suárez, 1988; Castillo Ruiz, 1990; Martín-Suárez et al., 2001; Minwer-Barakat, 2005; García-Alix et al., 2008a; García-Alix et al., 2009). To avoid the over-representation of a taxon, we used the total number of teeth of each taxon, divided by its number of diagnostic elements (Murinae, Cricetidae, Gerbillidae and Trilophomyidae: 12 molars; Gliridae: 16 teeth; Soricidae: 20 teeth; Erinaceidae and Talpidae: 44 teeth; Lagomorph: 22 jugal teeth).

Institutional Abbreviations—IPHES, Institut Català de Paleoecologia Humana i Evolució Social; **IPS**, Institut de Paleontologia de Sabadell.

Anatomical Abbreviations—**L**, length; **W**, width; **tma**, anterocentral cusp; **c1**, posterior accessory cusp; **t1–t12**, numbered tubercules from 1 to 12; **L1**, occlusal surface length; **L2**, crown maximum length; **L3**, crown base length.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821

Family CRICETIDAE Rochebrune, 1883

Subfamily CRICETINAE Fischer, 1817

Genus *APOCRICETUS* Freudenthal, Mein and Martín Suárez, 1998

APOCRICETUS BARRIEREI (Mein and Michaux, 1970)

(Fig. 2A–F)

Ocurrence and Material—Baza-1: 16 M1s (BA1-2001-R1/1–7, IPS89207, IPS89209–89216), 26 M2s (BA1-2001-R1/8–22, IPS89217–89227), 20 M3s (BA1-2001-R1/23–32, IPS89228–89237), 25 m1s (BA1-2001-R1/33–44, IPS89208, IPS89238–89249), 30 m2s (BA1-2001-R1/45–64, IPS89250–89259), 19 m3s (BA1-2001-R1/65–74, IPS89260–89268).

Measurements—See Table 1.

Description—The m1s are simple and have a crest-like anteroconid in most of the specimens. However, there is slight evidence of bifid (three specimens) or trifid (three specimens) anteroconid. The anterolophulid is usually double, connecting the anteroconid to the prelophid. However, there are two cases of simple anterolophulid, labial in one case and directed to the middle of the anteroconid in another case. The prelophid is wide in six specimens and short in another six. The mesolophid is always absent except in one individual, in which a very small mesolophid can be observed. The metalophid and the protolophid are always anterior. The posterolophid is directed to the base of the entoconid, without closing the posterosinusid. In m2s the anterosinusid is absent. The labial cingulum is well developed and descends to the base of the protoconid. The protolophid is anterior in all the individuals. The mesolophid is absent. The metalophid is anterior in all individuals. The posterolophid is directed to the base of the entoconid, closing the posterosinusid in one specimen. The m3s have the anterosinusid absent. The well-developed labial cingulum reaches the base of the protoconid. In one individual, a small lingual cingulum delimitates a small anterosinusid. The protolophid is anterior in all the specimens. A well-developed mesolophid is present in one case and small or vestigial in seven. The metalophid is anterior. Sinusid and mesosinud closed at the base by low cingula. The posterolophid is directed to the base of the entoconid, closing the posterosinusid in all the individuals.

The M1s display double anterocone. The two cusps of the anterocone are connected anteriorly. A well-developed cingulum ridge at the base of the anterocone is present in all the cases. All the specimens have double anteroloph, each branch connecting the two cusps of the anterocone to the preloph. The protolophule is posterior in most of the cases, except in two specimens with double protolophule and another case in which a small anterior protolophule is observed at the base of the anterosinus, not reaching the paracone. Except in two cases, there is always a well-developed entoloph. The mesoloph is absent. There is a well-developed anterior metalophule which reaches the anterior wall of the metacone. Labial and lingual sinuses closed at the base by basal cingula. A posterior metalophule is present in three individuals, delimiting a posterorsinus. The posteroloph is connected directly to the posterior wall of the metacone. In M2s there are a well-developed lingual anteroloph. A labial anteroloph is present in 17 specimens at the base of the crown. A posterior protolophule is present in most of the specimens, whereas a double protolophule is present in three cases. The very small entoloph, the posterior arm of the protocone, the posterior protolophule, the anterior metalophule and the anterior arm of the hypocone performing an X-like shape. The anterior metalophule is always present (except in one individual), connecting with the anterior wall of the metacone. The posterior metalophule is absent, so the posterior posteroloph is directly connected to the posterior wall of the metacone. The M3s show a well-developed labial anteroloph which connects to the base of the paracone. The posteroloph is posterior in all except one case, in which a double protolophule is observed. There is a well-developed entoloph. The metalophule is anterior in all the specimens. The posterior metalophule is absent, so the posterior posteroloph is directly connected to the posterior wall of the metacone. Sinus and mesosinus closed at the base by basal cingula.

Remarks—*Apocricetus barrierei* was originally identified in the early Pliocene of Southern France (Hautimagne, Chabrier, Celleneuve, Vendargues; Mein and Michaux, 1970), but later recognized in many sites from Spain: Vilafant, Caravaca, Alcoy 4B, La Alberca, Botardo-C and D, Gorafe 4 and others (Gibert et al., 1980; Freudenthal et al., 1998). Despite the wide geographic range of this species, its dental variability has been badly known, because it is usually represented by a small number of teeth. The large sample from Baza-1, with more than 120 teeth permits to constrain the features of this species. Quite surprinsingly, the new material indicates a remarkable uniform population, with a quite stable dental pattern. Variability is restricted in the lower molars somehow to the shape of the anteroconid, which can be rarely bifid or trifid, the width of the prelofid and the rare presence of a small mesolophid. The variability of the upper molars is even more restricted, only affecting to the presence of a lingual anteroloph in some M2 specimens. The stability of this design is in contrast with the high variability observed in populations of *Apocricetus alberti* (Mansino et al., 2014a). In terms of size, the sample from Baza-1 is comparable to the original material described by Mein and Michaux (1970) from the type-locality of Chabrier and other Southern France sites. In contrast, *Apocricetus barrierei* from Baza-1 displays larger teeth than the scarce material coming from the early Pliocene sites of Botardo-C and D, in the same Guadix-Baza Basin (Freudenthal et al., 1998), probably indicating a younger age.

Subfamily CRICETODONTINAE Stehlin and Schaub, 1951

Genus *RUSCINOMYS* Depéret, 1890

RUSCINOMYS cf. *LASALLEI* Adrover, 1969

(Fig. 3A, B)

Ocurrence, Material, and Measurements—Baza-1: seven fragments (BA1-2001-R2/1–7) and one partial M1 (IPS89340). The poor preservation of the molars does not allow take measurements, except the length in the fragment of M1 (4.52 mm).

Description—The only recognizable tooth of *Ruscinomys* is a fragmented M1, which preserves the lingual wall and the anterocone. The anterocone is double, with a deep and long groove on the anterior wall of the tooth separating its two lobes. The posterior wall of the protocone is backward projected to the anterior wall of the hypocone. The rest of fragments can not be identified, but they are large and have thick enamel and high crown.

Remarks—The few specimens are incomplete, but the great hypsodonty of the fragments, the large size and the enamel thickness, allow us to ascribe these specimens to the genus *Ruscinomys*. The only reconognizable tooth agrees in size and morphology with the species *Ruscinomys lasallei*. Due to the scarcity of fossils we adscribe it to *Ruscinomys* cf. *lasallei*. This genus was created by Depéret in 1890 to define a large-sized and high-crown cricetid from the Pliocene of Perpignan, *Ruscinomys europaeus*. In the late Miocene and early Pliocene of Western Europe, this genus is frequent, showing increase of tooth size and the crown height over time (Minwer-Barakat et al., 2009). The Guadix-Baza Basin has yielded a very scarce sample of the genus *Ruscinomys*. Localities where they have been identified within the referred basin are: Pino Mojón with *Ruscinomys* cf. *schaubi* (Sesé, 1989), Gorafe A with *R. lasallei* (Ruiz Bustos et al., 1984), Gorafe 5 and Barranco Cañuelas 5 with *R. europaeus* (Martín Suárez, 1988; Sesé, 1989), Gorafe 1, Colorado 2 and Negratín-1with *Ruscinomys* sp. (Guerra-Merchán et al., 1991; Minwer-Barakat et al., 2009). In the Granada Basin there is a continuous record of *Ruscinomys* from the late Turolian to the early Ruscinian, corroborating the lineage between *R. schaubi* and *R. lasallei* (García-Alix et al., 2008b). In the Teruel Basin *Ruscinomys* is very abundant in the middle Turolian, but scarce in late Turolian and Ruscinian localities, so some sort of ecological control is supposed (Adrover et al., 1993).

Genus TRILOPHOMYS Depéret, 1890

TRILOPHOMYS cf. *VANDEWEERDI* Brandy, 1979a

(Fig. 4A, B)

Occurrence, Material, and Measurements—Baza-1: two m1s (IPS89338, L1: 2.64 mm, L2: 2.87 mm, L3: 2.48 mm, width: 1.65 mm; IPS89339, L1: 2.28 mm, L2: 3.19 mm, L3: 2.81 mm, width: 1.68 mm), one M3 (IPS89345, L1: 1.21 mm, L2: 1.44 mm, L3: 1.48 mm, width: 1.51 mm).

Description—The m1s have three tranversal lobes connected by a longitudinal crest. The salient angles of these lobes are acute and romboid in one specimen and rounded in the other. In both cases the anterior lobe displays a shallow lingual re-entrant angle. In one individual a very tiny salient angle is observed on the labial wall of the anterior lobe. In both molars the lingual re-entrant angles are deeper than the labial ones. The end of these re-entrant angles is acute in one case and rounded in the other. The two cusps of the medial lobe are opposed in one individual, forming a romboid pattern. In the other case, the labial cusp is somewhat advanced with respect to the lingual one, therefore forming a sigmoid pattern.

The M3 is formed by two lobes. The anterior lobe is formed of two cusps, the lingual one being very elongated. On the anterior wall of the labial one a small anterolophid is present. The lingual re-entrant fold is very deep, whereas the labial one is much shallower.

Remarks—*Trilophomys* cf. *vandeweerdi* from Baza-1 is considerably larger than *Trilophomys castroi* from the Teruel Basin (Adrover, 1986) and comparable in size to the samples from the Pliocene sites of Layna, Mas Senegals and Balaruc IV (Brandy, 1979a). Its presence at the early Pliocene of Baza-1 reinforces the argument about the existence of more than one lineage in this genus. In the Guadix-Baza Basin, *T. vandeweerdi* has been quoted at the sites of Tollo de Chiclana 1B (Minwer-Barakat, 2005), Gorafe A (Ruiz Bustos et al., 1984), Rambla del Conejo (Sesé, 1989), Yeguas (Soria Mingorance and Ruiz Bustos, 1991) and Nuca 1 (Ruiz Bustos, 1991). Another species of the genus *Trilophomys* found in the basin is *Trilophomys* cf. *castroi*, identified at the localities of Gorafe 3, 4 and 5 (Martín Suárez, 1988). Hitherto *T.* cf. *vandeweerdi* from Baza-1 represents the oldest record of that genus in the Guadix-Baza Basin.

Family MURIDAE Illiger, 1811

Subfamily MURINAE Illiger, 1811

Genus *STEPHANOMYS* Schaub, 1938

STEPHANOMYS CORDII Ruiz Bustos, 1986

(Fig. 5A–F)

Ocurrence and Material—Baza-1: three M1s (BA1-2001-R3/1, IPS89341, IPS89271), five M2s (BA1-2001-R3/2–5, IPS89342), two M3s (BA1-2001-R3/12, IPS89289), two m1s (BA1-2001-R3/6, BA1-2001-R3/13), three m2s (BA1-2001-R3/14, IPS89343, IPS89344), five m3s (BA1-2001-R3/7–11).

Measurements—See Table 2.

Description—The lower molars have a well-developed longitudinal crest which connects the hypoconid-entoconid to the protoconid-metaconid junction. The m1s have the anteroconid slightly asymmetrical, with anterolingual cusp softly elongated ahead. The tma is absent. The hypoconid is displaced backward. The posterior heel is larger than c1 and lingually displaced. The shape may be triangle or almost laminar, and in one out of two molars (BA1-2001-R3/6) continues through a ridge up to posterolingual base of the hypoconid. The labial cingulum may be weak or moderate. The c1 is low, round and connected to the hypoconid. Another accessory cusp may be present. The terminal heel is oval, large and isolated. In m2s the longitudinal crest is lingually displaced. The anterolabial cusp is elongated toward the small labial cingulum. The c1 is low, small and crest-shaped. The posterior heel is oval, low and may be large or small. The m3s have a longitudinal crest joined to the protoconid. It is interrupted in some specimens. The anterolabial cusp is low, poorly developed and connected to the protoconid.

The upper molars display a great stephanodonty. M1s have the t1 displaced backward. The t1 and t3 have a symmetric disposition with respect to the t2. There are t1bis and t2bis. Both the labial crest (t3–t5 connection) and the lingual crest (t1–t5 connection) are present. Even t4 is connected to t8 by a ridge. In IPS89341 the t1–t5 and t4–t8 connections are very low. The t7 is absent. The t12 is present as a small salient angle of the t8. In M2s the t1 is large. In one out of five molars there is a t1bis (BA1-2001-R3/4). The posterior crests of t1 and t3 are well developed and connected to the t4-t5 and t5-t6 intersection respectively. The t12 is absent except in one specimen (BA1-2001-R3/2), in which it appears as a thickening of the t8-t9 crest. The M3s have a large t1 connected to the t5. The t3 is absent. The t8 is connected to the t4-t6 intersection by a low ridge.

Remarks—The morphology of the studied teeth is consistent with that of the genus *Stephanomys*: high crown, longitudinal crest in the lower teeth, and posterior crests and spurs of t1 and t3 in the upper teeth (see Fig. 5A, B). These specimens are higher crowned, larger and more stephanodont than those of Miocene species such as *Stephanomys stadii* and *Stephanomys ramblensis*. The size of *Stephanomys* from Baza-1 is smaller than other Pliocene species such as *Stephanomys vandeweerdi*, *Stephanomys donnezani*, *Stephanomys calveti*, *Stephanomys thaleri* and *Stephanomys balcellsi*. Although some of our specimens fall within the size range of *Stephanomys minor*, they differ in the tubercular shape of the posterior heel. The measurements of our population are larger than most *Stephanomys dubari* populations, but seem to be close to those of Castelnou 3 (type locality, Aguilar et al., 1991), PUR-13 (García-Alix et al., 2008c), La Gloria 4 and Peralejos E (Adrover et al., 1993). Nevertheless the mean values of the studied sample are closer to the maximum values of the former populations. Adrover et al. (1993) identified *Stephanomys medius* in La Gloria 4 and Peralejos E. *Stepanomys medius* is a “nomen nudum” because the PhD dissertation of Cordy (1976), which originally described this species, was not published in a peer-reviewed journal. According to López Martínez et al. (1998) its correct denomination is *Stephanomys donnezani cordii*. García-Alix et al. (2008c) elevated this taxon to species level and called it *Stephanomys cordii*. However they considered the populations from La Gloria 4 and Peralejos E as *Stephanomys dubari*. The measurements of some of the teeth match those of *Stephanomys margaritae*. However, one of the diagnostic traits of the last species is the size of the M2 (Adrover, 1986), and the populations with measurements, such as Aldehuela, Arquillo 3 (Adrover 1986), Villalba Alto Río (Adrover et al., 1988), and Gorafe 5 (Martín Suárez, 1988) have a larger size than the specimens from Baza-1.

The mean values of *Stephanomys* from Baza-1 are similar to those of the type locality of *S. cordii* (Alcoy), and its size lies within the range of variation of *S. cordii* from Alcoy 2D (Mansino et al., 2013), and Celadas 9 (Adrover et al., 1993). In addition, they show the typical traits of *S. cordii*, such as symmetric disposition of t1 and t3 with respect to the t2 in the M1, reduced labial cingulum in m1 and m2, tubercular posterior heel and m3 with a poorly-developed anterolabial cusp and longitudinal crest joined to the protoconid (Cordy, 1976). Accordingly, the material from Baza-1 is identified as *S. cordii*.

Freudenthal and Martín Suárez (1999) reported that the evolutionary trends of *Stephanomys* genus are increasing crown height, development of longitudinal crests in both upper and lower molars, and increasing stephanodonty. Aguilar et al. (1991) defined *S. dubari* as an intermediate species between *S. ramblensis* and *S. cordii*; and Adrover (1986) consider *S. margaritae* to be a descendant of *S. cordii*. Minwer-Barakat (2005) proposed a single evolutionary line in which there is a continued increase in size, crown height and stephanodonty: *S. ramblensis* – *S. dubari* – *S. cordii* – *S. margaritae* – *S. vandeweerdi*. This justifies the overlap of the size of *S. cordii* from Baza-1 with the maximum size of *S. dubari* and the minimum size of *S. margaritae* from some populations.

Genus *APODEMUS* Kaup, 1829

APODEMUS GORAFENSIS Ruiz Bustos, Sesé, Dabrio, Peña and Padial, 1984

(Fig. 5G–L)

Occurrence and Material—Baza-1: four M1s (BA1-2001-R4/1–4), four M2s (BA1-2001-R4/5–8), one M3 (BA1-2001-R4/9), one m1 (BA1-2001-R4/10), three m2s (BA1-2001-R4/11–13), six m3s (BA1-2001-R4/14–16, IPS89321, IPS89322, IPS89324).

Measurements—See Table 3.

Description—The m1 has a large tma. The connection between the symmetric anteroconid and the tma forms a funnel. The anteroconid, protoconid and metaconid are separated. There is a well-developed labial cingulum contacting the labial anteroconid. There are two small accessory cusps, and a large and oval c1. The posterior heel is oval and smaller than c1. The m2s have a small and low anterolabial cusp. There is a well-developed labial cingulum. The c1 is small and round. There is no presence of other accessory cusps. The posterior heel is large and oval. In m3s the anterolabial cusp is very weak. Two specimens develop a reduced labial cingulum. There is no c1.

In M1s the t1 is posterior to t2 and t3. The t1-t2 connection is very low. One specimen (BA1-2001-R4/2) has t2bis. There is a small posterior spur in t3 directed to t5-t6 intersection. Three out four individuals have a deep and wide separation between t1 and t4, and t3 and t6. The elongated t7 may be separated from t4 by a small valley or connected. The t6-t9 connection is very low. The well-developed t12 is low. In M2s the t1 is large and may have a posterior spur directed to the posterior side of t5. The t1 is larger than t3. The t7 is large and elongated. The t4-t7 and t6-t9 connections are very low. These tubercles are separated by a small valley in one specimen (BA1-2001-R4/8). The t12 is well developed and elongated. It is connected to the posterolabial face of t8, and separated from t9. The M3 has a large and oval t1 in contact with t5. The t3 and t9 are absent. The large t8 is isolated, showing a small valley in the t8-t4 and t8-t6 intersection.

Remarks—The studied teeth share the main features of the genus *Apodemus*: connecting crest between t4 and t8 in the upper molars (which over time forms a t7), t6 and t9 united, presence of t12, t1 in an anterior position, absence of t1bis in M2, longitudinal crest is usually absent in the lower molars, and tma is practically always present (Martín Suárez and Mein, 1998). Our specimens are larger than those of Miocene species, including *Apodemus lugdunensis*, *Apodemus barbarae* and *Apodemus meini*. Besides, the size of *Apodemus* from Baza-1 is larger than the medium-small-sized species such as *Apodemus atavus*, *Apodemus mystacinus*, *Apodemus sylvaticus* and *Apodemus flavicollis*. The studied material differs from *Apodemus gudrunae* by its more developed t7 and larger size. The size values resemble to those of *Apodemus agustii* from its type locality Cañada del Castaño-1 (Guadix-Baza Basin, Martín Suárez, 1988), but our specimens are narrower. Moreover, *A. agustii* is characterized by the absence of stephanodonty in the upper molars and the development of a funnel in the m1, delimited by the anteroconid, protoconid and metaconid, features which are lacking in our sample. The size of the studied material is similar to that of *Apodemus jeanteti*, but differs mainly in the morphology: the studied material has a well-developed tma in m1 and a weaker connection between t6 and t9 in the upper molars. The population from Baza-1 agrees both in size and morphology with *Apodemus gorafensis* from the type locality Gorafe A (Ruiz Bustos et al., 1984), showing t7, a weak t6-t9 connection, a large tma and a well-developed labial cingulum. However, the material from Baza-1 displays a larger variability than that of *A. gorafensis* from its type locality. Measurements are also quite close to *A. gorafensis* from Gorafe 4 (Martín Suárez, 1988), DHS-16, MNA-4, MNA-2, CLR-1, CAC-11 (García-Alix et al., 2008c), Perpignan and Sète (Bachelet, 1990).

Martín Suárez (1988) and García-Alix et al. (2008b) noted a trend towards increasing size in the populations of *A. gorafensis* from the Guadix-Baza and Granada basins over time. We observe that our specimens matches both Miocene and Pliocene populations. *Apodemus gorafensis* is present in the Guadix-Baza Basin from the late Turolian to the late Ruscinian. This species becomes extinct beside other large-sized *Apodemus*, coinciding with the spread of the arvicolids. Since then, only the medium and small-sized *Apodemus* remain, which is true to this day (Martín Suárez, 1988).

Genus *CASTILLOMYS* Michaux, 1969

CASTILLOMYS GRACILIS Van de Weerd, 1976

(Fig. 6A–D)

Ocurrence and Material—Baza-1: four M1s (BA1-2001-R5/1, IPS89333–89335), one M2 (BA1-2001-R5/2), two m1s (BA1-2001-R5/3, IPS89336), two m2s (BA1-2001-R5/4, IPS89337).

Measurements—See Table 4.

Description—In m1 the entoconid and hypoconid are connected to the lingual part of the protoconid by a longitudinal crest. There is a symmetrical anteroconid. The tma is absent. The labial cingulum is interrupted at the height of the protoconid. The anterolabial cusp is attached to it. There are no other accessory cusps. The small posterior heel may be subriangular or elongated. It reaches the postero-lingual base of the hypoconid through a small crest in one individual (BA1-2001-R5/3). The c1 is low, oval, and larger than the posterior heel. It is connected to the protoconid by a weak crest. The m2s have a hint of longitudinal spur. The labial cingulum is poorly developed. It has attached a large and oval anterolabial cusp. Posterior heel is oval and weak. The c1 is much worn.

In M1s the t1 is displaced backward. The posterior spurs of t1 and t3 are poorly developed. The t1bis can appear as a thickening of the enamel. The t2bis is absent. There is no t4-t8 connection. The t3, t6 and t9 are not much more developed than t1 and t4, except in IPS89333. The t3 is far apart from t6. The t7 is absent. The t12 is present as a bulge between t8 and t9. The M2 is fractured by the t9 part. The t1 and t5 are connected by a well-developed lingual longitudinal crest. The t1 is elongated, and have a spur directed toward the antero-lingual side of t5. The t3 is isolated. The t12 is poorly developed.

Remarks—The morphology of the studied molars agrees with that of genus *Castillomys*: absence of t7, longitudinal spur in m1 and presence of a posterior spur in t1 and t3 in M1. Our specimens are smaller and have less-developed spurs and crests than those of *Castillomys crusafonti*, *Castillomys rivas* and *Castillomys africanus*. The adscription to *Castillomys margaritae* is also discarded because the t1 and t4 of the studied sample as large as t3, t6, and t9. To the contrary, the morphology of our teeth corresponds to that of *Castillomys gracilis*: absence of longitudinal crest and weak posterior heel in m2, poor development of posterior spurs in t1 and t3 of the M1, t8 isolated in M1, and t3 isolated in M2. The size values also fit the range of *C. gracilis* from Caravaca (type population), Orrios 1 (Van de Weerd, 1976), Gorafe 4 (Martín Suárez, 1988), Aldehuela (Adrover, 1986), and La Bullana 2B (Mansino et al., 2015). This species was originally defined by Van de Weerd (1976) as *Castillomys crusafonti gracilis*, but Martín Suárez and Mein (1991) elevated it to the species level (*Castillomys gracilis*). These authors proposed an anagenetic evolutionary lineage, including *C.*

gracilis, *C. crusafonti* and *C. rivas*. In this lineage, *C. gracilis* and *C. rivas* represent the extreme points of variability, whereas *C. crusafonti* has an intermediate mosaic distribution between the latter two. This explains why the studied material overlaps with the minimum biometric distribution of some population of *C. crusafonti* such as TCH-1B (Minwer-Barakat et al., 2005), Arquillo 3 (Adrover, 1986) and Asta Regia 3 (Castillo and Agustí, 1996). A size increase from the oldest towards the youngest populations was noticed by Martín Suárez and Mein (1991).

Genus *PARAETHOMYS* Petter, 1968

PARAETHOMYS MEINI (Michaux, 1969)

(Fig. 6E–H)

Ocurrence, Material, and Measurements—Baza-1: one M3 (BA1-2001-R6/4, length: 1.16 mm, width: 1.12 mm), three m1s (BA1-2001-R6/1, length: 2.00 mm, width: 1.31 mm; BA1-2001-R6/2, length: 1.95 mm, width: 1.23 mm; IPS89307, length: 1.95 mm, width: 1.25 mm), one m2 (BA1-2001-R6/3, length: 1.40 mm, width: 1.33 mm), two m3s (BA1-2001-R6/5, length: 1.23 mm, width: 1.13 mm; BA1-2001-R6/6, length: 1.22 mm, width: 1.15 mm).

Description—The m1s have a slightly asymmetrical anteroconid. The tma is absent or very weak. The connection between the anteroconid and the protoconid-metaconid complex develops a round funnel. The labial cingulum can be weak or moderate. It is connected to the anteroconid. The large c1 is round or oval. There are two small accessory cuspids between the c1 and the postero-labial base of the protoconid. The small and low posterior heel may be elongated or round. In m2 the anterolabial cusp is in contact with the poorly-developed labial cingulum. The c1 is small, oval, and separated from the hypoconid. There is a weak and laminar posterior heel. The anterolabial cusp has medium-sized and is oval. In m3s the anterolabial cusp and c1 are absent. The hypoconid-entoconid pair is separated from the anterior complex.

In M3s the t1 is isolated. It is similar in size to t4 and t8. There is no t3. The union t4-t5-t6-t8 forms a closed depression. This funnel is softly broad in the t4-t8 and t8-t6 contact.

Remarks—Baza-1 has yielded 161 molars corresponding to the genus *Paraethomys*. This sample shows two groups which can be distinguished on the basis of size. Therefore, 7 out of 152 specimens are very small when compared to the remaining teeth. This reduced sample is much smaller than *Paraethomys jaegeri* and *Paraethomys abaigari*. *Paraethomys belmezensis* has a well-developed tma connected to the lingual lobe of the anteroconid, and despite that by size the m1 from Baza-1 fit the range of *P. belmezensis*, the remaining molars are smaller and the tma is very weak or absent. The measurement of our specimens falls within the range of *Paraethomys meini* from PUR-4 (García-Alix et al., 2008c), Celadas 9 (Adrover et al., 1993), Villalba Alta (Adrover, 1986), Peralejos E and Villalba Alta Río (Adrover et al., 1988). In addition, some morphological traits are consistent with those of *P. meini*: weak or medium-sized labial cingulum in the lower molars and an absent or weak tma. Otherwise the measurements of the studied individuals are close to those of *P. meini* from Sète (type locality) and Aldehuela (Adrover, 1986), Orrios (Van de Weerd, 1976), La Juliana (Montenat and de Bruijn, 1976), Zorreras-3A (Martín-Suárez et al., 2000), PUR-3, 7, BRA-5B, CLC-5A, CAC-9, DHS-4A, 4B, 15B, MNA-4 (García-Alix et al., 2008c), Alcoy 2C and 2D (Mansino et al., 2013), La Bullana 2B (Mansino et al., 2015).

The size of our specimens are also similar to that of *Paraethomys anomalus* from Crevillente 6 (de Bruijn et al., 1975) and La Gloria 4 (Adrover et al., 1993), and *Paraethomys miocaenicus* from Khendek el Ouaich (Adrover, 1986), Librilla and Salobreña (Brandy, 1979b). Neverthless, *P. anomalus*, *P. miocaenicus*, and *P. meini* are considered synonymous by several authors (Montenat and de Bruijn, 1976; Van de Weerd, 1976; Adrover, 1986; Martín Suárez, 1988; Castillo Ruiz, 1990; Minwer-Barakat et al., 2005; García-Alix, 2006). Following Agustí et al. (2006) the first occurrence of *Paraethomys* in Iberian Peninsula took place in the Fortuna Basin (Southern Spain) prior to Messinian Salinity Crisis (at about 6.2 Ma). The *Paraethomys* dispersal is probably associated with the entry of camels of the genus *Paracamelus* into southern Spain, and the presence of both taxa in the Messinian beds can be explained as part of the same dispersal event likely from northern Africa (Pickford et al., 1994; Garcés et al., 1998; Agustí et al., 2006).

PARAETHOMYS aff. *ABAIGARI* (Michaux, 1969)

(Fig. 5M–R)

Occurrence and Material—Baza-1: 21 M1s (BA1-2001-R7/1–16, IPS89269, IPS89270, IPS89272, IPS89273, IPS89274), 26 M2s (BA1-2001-R7/17–31, IPS89217–89227), 11 M3s (BA1-2001-R8/17–20, IPHES-Bz-1-R8/22, IPS89287, IPS89288, IPS89292–89295), 33 m1s (BA1-2001-R7/32–54, IPS8297–82306), 39 m2 (BA1-2001-R7/55–81, IPS89308–89319), 24 m3s (IPHES-Bz-1-R8/1–16, IPHES-Bz-1-R8/21, IPS89320, IPS89323, IPS89325–89329).

Measurements—See Table 5.

Description—The teeth are medium-sized. The m1s have a sligh asymmetrical anteroconid. The tma is absent or very weak. The connection between the anteroconid and the protoconid-metaconid complex develops a round funnel in some specimens. The longitudinal spur may be small or absent. The labial cingulum is moderately developed. There are up to three accessory cusps. The large c1 is displaced lingually, and may be oval or elongated. The c1 usually develops a distal spur connected to the labial face of the hypoconid. There is occasionally another spur in contact with the posterior face of the hypoconid. The posterior heel may be small or moderate, and laminar or oval. In m2s the moderate-sized anterolabial cusp can be oval or round. There is an absent or poorly-developed labial cingulum which occasionally presents a small c1. The longitudinal spur is very weak or absent. The variable posterior heel is displaced lingually. It may be small or large, and oval or laminar. In m3s the anterolabial cusp is absent in most of specimens (very weak in BA1-2001-R8/11, IPS89320 and IPS89327). The c1 is absent or weak if present. The posterior complex is separated from the protoconid-metaconid complex.

In M1s the t1 is somewhat displaced backward. The t1 and t3 develop a distal spur toward the t4-t5 and t5-t6 intersection, respectively. It is less developed in t1. The t2-3 connection is higher than that of t1-2. The t6-t9 crest is high, and that of t4-t8 is low. There is a small t12 in all the specimens. The M2s display a large t1. It is usually isolated and develops a distal spur. The small and round t3 is isolated. It may develop a small distal spur. The t9 is reduced to a crest connecting t6 and t8. It is inflated in some specimens. The t4-t5 connection is low. There is a narrow ridge between the t4 and t8. The t12 is absent. In M3s the t1 is large and isolated. There is no t3. The t4-t8 and t6-t8 connection is low. The union t4-t5-t6-t8 forms a funnel.

Remarks—The large-sized *Paraethomys* of Baza-1 is clearly larger than *Paraethomys meini* and shows a further development of distal spurs in t1 and t3. The molars of *Paraethomys belmezensis* are smaller than the studied molars (Castillo Ruiz, 1992) and the diagnostic features are different. The average and the relative width of the studied population are in general smaller than those of *Paraethomys jaegeri*. The features of the specimens from Baza-1 are close to those of *Paraethomys abaigari* from its type localitiy (Villalba Alta Río): distal spur in t1 and t3 but less developed in t1, and high t6-t9 and t4-t8 connection in M1; large t1 with distal spur in M2; reduced longitudinal spur, moderate labial cingulum, large c1 and moderate posterior heel in m1 (Adrover et al., 1988). In size, the mean values match with that of minimum values of *P. abaigari* from Villalba Alta Río and La Judería. In general, the studied material is slightly smaller than *P. abaigari* (except for m2s and m3s), but is very similar to *Paraethomys* aff. *abaigari* from La Gloria 4 and Celadas 9 (Adrover et al., 1993), PUR-13 and CLC-5 (García-Alix et al., 2008c), AL2C and 2D (Mansino et al., 2013), and La Bullana 2B and 3 (Mansino et al., 2015). Thus we ascribe the large-sized *Paraethomys* from Baza-1 to *Paraethomys* aff. *abaigari*.

The association of a big-sized form with a small-sized form of *Paraethomys* has been identified in several Pliocene localities. *Paraethomys meini* (small form) and *P.* aff. *abaigari* (large form) coexisted at the Teruel Basin in the Ruscinian localities of Celadas-14, Celadas-5, Celadas-5A, La Gloria 4 and Celadas 9 (Adrover et al., 1993). The same association is found in CLC-5A and PUR-13 in the Granada Basin (García-Alix et al., 2008c), and in some localities from the Alcoy Basin such as Alcoy 2, AL2C, AL2D and La Bullana 2B (Esteban Aenlle and Lacomba, 1988; Mansino et al., 2013; Mansino et al., 2015). The coexistence of *P. abaigari* and *P. meini* has been recorded in La Judería, Celadas 6 and Villalba Alta Río (Teruel Basin, Adrover et al., 1988).

Paraethomys meini coexists with the big-sized *P. jaegeri* and with *P.* aff. *jaegeri* in Sète and Villalba Alta, respectively (Adrover et al., 1988). Montenat and de Bruijn (1976) recognized *P. jaegeri* and *P. meini* in the Ruscinian locality of La Juliana (Murcia), and Castillo and Agustí (1996) identified *P. jaegeri* and *P.* cf. *meini* in the early Pliocene locality of Asta Regia 3.

According to Mein et al. (1990) both the small-sized lineage of *Paraethomys* (*P. meini*) and the large-sized one (*P.* aff. *abaigari* – *P. abaigari* – *P.* aff. *jaegeri* – *P. jaegeri*) tend to increase in size through time. However, their origin is uncertain. *Paraethomys abaigari* could evolve from *P. meini* or may be an inmigrant taxon (García-Alix et al., 2008c).

Genus *OCCITANOMYS* Michaux, 1969

OCCITANOMYS cf. *BRAILLONI* Michaux, 1969

(Fig. 5S–X)

Ocurrence, Material and Measurements—Baza-1: two M1s (IPHES-Bz-R9/1, length: 2.17 mm, width: 1.48 mm; BA1-2001-R9/2, length: 2.27 mm, width: 1.63 mm), three M2s (IPHES-Bz-R9/3, length: 1.68 mm, width: 1.50 mm; IPS89330, length: 1.57 mm, width: 1.36 mm; IPS89331, length: 1.49 mm, width: 1.37 mm), two M3s (BA1-2001-R9/4, length: 1.16 mm, width: 1.15 mm; IPS89290, length: 1.10 mm, width: 1.11 mm), one m1 (BA1-2001-R9/5, length: 1.91 mm, width: 1.32 mm), two m2s (BA1-2001-R9/6, length: 1.42 mm, width: 1.30 mm; IPS89332, length: 1.43 mm, width: 1.38 mm), one m3 (BA1-2001-R9/7, length: 1.22 mm, width: 1.09 mm).

Description—The medium-sized teeth have an intermediate stephanodonty. The m1 has a slight asymmetrical anteroconid. The tma is absent. There is no longitudinal spur. The labial cingulum is wide and well developed. The oval c1 is small and low. There are no other accessory labial cusps. The small posterior heel has an oval shape. In m2s the longitudinal spur is not present. The labial cingulum is well developed and rugous. Accessory labial cusps are not observed. The large and round anterolabial cusp is higher than the labial cingulum. It is separated from the protoconid by a narrow valley. The posterior heel is oval. In m3 the protoconid and metaconid are symmetric. They are separated from the large hypoconid-entoconid complex. The anterolabial cusp and c1 are absent.

In M1s the t1 is displaced backward. It is connected to t5 by a low or high crest. There is a well-developed t1bis. The t2bis is small. The t3 is separated from the t5. It has an undeveloped distal spur directed to the t4-t5 connection. The t6 is inclined toward t9, being closer to this latter than to t3. The t12 is well developed. The t7 is absent. One out of two specimens (BA1-2001-R9/2, Fig. 5S) has three small, round and isolated extra tubercles. One of them is placed in the basal part of t9, another one between t1 and t4, and the last one in the posterior face of t2. In M2s the t1 is connected to t5 by a low crest. There is a round t1bis. The small t3 is isolated. The t4 is much larger than the t9. The t12 can appear as a small and thin crest directed to t9. The t5-t6 crest develops a small fold toward the t3 in two out of three specimens. The M3s have a duplicated t1 (t1bis). Both tubercles form an isolated complex. The t4, t5, t6, t9 and t8 are connected. The t3 is absent. The t8 has a spur directed anteroposteriorly in BA1-2001-R9/4 (Fig. 5U).

Remarks—The morphological features of the sample from Baza-1 agrees with that of genus *Occitanomys*: medium-sized teeth with stephanodonty more developed than in *Apodemus* but less advanced than in *Stephanomys* and *Castillomys*, t1 placed posteriorly, and t6 strongly inclined and much closer to t9 than to t3 (Michaux, 1969; Martín Suárez and Mein, 1991).

The material from Baza-1 is larger than oldest species of *Occitanomys* (*Occitanomys hispanicus* and *Occitanomys sondaari*). Our specimens are also larger than *Occitanomys alcalai*, *Occitanomys debruijni* and *Occitanomys vandami*. Although the mean size values of *Occitanomys adroveri* are smaller than *Occitanomys* from Baza-1, some of maximum size values may overlap with it, such as in the population from Los Masuetos (type locality). Neverthless we reject to assign the Baza-1 specimens to be *O. adroveri* due to the greater mean of size. Our material fits the size range of *O. brailloni* from Layna (type locality, Michaux, 1969), Arquillo 3 (Adrover, 1986) and Ptolemais 3 (Van de Weerd, 1979). In addition, the morphology is consistent with *O. brailloni*, displaying the m1 without tma, the accessory cusps less developed than *Apodemus*, t1bis developed in M1, and t1 connected to t5 and small t3 in M2. It is noteworthy that the studied specimens show some archaic features such as the weak connection between t1 and t5 in M1, and the absence of a longitudinal spur in m1, as is also the case of *Occitanomys* cf. *brailloni* from Gorafe A (Ruiz Bustos et al., 1984). Further, in contrast to the population from Layna (type locality) the studied specimens have well-developed t12. Thereby we prefer to ascribe the sample from Baza-1 to *Occitanomys* cf. *brailloni*.

Occitanomys brailloni is distributed in the Mediterranean area. It is a common species during late Ruscinian, but it has also been identified in early Ruscinian sites (Van de Weerd, 1979; Ruiz Bustos et al., 1984; Adrover, 1986; Guerra-Merchán and Ruiz Bustos, 1991; Guerra Merchán et al., 1991, 2013).

Subfamily TATERILLINAE Chaline, Mein and Petter, 1977

Genus *DEBRUIJNIMYS* Castillo and Agustí, 1996

DEBRUIJNIMYS JULII Castillo and Agustí, 1996

(Fig. 7A–C)

Occurrence, Material, and Measurements—Baza-1: one M1 (IPHES-Bz-R11/1, length: 3.16 mm, width: 2.23 mm), one M2 (IPHES-Bz-R11/3, length: 1.96 mm, width: 1.97 mm), two m1s (IPHES-Bz-R11/2, length: 3.05 mm, width: 2.14 mm; BA1-2001-R11/4, width: 1.97 mm).

Description—There are two specimens of m1. One of them is highly worn, whereas the second is fractured. The simple anteroconid is wide and assymetrical. Its labial side is larger than the lingual one. Both ends of the anteroconid bear cingula that are directed toward the protoconid and the metaconid. An indentation can be observed on the labial wall of the anteroconid. The protoconid and metaconid are widely fused, forming a transversal ridge. The anteroconid is connected to this crest. The posterior wall of the metaconid has a small posterior spur. A longitudinal spur connects the protoconid and metaconid to the hypoconid-entoconid lobe. The hypoconid and entoconid are completely fused, forming a romboid tranversal ridge. A very small posterior spur can be distinguished at the posterior wall of the hypoconid.

The M1 is a rather worn specimen. The anterocone is simple. A posterior longitudinal crest connects this cusp to the lobe formed by the protocone and the paracone. The protocone and paracone are fused, forming a transverse ridge. The protocone displays a posterior spur connected basally to the hypocone. The metacone and hypocone are equally fused. The hypocone has an anterior spur connected to the base of the posterior spur of the protocone. There is no evidence of posterostyle. In M2 the protocone and paracone are fused. Both have a posterior spur connected to the base of the hypocone and metacone respectively. The metacone and hypocone are equally fused. The hypocone displays an anterior spur that connects to the base of the posterior spur of the protocone. As in the case of the M1, there is no evidence of posterostyle.

Remarks—The specimens from Baza-1 are assigned to the genus *Debruijnimys* on the basis of morphological characters: presence of a longitudinal crest in m1 connecting the anteroconid to the protoconid and the metaconid, and a second longitudinal ridge connecting the protoconid to the hypoconid-entoconid; and tendency to the connection in M1 between the protocone and the hypocone and between the paracone and the metacone.

In addition to *D. julii*, Agustí and Casanovas-Vilar (2003) included within the genus *Debruijnimys* the species *Protatera almenarensis* from Almenara-Casablanca M, and the specimens originally reported as Gerbillidae indet. or *Protatera* sp. from southern Spain, in localities such as Alcoy 4B (Agustí, 1991), Botardo-C (Martín Suárez, 1988), Gorafe 1 and Caravaca (de Bruijn, 1974); as well as the African species *Protatera davidi*. Following these authors, all the specimens from Europe assigned to *Protatera* actually correspond to *Debruijnimys*.

The dimensions of our specimens are fairly larger than those of *Debruijnimys davidi* from Lissasfa (Geraads, 1998). The first upper molars of *Debruijnimys almenarensis* (recorded in Salobreña, Aguilar et al., 1984; Almenara-Casablanca M, Agustí, 1990b; Negratín-1, Minwer-Barakat et al., 2009; Zorreras-3A Martín-Suárez et al., 2000; Gafares 2B, García-Alix et al., 2016) are slightly smaller than the specimens from Baza-1, but the morphology is very similar. Nevertheless, the studied teeth differ from *D.*

almenarensis mainly in the presence of a longitudinal ridge which connects the anteroconid to the protoconid-metaconid pair in m1, and in the development of posterior spurs in the backside of the paracone and protocone that tend to join to the metacone and hypocone respectively in M1. These morphological features are typical of *D. julii*. In addition, the size of our specimens is rather similar to those of *D. julii* from its type locality, Asta Regia-3 (Castillo and Agustí, 1996), and Bacochas-1 (Sesé, 1989). Thus we ascribe the gerbil from Baza-1 to *Debruijnimys julii*.

Debruijnimys julii is one of the youngest representatives of its genus, and appears also in Gorafe 1, Alcoy 4B and as *D.* cf. *julii* in La Bullana 2B (Mansino et al., 2015). According to Agustí and Casanovas-Vilar (2003) the origin of *Debruijnimys* lies directly in a primitive species of *Abudhabia*, from Sahabi (Libya). *Debruijnimys* settled on the Iberian Peninsula at least twice during the Miocene-Pliocene transition through two different immigrations waves from Northern Africa. The first one had to do with *D. almenarensis* from late Miocene, and the second one corresponded to those representatives who might be the ancestors of *D. julii*, i.e. *Debruijnimys* from the early Pliocene localities of Alcoy, Gorafe, Caravaca and La Gloria 4 (Castillo and Agustí, 1996; Agustí and Casanovas-Vilar 2003).

Family GLIRIDAE Thomas, 1897

Genus *ELIOMYS* Wagner, 1840

ELIOMYS INTERMEDIUS Friant, 1953

(Fig. 5Y–AC)

Occurrence and Material—Baza-1: one D4 (BA1-2001-R10/1), two P4 (IPS89347, IPS89348), nine M1–2s (BA1-2001-R10/2–4, IPS89349–89354), one M3 (BA1-2001-R10/5), one d4 (BA1-2001-R10/6), two p4s (BA1-2001-R10/7, IPS89355), 11 m1–2s (BA1-2001-R10/8–12, IPS89356–89361), four m3s (BA1-2001-R10/13, BA1-2001-R10/14, IPS89362, IPS89363).

Measurements—See Table 6.

Description—The d4 displays a subtriangular occlusal outline. In the anterior part of the tooth, the anterolophid and protolophid form a ring. In the posterior part of the teeth, a posterotropid can be recognized between the mesolophid and the posterolophid. As in the former case, the occlusal outline of the p4 is subtriangular. Although very reduced, the anterolophid, protolophid, mesolophid and posterolophid can be recognized. There is no centrolophid. The hypoconid is anteriorly directed toward the mesoconid, but they do not contact. There is a well-developed posterotropid. All the m1s have a well-developed anterolophid, which is connected to the protoconid in three out of five specimens. The anterotropid is absent. The centrolophid is long in three individuals, medium-length in one and absent in another case. In one tooth it connects to the anterior wall of the metalophid. The posterotropid is long in four cases and medium-length in one. In one specimen it is connected labially to the mesolophid. The m2s possess a well-developed anterolophid, which in two cases is connected to the protoconid. The anterotropid is absent. The centrolophid is medium-length in two individuals and long in another two. In one of the latter cases it is connected to the anterior wall of the metalophid. The labial ends of the mesolophid and posterolophid are anteriorly directed. The posterotropid is short in one case and long in the other specimens. The m3s have a well-developed anterolophid. It is connected to the protoconid in one molar. The anterotropid is absent. The centrolophid is medium-length in two individuals and long in another one. The metalophid is connected to the metaconid. The labial ends of the mesolophid and posterolophid are anteriorly directed. The posterotropid is absent, except in one case in which it is reduced to a vestigial cuspule.

The P4s display a short anteroloph in one specimen and a very short or vestigial in the other. The precentroloph is absent in one individual and small in the other. There is a medium-length postcentroloph in one individual. In the remaining teeth it is almost vestigial. This crest is not connected to the metaloph. The long posteroloph is fused to the endoloph in one specimen. The occlusal surface of the M1s is concave. A continuous endoloph is present in all the cases. The paracone and metacone are prominent. The precentroloph is from medium-length to long. It is connected to the metaloph in one specimen. The postcentroloph is short in three specimens and medium-length in one. A small prototrope is present in one molar. In one case the posteroloph is isolated, not connected to the endoloph. The oclusal surface of M2s is also concave. The endoloph is continuous. There is a prominent paracone and metacone. The medium-length precentroloph is not connected to the metaloph. The short postcentroloph is not connected to the anterior centroloph. The M3s have continuous endoloph. The precentroloph is medium-length in two cases. It is absent in another individual. The precentroloph never reaches the metaloph. A short postcentroloph is present in one case and absent in the others.

Remarks— *Eliomys intermedius* from Baza-1 is clearly larger than *Eliomys yevesi* from Venta del Moro and Alcoy (Mansino et al., 2014b). It fits in size and morphology with previously described samples of this species, such Arquillo 3, Orrios 3 and Villalba Alta in the Teruel Basin (Adrover, 1986) and Tollo de Chiclana 1, 1B, 3 and 13 from the Guadix Basin (Minwer-Barakat, 2005). It differs from late early and middle Pleistocene samples of *Eliomys quercinus* (Huéscar 1, Cúllar de Baza 1; Sesé, 1989) by the presence of a well-developed posterotropid in the first and second lower molars, and well-developed pre and postcetrolophs in the upper molars.

Eliomys intermedius is a species widely represented in the Pliocene and early Pleistocene of the Guadix-Baza Basin. Until now the oldest record of this species in the basin was established at the sites of Gorafe 1 and Gorafe 4, in the early Pliocene (*Trilophomys* Zone; Agustí and Martín Suárez, 1984). It is also present in late Pliocene sites such as Gorafe 5 and Tollo de Chiclana 1B (*Dolomys* adroveri Zone; Agustí and Martín Suárez, 1984; Minwer-Barakat, 2005; Piñero and Agustí, 2015). The youngest record of this species in the basin comes from the early Pleistocene sites of Venta Micena 1 and 2 (Agustí et al., 1987a) and the late early Pleistocene sites of Barranco Léon 2 and Orce 3 (Agustí et al., 1987b).

Eliomys intermedius has not been reported so far from early Pliocene levels from the Guadix-Baza Basin. The Baza-1 specimens are the oldest record of this species in this basin.

DISCUSSION

Biostratigraphic Correlation

We estimate the age of Baza-1 based on the comparison of the rodent composition in this site with those from other areas located in the Guadix-Baza, Granada, Teruel and Alcoy basins.

The coexistence of a large and a small-sized species of *Paraethomys* has been reported in a number of Ruscinian localities (Mein et al., 1990; Adrover et al., 1993; Castillo and Agustí, 1996; García-Alix et al., 2008c; Mansino et al., 2013, 2015; among others). In addition, *Apocricetus barrierei* has been used to characterize the Pliocene in the Betic Cordillera (Ruiz Bustos, 1990; Sesé et al., 2001) and it is indicative of early Ruscinian age according to García-Alix et al. (2008b). The quotation of the gerbil *Debruijnimys julii* in Baza-1 has a biostratigraphical interest, indicating a higher biostratigraphic position than the Gerbil Event proposed by Agustí et al. (2006). This event took place between 5.96 and 5.33 Ma, involving the entry into the Western Mediterranean of rodents of African affinities, such as members of the genera *Myocricetodon* and *Debruijnimys*. It has been recorded in the late Miocene (MN13) localities of Almenara-Casablanca M (Agustí et al., 2006), Negratín-1 (Minwer-Barakat et al., 2009), Gafares 2B (García-Alix et al., 2016) and Zorreras-2B (Martín-Suárez et al., 2000), where *Debruijnimys almenarensis* has been reported. The association of *Stephanomys cordii*, *Apodemus gorafensis*, *Paraethomys meini*, *Castillomys gracilis* and *Apocricetus barrierei* is characteristic of the early Ruscinian, MN14 (Minwer-Barakat, 2005; García-Alix et al., 2008d), between ca. 4.9–4.2 Ma (Agustí et al., 2001a).

Regarding other Guadix-Baza Basin localities, the assemblages from Gorafe 2, 3, 5 (Martín Suárez, 1988), with the presence of an arvicolid identified as *Dolomys occitanus*, Galera-C (Agustí et al. 1997) with *Dolomys adroveri* and *D. occitanus*, and Tollo de Chiclana 1 (Minwer-Barakat et al., 2005) with *D. adroveri* and *Stephanomys donnezani*, indicate a younger age than Baza-1. Otherwise, the species *Apodemus gudrunae* (ancestor of *A. gorafensis*, Martín Suárez and Mein, 1998) and *Cricetus* cf. *kormosi* (redefined as *Apocricetus barrierei* by Freudenthal et al., 1998) in Botardo-C

(Martín Suárez, 1988), besides *Debruijnimys almenarensis* and *Myocricetodon jaegeri* in Negratín-1 (Minwer-Barakat et al., 2009) and *Myocricetodon* sp. in Pino Mojón (Sesé, 1989) determine an older age for these localities compared to Baza-1, all being included in the *Apodemus gudrunae* Biozone (late Miocene, MN13) from the Guadix Basin (Minwer-Barakat et al., 2012).

The studied rodent fauna is very similar to those of Gorafe A (Ruiz Bustos et al., 1984), Gorafe 1 (de Bruijn, 1974), Gorafe 4 (Martín Suárez, 1988) and Yeguas (Soria Mingorance and Ruiz Bustos, 1991; Minwer-Barakat et al., 2005), all within the *Trilophomys* Biozone from the Guadix Basin, assigned to upper part of MN14 and characterized by the occurrence of *A. barrierei*, *S. cordii*, *C. gracilis*, *A. gorafensis*, *P. meini* and *Trilophomys* (Minwer-Barakat et al., 2012). Therefore, we consider that Baza-1 is close in age to these localities (Fig. 8). The novelty for the Guadix-Baza Basin lies in the joint presence of two species of *Paraethomys*. The only previous mention was that of Aljibe 2 and 3 (*P. jaegeri* and *P.* cf. *meini*), but there are neither descriptions nor figures to check the information. Adrover et al. (1988) pointed out that Gorafe 1 and Gorafe A have a big-sized *Paraethomys*. Effectively, the size and morphology of *P.* cf. *meini* from Gorafe A and *P. meini* from Gorafe 1 fit well to those of *P.* aff. *abaigari*. In contrast, the sites of Gorafe 4 and Yeguas only record a small species. This indicates that either the two species are mutually exclusive or there is a bias in the record. The latter is most likely, but owing to the large sample of Baza-1, the coexistence of two *Paraethomys* has been corroborated in the Guadix-Baza Basin.

The faunal assemblage from Baza-1 shares species with other localities of the Iberian Peninsula such as PUR-4 in the neighbour Granada Basin (García-Alix et al., 2008d). It shares with our site the appearance of *A. gorafensis*, *A. barrierei*, *P. meini* and *E. intermedius*. Nevertheless this site is included in the *Apocricetus barrierei* Biozone, immediately prior to the zone with two *Paraethomys* species. The specimens of *A. barrierei* from PUR-4 are smaller than those of this species from Baza-1, which is congruent with a younger age for the latter, since the size of this species increases through the time (Minwer-Barakat et al., 2012). Also the localities of AL2D and AL2C have a similar assemblage to Baza-1 (e.g. *P. meini*, *P.* aff. *abaigari*, *Trilophomys*), suggesting a close age.

The *Apocricetus barrierei* Biozone from the Granada Basin is correlated with the *Celadensia* Biozone from the local biostratigraphy of the Teruel Basin (Mein et al., 1990). The site of Peralejos E is included in the former biozone and records some species also found in Baza-1 (*A. gorafensis*, *P. meini*, and *A. barrierei*; Adrover et al., 1988). However it only includes one species of *Paraethomys* and although it shows a great variability in size, it is not possible to differentiate two species. This fact determines Peralejos E to be in a lower biostratigraphic position than Baza-1. La Gloria 4 and Celadas 9 (Adrover et al., 1993) are assigned to the Two *Paraethomys* + *Promimomys* Biozone (Mein et al., 1990), with *P.* aff. *abaigari* and *P. meini* well separated as is also the case in Baza-1. These two *Paraethomys* are not accompainned by *Promimomys* in our site as it is the case in La Gloria 4 and Celadas 9 because the range of this genus within the Iberian Peninsula is limited to the Teruel region (Mein et al., 1990). They have many species in common such as *A. gorafensis*, *C. gracilis*, *P. meini* and *P.* aff. *abaigari*. In addition, the rodent list of La Gloria 4 includes *A. barrierei* (similar in size to that of Baza-1) and a representative of *Debruijnimys* (reported as *Protatera*), whereas Celadas 9 incorporates *S. cordii*. However, both La Gloria 4 and Celadas 9 were deposited inmediatley prior to the first entry of *Trilophomys*. Accordingly Baza-1 has a somewhat younger age. In contrast, Villalba Alta Río 1 (Mein et al., 1990) and Aldehuela (Adrover, 1986), based on the *Triolophomys* Biozone (Mein et al., 1990), are younger than Baza-1 according to the presence of *Ruscinomys europaeus* and *Stephanomys margaritae*, descendants of *R. lasallei* and *S. cordii*, respectively.

The localities of PUR-13 and CLC-5A are included in the local *Paraethomys* aff. *abaigari* Biozone (García-Alix et al., 2008d). PUR-13 has in common with Baza-1 the occurrence of *A. gorafensis*, *P. meini*, *P.* aff. *abaigari*, *C. gracilis* and *E. intermedius*, whereas CLC-5A only shares the two *Paraethomys* (García-Alix et al., 2008d). Although these sites have key element in common, the presence of *S. dubari* (instead its descendant *S. cordii*) and the absence of *Trilophomys* in PUR-13 and CLC-5A determines a somewhat older age than Baza-1.

Therefore, Baza-1 represents the first locality within the Guadix-Baza Basin where the joint occurrence of two species of *Paraethomys* has been confirmed.

Paleoecological Inferences

Small mammals have been widely used as paleoclimatical and paleoecological indicators. Studies of rodent assemblages in particular provide interesting information on the past environmental and climatic conditions (Martín-Suárez et al., 2001; Minwer-Barakat et al., 2005; Montuire et al., 2006; García-Alix et al., 2008a; among others). Neverthless, in some cases, as García-Alix et al. (2013, 2015) and Freudenthal et al. (2014) noticed, the paleoecological and paleoenvironmental inferences (specially paleo-humidity conditions) could be affected by the paleogeography of the area, recording physical landscape changes rather than global or regional climatic trends. Minwer-Barakat (2005) suggested using rodent and insectivores associations with a minimum sampling effort of 100 specimens for paleoecological studies. Our sample consists of 447 specimens (adding insectivores and lagomorphs).

The micromammal assemblage (except Chiroptera indet.) from Baza-1 is dominated by two species from two different families: *Paraethomys* aff. *abaigari* (Muridae) and *Apocricetus barrierei* (Cricetidae) with a prevalence of 36.80% and 32.50% respectively (Table 7). Nevertheless, murids are the most abundant with a relative abundance of 52.57% for the whole association. The families Gliridae, Gerbillidae and Trilophomyidae are very scarce with 5.56%, 0.96% and 0.72% respectively. The Insectivora association only accounts for 0.71% and the Lagomorpha for 5.08%.

Determination of the ecological requirements of an extinct taxon is based on the phylogenetic relationships with extant species, dental modifications and association with taxons with known ecological preferences (García-Alix et al., 2008a). We have followed the paleoecological requirements used by Minwer-Barakat (2005) and García Alix et al. (2008a) for most taxa. They interpreted *Castillomy*s and *Stephanomys* as eurytopic taxons. However both groups display morphological features in their dental pattern associated with the stephanodonty (development of longitudinal ridges among molar cusps). Some authors interpreted these characters as indicative of a diet based on fibrous components (van Dam and Weltje, 1999; Renaud et al., 2005; Gomes Rodrigues et al., 2013; Gómez Cano et al., 2013; Piñero et al., 2015b). Accordingly we consider in this paper both *Castillomys* and *Stephanomys* as inhabitant of open herbaceous meadows. Regarding the lagomorphs, *Trischizolagus maritsae* is considered to be a possible ancestor of extant *Oryctolagus* (López Martínez, 2008), so similar ecological requirements have been speculated (warm temperatures, open meadows and eurytopic for the humidity). About *Prolagus michauxi*, López Martínez (2001) indicated ecological preferences analogous to that of the living leporid *Sylvilagus palustris*, i.e. subtropical swamp (warm and humid conditions and edge-water areas).

Two taxa have unknown ecological affinities (*Paraethomys* aff. *abaigari* and *Occitanomys* cf. *brailloni*), involving a prevalence of 40% (Table 7).

The micromammal assemblage from Baza-1 is mostly formed by taxa interpreted as inhabitants of open and herbaceous habitats (46%) such as *Castillomys gracilis*, *Stephanomys cordii*, *A. barrierei*, *Ruscinomys* cf. *lasallei*. *Trilophomys* cf. *vandeweerdi* and *T. maritsae*. The woodland elements are poorly represented (5%) with only *Eliomys intermedius*. The open bare habitat representation is also very scarce (1%), represented only by *Debruijnimys julii*. The 6% of the association is considered as eurytopic in terms of habitat preferences. The existence of open herbaceous areas is supported by the coexistence of large herbivores taxa in Baza-1 site the two mega-herbivorous *Mammut borsoni* and *Anancus arvernensis*, *Stephanorhinus* sp. cf. *S. jeanvireti*, *Alephis* sp., as well as *Hipparion* sp., whereas the presence of forested areas agrees with the occurrence of Cervidae indet. (Ros-Montoya, 2010; Martínez-Navarro et al., 2015). The presence of taxa linked to a semi-aquatic mode of life or edge-water environments (1%), such as desmanines (desmans) and *P. michauxi*, allow verifying the development of a constant water courses close to the site, consistent with the basin margin alternating lacustrine-palustrine environments and the appearance of many freshwater fish remains, belonging to the family Cyprinidae. These results agree with a landscape dominated mainly by open grassed meadows with a scarce proportion of forest patches and the development of stable water courses in the vicinity of Baza-1 during the accumulation of the level.

Regarding the temperature, the faunal assemblage is dominated by indicators of warm climatic conditions (45%) like *Apodemus gorafensis*, *Paraethomys meini*, *A. barrierei*, *D. julii*, *T. maritsae* and *P. michauxi*, whereas relatively cold elements only are represented by *R.* cf. *lasallei* and *T.* cf. *vandeweerdi* (3%). In addition, the arvicolids (characteristic of cold climate) are absent in our site, whereas they appear in northernmost sites contemporaneous to Baza-1 within the Iberian Peninsula such as Celadas 9 and La Gloria 4 (Adrover et al., 1993; Minwer-Barakat, 2005). *Stephanomys cordii*, *E. intermedius* and Erinaceinae indet. are indifferent with respect to the temperature (13%). In the same way *A. gorafensis*, Desmaninae indet., cf. *Sorex* sp., cf. *Sorex minutus* and *P. michauxi* represents wet environmental conditions (6%). *Paraethomys meini*, *A. barrierei*, *R.* cf. *lasallei* and *D. julii* are considered as dry environment indicators (37%). *Castillomys gracilis*, *S. cordii*, *E. intermedius*, *T.* cf. *vandeweerdi*, Erinaceinae indet. and *T. maritsae* do not represent specific humidity conditions (18%). According to the rodent assemblage and the scarcity of insectivores, it seems clear that warm and dry conditions were dominant during early Ruscinian in the surrounding of Baza-1 site. Nevertheless the occurrence of species which require constant watercourses indicates some minimal conditions of humidity. It is probable that the general conditions were dry but with a possibility of the development of wet environments near to the water areas.

Among the preliminary list of amphibians and reptiles from the Pliocene of Baza-1, two ophidian taxons suggest interesting paleoenvironmental and paleoclimatic data like scolecophidians (blind snakes) and elapids (cobras). Scolecophidian snakes are represented today in Southeastern Europe and Anatolia, as well as in the Middle East and North Africa (Sindaco et al. 2013), despite their main range currently includes mostly tropical and subtropical areas from Africa, Asia and South America. Elapids are venomous snakes found in tropical and subtropical regions around the world. Among elapids, cobras occur in regions throughout Africa, Southwest Asia, South Asia and Southeast Asia (Sindaco et al. 2013) and live in a wide variety of habitats like, steppes, dry to moist savannas, arid semi-desert regions with some water and vegetation. The presence of these two snakes in Baza-1 suggests warm and relatively dry conditions (although with certain local humidity) in accordance with the results from the micromammalian assemblage.

The climate during the Pliocene became cooler, drier, and more seasonal (deMenocal, 2004). The early Pliocene was a warm period, ~3ºC higher global surface temperatures than today (Raymo et al., 1996) and low amplitude changes, which progressively grew cooler (Suc et al., 1995). Fauquette et al. (1999) determined for the early Pliocene in southern Spain annual temperatures 6 ºC higher than today and precipitation as low as it is nowadays. Our data are consistent with this result, indicating warm and dry conditions.

According to Hernández Fernández et al. (2007) the Iberian Peninsula Ruscinian is characterized by subtropical temperatures and summer rains. Suc et al. (1995) through pollen data proposed that in SW Europe open habitats with richness of herbaceus vegetation and scarce woodlands predominated from 5.3 Ma (Mio-Pliocene transition) to 4.5 Ma. These authors identified cooling at 4.5 Ma followed by a warmer period, but did not induce large changes in the vegetation of SW Europe (Fauquette et al., 1998). The results for Baza-1 are consistent with this interpretation.

Our analysis suggests that the deposition of the site occurred during the warm period before the aridity maximum at 3.95 Ma (correlates with the eccentricity minimum at about 4 Ma) identified by Agustí et al. (2001b) in the Zújar section (Guadix-Baza Basin), because this peak could mark the first entry of *Trilophomys* in the southern Spain. The presence of *Trilophomys* in Baza-1 may be a first indication of the first early Pliocene cooling events before the onset of the glacial-interglacial dynamics at 2.6 Ma (Agustí et al., 2001b).

CONCLUSIONS

The rodent sample from Baza-1 is formed by more than 400 specimens. The assemblage includes two cricetids (*Ruscinomys* cf. *lasallei*, *Apocricetus barrierei*), six murids (*Stephanomys cordii*, *Apodemus gorafensis*, *Castillomys gracilis*, *Paraethomys meini*, *Paraethomys* aff. *abaigari*, *Occitanomys* cf. *brailloni*), one gerbil (*Debruijnimys julii*), one glirid (*Eliomys intermedius*) and one representative of the family Trilophomyidae (*Trilophomys* cf. *vandeweerdi*). The latter two taxa at Baza-1 record their oldest occurrence in the Guadix-Baza Basin. The faunal assemblage indicates an early Ruscinian age, MN14 (between ca. 4.9–4.2 Ma). This association is very similar to those of Gorafe A, Gorafe 1, Gorafe 4 and Yeguas, all within the *Trilophomys* biozone from the Guadix Basin.

The amount of small mammal specimens yielded by Baza-1 is enough to perform a paleoecological analysis. The relative proportions of the species in relation with their ecological preferences suggests the dominance of open grassed meadows during the formation of Baza-1, with the occasional presence of woodland patches and the development of stable water courses. It is probable that the climate conditions were warm and dry, under the warm period after the cooling at 4.5 Ma, and prior to the aridity maximum at 3.95 Ma.

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TABLE 1. Measurements (mm) of the teeth of *Apocricetus barrierei* from Baza-1.

	Length				Width			
Element	N	min	mean	max	N	Min	mean	max
M1	14	2.61	2.81	2.96	13	1.63	1.80	1.88
M2	24	2.00	2.16	2.35	24	1.71	1.82	1.98
M3	20	1.68	1.90	2.10	20	1.55	1.70	1.79
m1	22	2.35	2.61	2.78	23	1.39	1.52	1.62
m2	28	1.90	2.17	2.42	27	1.48	1.71	1.90
m3	15	2.12	2.30	2.50	13	1.53	1.65	1.82

TABLE 2. Measurements (mm) of the teeth of *Stephanomys cordii* from Baza-1.

	Length				Width			
Element	N	min	mean	max	N	Min	Mean	max
M1	3	2.53	2.58	2.62	3	1.78	1.82	1.85
M2	4	1.63	1.73	1.82	5	1.63	1.77	1.87
M3	2	1.18	1.19	1.20	2	1.06	1.07	1.08
m1	2	2.16	2.21	2.26	2	1.43	1.43	1.44
m2	3	1.67	1.69	1.72	3	1.49	1.52	1.56
m3	5	1.30	1.34	1.40	2	1.28	1.33	1.40

TABLE 3. Measurements (mm) of the teeth of *Apodemus gorafensis* from Baza-1.

	Length				Width			
Element	N	min	mean	max	N	min	mean	max
M1	3	2.36	2.52	2.64	4	1.45	1.56	1.65
M2	4	1.48	1.57	1.68	4	1.37	1.45	1.54
M3	1		1.08				1.06	
m1	1		2.36			1	1.46	
m2	3	1.56	1.62	1.68	3	1.34	1.39	1.43
m3	6	1.15	1.23	1.27	6	0.98	1.15	1.22

TABLE 4. Measurements (mm) of the teeth of *Castillomys gracilis* from Baza-1.

	Length				Width			
Element	N	min	mean	max	N	Min	Mean	max
M1	4	1.45	1.53	1.59	4	1.03	1.07	1.10
M2	1		1.15		1		1.04	
m1	2	1.40	1.42	1.43	2	0.85	0.88	0.90
m2	2	0.95	0.97	0.98	2	0.89	0.91	0.93

TABLE 5. Measurements (mm) of the teeth of *Paraethomys* aff. *abaigari* from Baza-1.

	Length				Width			
Element	N	min	mean	max	N	min	mean	max
M1	17	2.47	2.65	2.79	19	1.70	1.77	1.88
M2	24	1.82	1.91	2.03	24	1.61	1.71	1.85
M3	9	1.25	1.32	1.42	11	1.21	1.31	1.41
m1	29	2.24	2.41	2.60	31	1.37	1.53	1.69
m2	35	1.64	1.74	1.85	37	1.44	1.57	1.71
m3	24	1.39	1.50	1.65	23	1.21	1.34	1.43

TABLE 6. Measurements (mm) of the teeth of *Eliomys intermedius* from Baza-1.

	Length				Width			
Element	N	min	mean	max	N	min	Mean	max
D4	1		1.47		1		0.80	
P4	2	0.95	1.03	1.10	2	1.35	1.51	1.67
M12	8	1.30	1.41	1.60	8	1.63	1.78	1.96
M3	1		1.20					
d4	1		1.18				1.11	
p4	2	1.35	1.39	1.43	2	1.30	1.32	1.33
m12	10	1.29	1.49	1.59	10	1.44	1.64	1.76
m3	4	1.31	1.35	1.43	4	1.46	1.53	1.59

TABLE 7. Relative abundances (RA) of each taxon from Baza-1 [calculated dividing the number of specimens (N) by the number of diagnostic elements (DE) of each group] with its paleoecological affinities. **Abbreviations**: **C**, cool; **D**, dry; E, eurytopic; **EW**, edge-water/(semi)aquatic; **F**, forested; **H**, humid; **OB**, open/bare; **OH**, open/herbaceous; **U**, unknown; **W**, warm.

	N	DE	N/DE	RA (%)	Habitat	Temperat.	Humidity
Ruscinomys cf. *lasallei*	8	12	0.67	1.91	OH	C	D
Apocricetus barrierei	136	12	11.33	32.50	OH	W	D
Stephanomys cordii	20	12	1.67	4.78	OH	E	E
Apodemus gorafensis	19	12	1.58	4.54	E	W	H
Castillomys gracilis	9	12	0.75	2.15	OH	E	E
Paraethomys meini	7	12	0.58	1.67	E	W	D
Paraehtomys aff. *abaigari*	154	12	12.83	36.80	U	U	U
Occitanomys cf. *brailloni*	11	12	0.92	2.63	U	U	U
Eliomys intermedius	31	16	1.94	5.56	F	E	E
Debruijnimys julii	4	12	0.33	0.96	OB	W	D
Trilophomys cf. *vandeweerdi*	3	12	0.25	0.72	OH	C	E
Trischizolagus maritsae	34	22	1.55	4.43	OH	W	E
Prolagus michauxi	5	22	0.23	0.65	EW	W	H
Desmaninae indet.	1	44	0.02	0.07	EW	-	H
cf. *Sorex* sp.	4	20	0.20	0.57	-	-	H
Erinaceinae indet.	1	44	0.02	0.07	E	E	E
Total	447		34.87	100			
					OH: 46.49		
					OB: 0.96	C: 2.63	D: 37.08
					F: 5.56	W: 44.75	H: 5.83
					EW: 0.72	E: 12.56	E: 17.71
					E: 6.28	U: 39.43	U: 39.43
					U:39.43		

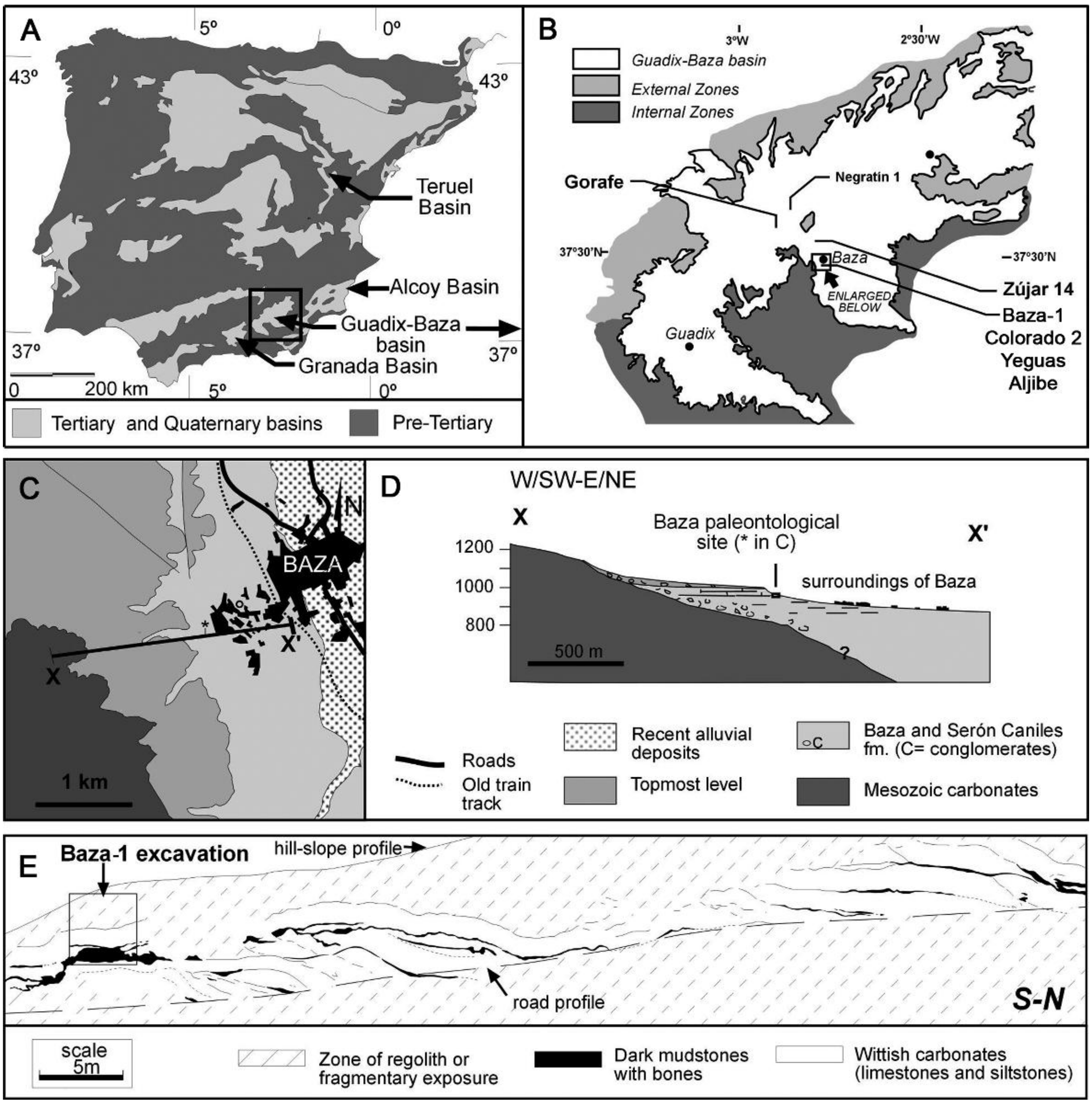


FIGURE 1. Geological setting of the Baza-1 site. **A**, Simplified map of the Iberian Peninsula, with indication of main Neogene and Quaternary basins referred in text; **B**, Guadix-Baza Basin with loction of Baza-1 site and other related localities; **C**, Setting around Baza-1 site and city; **D**, cross section of Baza-1 site (see location in 'C'); **E**, Baza-1 outcrop. [planned for page width]

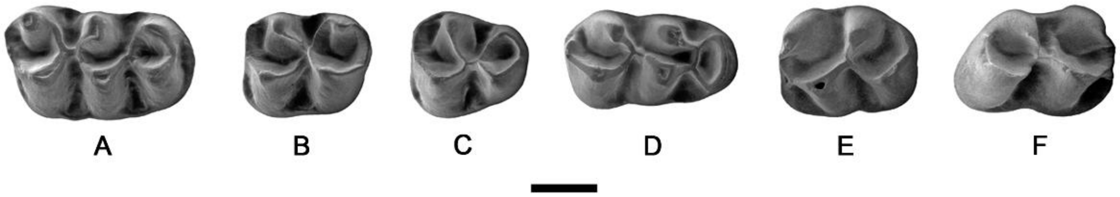


FIGURE 2. *Apocricetus barrierei* (Mein and Michaux, 1970) from Baza-1. **A**, right M1, BA1-2001-R1/3; **B**, left M2, BA1-2001-R1/10; **C**, left M3, BA1-2001-R1/28; **D**, right m1, BA1-2001-R1/38; **E**, left m2, BA1-2001-R1/54; **F**, right m3, BA1-2001-R1/70. Scale bar equals 1 mm. [planned for page width]

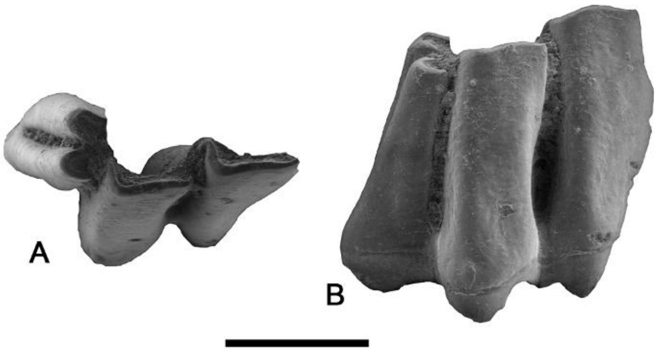


FIGURE 3. Left M1 of *Ruscinomys* cf. *lasallei* Adrover, 1969 from Baza-1, IPS89345. **A**, occlusal view; **B**, lingual view. Scale bar equals 2 mm. [planned for column width]

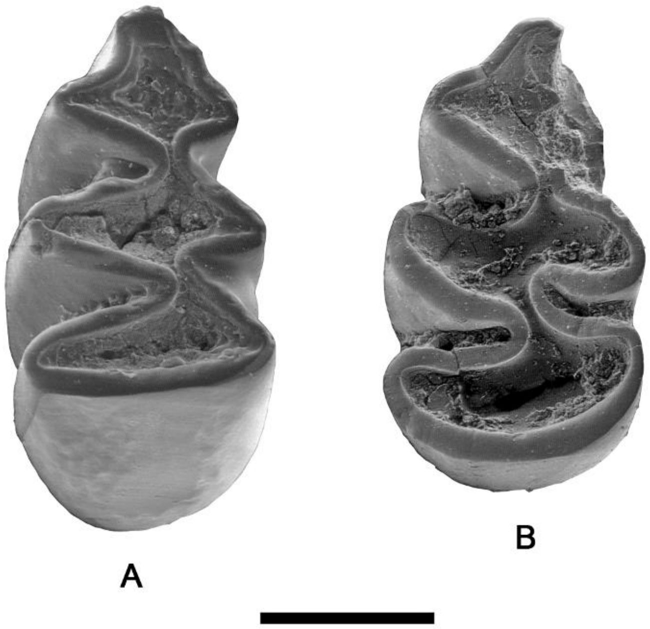


FIGURE 4. *Trilophomys* cf. *vandeweerdi* Brandy, 1979a from Baza-1. **A**, right m1, IPS89339; **B**, right m1, IPS89338. Scale bar equals 1 mm. [planned for column width]

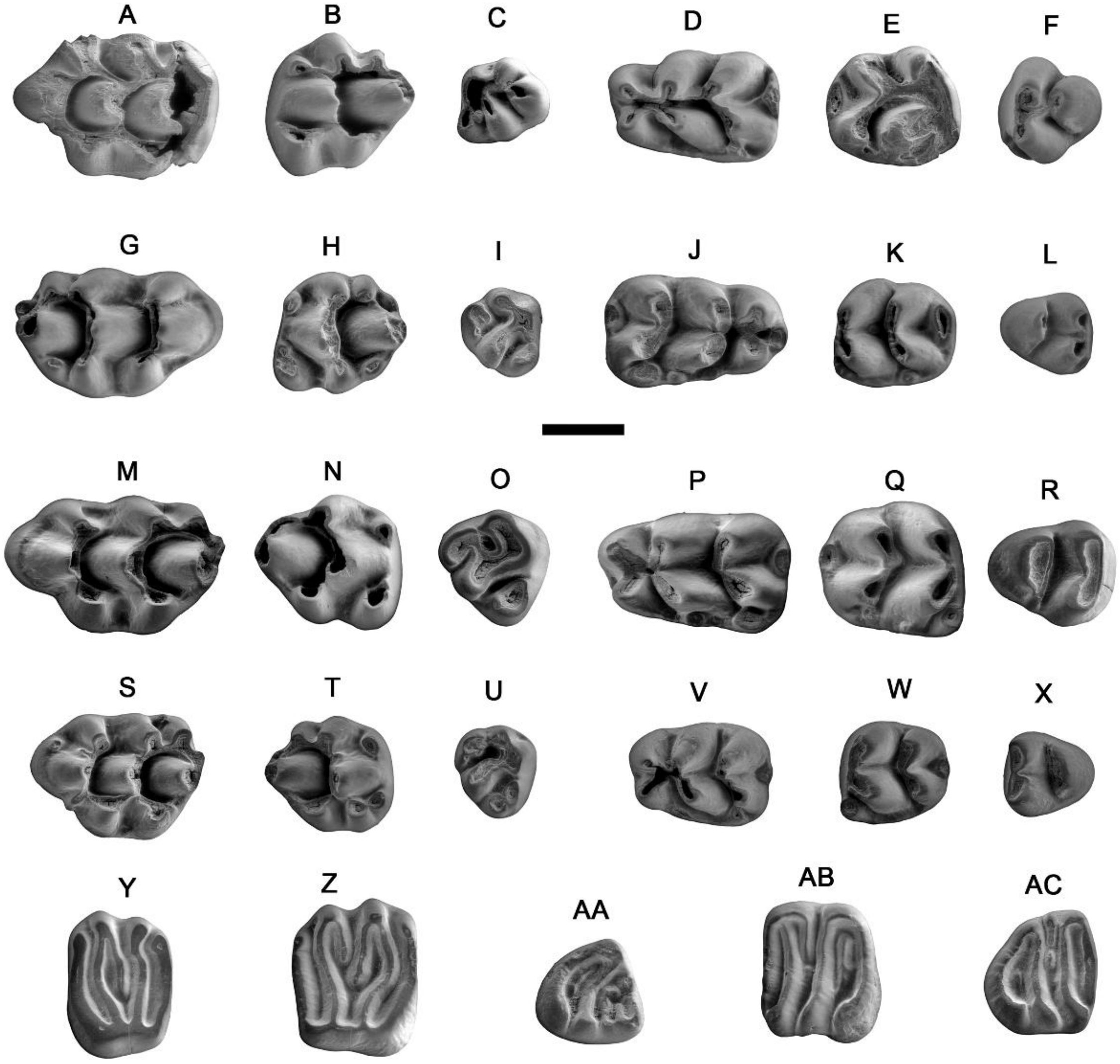


FIGURE 5. Murids and glirids from Baza-1. *Stephanomys cordii* Ruiz Bustos, 1986: **A**, left M1, BA1-2001-R3/1; **B**, left M2, BA1-2001-R3/2; **C**, left M3, BA1-2001-R3/12; **D**, left m1, BA1-2001-R3/6; **E**, right m2, BA1-2001-R3/14; left m3, BA1-2001-R3/9. *Apodemus gorafensis* Ruiz Bustos, Sesé, Dabrio, Peña and Padial, 1984: **G**, right M1, BA1-2001-R4/3; **H**, left M2, BA1-2001-R4/8; **I**, right M3, BA1-2001-R4/9; **J**, right m1, BA1-2001-R4/10; **K**, left m2, BA1-2001-R4/12; **L**, right m3, BA1-2001-R4/14. *Paraethomys* aff. *abaigari* (Michaux, 1969): **M**, left M1, BA1-2001-R7/2; **N**, right M2, BA1-2001-R7/25; **O**, right M3, BA1-2001-R8/17; **P**, left m1, BA1-2001-R7/43; **Q**, right m2, BA1-2001-R7/78; **R**, right m3, BA1-2001-R8/3. *Occitanomys* cf. *brailloni* Michaux, 1969: **S**, left M1, BA1-2001-R9/2; **T**, right m2, BA1-2001-R9/3; **U**, right M3, BA1-2001-R9/4; **V**, left m1, BA1-2001-R9/5; **W**, left m2, BA1-2001-R9/6; **X**, left m3, BA1-2001-R9/7. *Eliomys intermedius* Friant, 1953: **Y**, left M1, BA1-2001-R10/3; **Z**, right M2, BA1-2001-R10/4; **AA**, right p4 BA1-2001-R10/7; **AB**, left m2, BA1-2001-R10/11; **AC**, right m3, BA1-2001-R10/13. Scale bar equals 1 mm. [planned for page width]

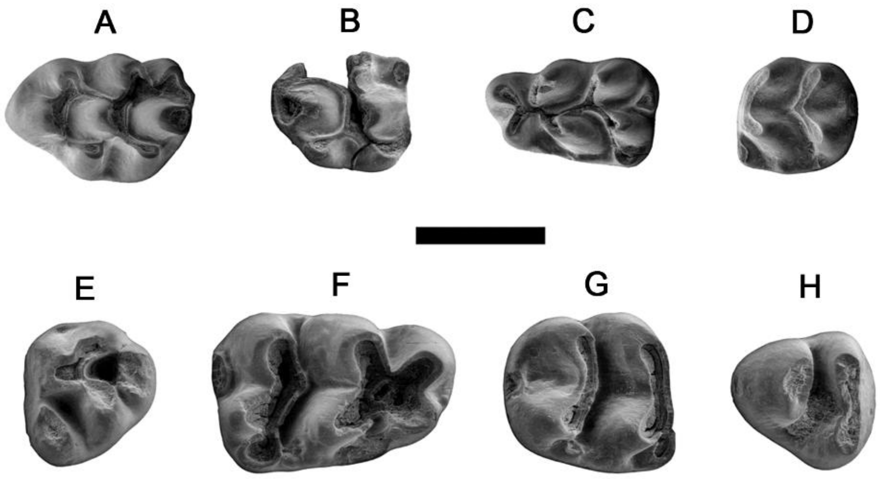


FIGURE 6. Murids from Baza-1. *Castillomys gracilis* van de Weerd, 1976: **A**, left M1, BA1-2001-R5/1; **B**, right M2, BA1-2001-R5/2; **C**, left m1, BA1-2001-R5/3; **D**, left, m2. *Paraethomys meini* (Michaux, 1969): **E**, left M3, BA1-2001-R6/4; **F**, right m1, BA1-2001-R6/1; **G**, right m2, BA1-2001-R6/3; **H**, right m3, BA1-2001-R6/5. Scale bar equals 1 mm. [planned for 2/3 page width]

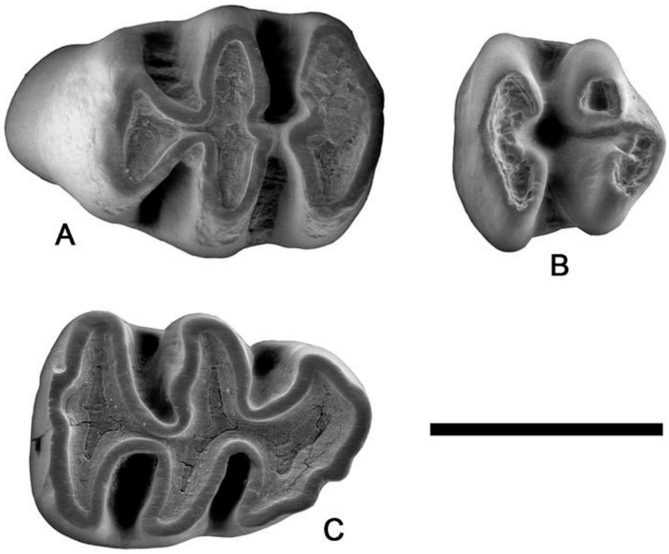
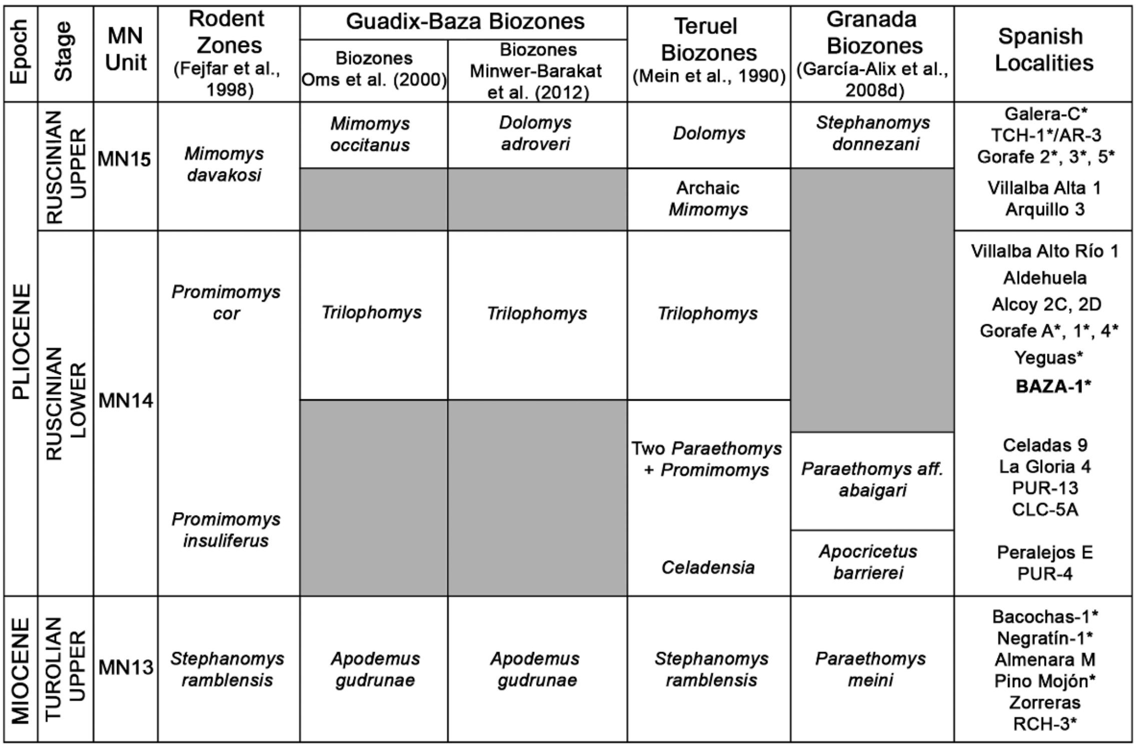


FIGURE 7. *Debruijnimys julii* Castillo and Agustí, 1996 from Baza-1. **A**, left M1, BA1-2001-R11/1; **B**, right M2, BA1-2001-R11/3; **C**, right m1, BA1-2001-R11/1. Scale bar equals 2 mm. [planned for column width]



Epoch	Stage	MN Unit	Rodent Zones (Fejfar et al., 1998)	Guadix-Baza Biozones		Teruel Biozones (Mein et al., 1990)	Granada Biozones (García-Alix et al., 2008d)	Spanish Localities
				Biozones Oms et al. (2000)	Biozones Minwer-Barakat et al. (2012)			
PLIOCENE	RUSCINIAN UPPER	MN15	*Mimomys davakosi*	*Mimomys occitanus*	*Dolomys adroveri*	*Dolomys*	*Stephanomys donnezani*	Galera-C* TCH-1*/AR-3 Gorafe 2*, 3*, 5*
				▨	▨	Archaic *Mimomys*	▨	Villalba Alta 1 Arquillo 3
	RUSCINIAN LOWER	MN14	*Promimomys cor*	*Trilophomys*	*Trilophomys*	*Trilophomys*		Villalba Alto Río 1 Aldehuela Alcoy 2C, 2D Gorafe A*, 1*, 4* Yeguas* **BAZA-1***
			Promimomys insuliferus	▨	▨	Two *Paraethomys* + *Promimomys*	*Paraethomys aff. abaigari*	Celadas 9 La Gloria 4 PUR-13 CLC-5A
						Celadensia	*Apocricetus barrierei*	Peralejos E PUR-4
MIOCENE	TUROLIAN UPPER	MN13	*Stephanomys ramblensis*	*Apodemus gudrunae*	*Apodemus gudrunae*	*Stephanomys ramblensis*	*Paraethomys meini*	Bacochas-1* Negratín-1* Almenara M Pino Mojón* Zorreras RCH-3*

FIGURE 8. Biostratigraphical position of the Baza-1 locality and its correlation with the biozonation proposed for the basins of Guadix-Baza, Granada and Teruel, placing other Spanish localities. The sites marked with an asterisk are within the Guadix-Baza Basin. **Abbreviations**: **AR-3**, Asta Regia 3; **CLC-5A**, Calicasas 5A; **PUR-4**, Barranco del Purcal 4; **PUR-13**, Barranco del Purcal 13; **RCH-3**, Rambla Chimeneas 3; **TCH-1**, Tollo de Chiclana 1 [planned for page width]

IX. LA SUCESIÓN DE ROEDORES DEL NEÓGENO SUPERIOR DE LA CUENCA DE GUADIX-BAZA (SE ESPAÑA) Y SU CORRELACIÓN CON LA ESCALA DE TIEMPO GEOMAGNÉTICA

The late Neogene rodent succession of the Guadix-Baza Basin (Southeastern Spain) and its correlation with Geomagnetic Time Scale

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ABSTRACT

In this paper a magnetostratigraphically calibrated biozonation of the Miocene–Pliocene continental record of the Guadix-Baza Basin (southeastern Spain) is presented. This biozonation is based on a rodent succession which ranges from the latest Miocene (*c*. 6 Ma) to the latest Pliocene (*c*. 2.6 Ma). A total of nine biozones have been defined for the late Miocene and Pliocene, all of them based on the range or concurrent-range of cricetid, murid and arvicolid species: *Apodemus gudrunae – Apocricetus alberti* Zone, *Apocricetus barrierei* Zone, *Paraethomys* aff. *abaigari* Zone, *Trilophomys* Zone, *Mimomys davakosi* Zone, *Dolomys adroveri* Zone, *Mimomys hassiacus* Zone, *Mimomys polonicus* Zone and *Kislangia ischus* Zone. A magnetobiostratigraphical correlation has been established between these biozones and the Standard ATNTS scale, on the basis of the paleomagnetic analysis carried out on the sections of Negratín, Botardo-1 and Gorafe. The correlation has been completed with previous paleomagnetic analysis in the sections of Galera and Zújar. As a result of this correlation, the time-span of each biozone can be established between 0.7 Myr, for the late Miocene – earliest Pliocene, to 0.1 Myr. The highest resolution is attained in the late early to late Pliocene, with durations between 0.1 and 0.45 Myr. The magnetobiostratigraphical correlation here established indicates a late Messinian age for the *Apodemus gudrunae – Apocricetus alberti* Zone, a Zanclean age for the *Apocricetus barrierei*, *Paraethomys* aff. *abaigari*, *Trilophomys* and *Mimomys davakosi* zones and a Piazencian age for the *Mimomys hassiacus*, *Mimomys polonicus* and *Kislangia ischus* zones. The *Dolomys adroveri* Zone is mostly Zanclean in age, but its uppermost part already belongs to the Piazencian. Therefore, the MN13 is correlated with the late Messinian, the MN14 is correlated with the early Zanclean, most of the MN15 is correlated with the late Zanclean, while the uppermost part of the MN15 and the MN16 are correlated with the Piazencian.

Keywords: late Miocene, Pliocene, biostratigraphy, magnetostratigraphy, rodents.

Several biozonations have been proposed for the late Neogene of the Guadix-Baza Basin (southeastern Iberian Peninsula). Most of the biozones have been defined on the basis of accurate studies of micromammals from several sites (Agustí 1986, 1990; Agustí *et al*. 1987; Martín Suárez 1988; Ruiz Bustos 1990; Agustí & Martín Suárez

1994; Minwer-Barakat *et al*. 2012*a*; Piñero & Agustí 2015). As a difference with these previous biozonations, in this paper, a complete calibrated rodent biozonation for the late Neogene of the Guadix-Baza Basin is presented for the first time. This is an extension of the calibrated biozonation for the early and middle Pleistocene from the same basin presented by Agustí *et al*. (2015).

This new information together with the revision of all Pliocene localities in the Guadix-Baza Basin and with few other data from the Iberian Peninsula provides a complete biostratigraphical record for the late Miocene to Pliocene micromammal succession. This record is further expanded for most of the Pleistocene (Oms *et al*. 2000; Agustí *et al*. 2015). The achieved palaeontological richness and stratigraphical continuity, makes the Guadix-Baza Basin a unique case in Western Europe and a reference for correlation with other areas from the late Miocene to the middle Pleistocene.

GEOLOGICAL SETTING

The Guadix-Baza Basin is an intramontane depression of Neogene and Quaternary age (Fig. 1) having an extension of approximately 3000 km^2. This basin is located in the Betic chain (southern Spain), an Alpine fold and thrust belt that mainly originated during the Miocene. At the contact area between the basement units or Internal Areas (located to the south and mainly of paleozoic age) and the cover units or External areas (located to the north and of mesozoic age) the Guadix-Baza Basin was developed. This basin was part of the corridors connecting the Atlantic and Mediterranean seas during part of Miocene (see general sedimentary schemes by Fernández *et al*. 1996; Soria *et al*. 1998). Towards the end of the Miocene the basin was disconnected from the sea and continental successions were deposited (Minwer-Barakat *et al*. 2009*a*, *b*, 2010, 2012*a*, *b*; Hüsing *et al*. 2010, 2012; Martín-Suárez *et al*. 2012). Thus, these successions provide an almost continuous continental record for the last 6 Myr. This unparalleled succession is recorded in several different palaeogeographic settings.

The Guadix-Baza Basin splits into two sub-basins: Guadix to the East and Baza to the West. Both sub-basins are separated by the Jabalcón threshold, being prominent reliefs of the External Zones. These two sub-basins underwent several connections and disconnections as a result of both tectonics and variations of the alluvial and fluvial network, which are regarded as the Guadix Formation (see Viseras 1991). This formation is build up of a main basin-axis aligned deposits (i.e. east-west) known as the longitudinal system. Other supplies were derived from the basin margins to the North and South known as the transversal systems. The alternating development of all these systems created confined lacustrine systems in different places of the basin (Fig. 1B). Thus, when the longitudinal system was more active, lacustine systems were mainly developed in the Baza sub-basin and are those of the Baza Formation. When transversal systems were more active, the main fluvial network was blocked and minor lacustrine systems formed in the Guadix sub-basin, known as Gorafe-Huélago and Solana formations, restricted to the Guadix sub-basin (Vera 1970). The basin was also infilled during the Pleistocene, but by 205 ka it was no longer endorheic and became a catchment area of the Guadalquivir River (see discussion in Oms *et al*. 2011).

The palaeontological sites considered in this study, in general terms belong to the lacustrine-palustrine systems of the Guadix and Baza sub-basins, but with some variations or peculiarities. A brief comment on sections which include new data it follows. The Negratín section is part of the Guadix sub-basin. This section is around 25 m thick (see figure 2 in Minwer-Barakat *et al*. 2009*a*) and is dominated by the distal alluvial-fluvial reddish mudstones, sandstones and conglomerates of the Guadix Fm. The Negratín-1 site is found at the very base of the section, where palustrine-lacustrine dark mudstones are found (Fig. 2A). The Botardo section is found in the Baza sub-basin and was introduced by Soria *et al*. (1987). It has a lower conglomeratic fluvial-alluvial part (from base to metre 23), and an upper part of the section built up of limestones and mudstones of lacustrine and palustrine origin that belong to the Baza Fm. The Botardo-C and D localities are found by metre 32 of the section (Fig. 2B). The Gorafe sites are found in the Gorafe Formation, which is restricted in the Guadix sub-basin. Some sites (Fig. 2C) are located in isolated outcrops (Gorafe-A and Gorafe-5; Ruiz Bustos *et al*. 1984; Martín Suárez 1988), while others (Gorafe-1 and Gorafe-2; de Bruijn 1974; Martín Suárez 1988) are found in stratigraphical succession. The basal part of this succession belongs to the Guadix Fm, while the rest are the lacustrine and palustrine Gorafe-Huélago Fm. Part of this section underwent a magnetostratigraphical study.

MAGNETOSTRATIGRAPHIC METHODS AND RESULTS

Three sections were sampled for magnetostratigraphic purposes: Negratín, Botardo-1 and Gorafe. Two other complementary outcrops containing micrommammals sites were also sampled close to the Gorafe section. Sampling was performed with an electrically powered drilling machine. Palaeomagnetic measurements were carried out in the Palaeomagnetism Laboratory at Institut de Ciències de la Terra Jaume Almera (SCT Universitat de Barcelona-CSIC). After sample preparation, specimens were demagnetized by means of a stepwise thermal treatment using a TSD-1 thermal demagnetiser (Schonstedt). Remanence measurements were acquired with a superconducting rock magnetometer (2G Enterprises). Bulk susceptibility was measured at room temperature and for each thermal demagnetization step with the Kappabridge KLY-2 susceptibilimeter (Geofyzika Brno).

Demagnetization protocol included the application of several demagnetization steps from room temperature until full demagnetization or until demagnetization plots displayed a spurious behavior. Sometimes this last fact was coincident with sudden susceptibility changes. Samples from Gorafe and Botardo sections were demagnetized until temperatures maximum around 400 ºC, while for Negratín section samples were demagnetized until temperatures higher than 600 ºC. Both the Gorafe and Negratín sections are flat lying so a fold/tilt test to check a primary origin of the characteristic remanent magnetization.

Figure 3 shows demagnetization plots from these sections. Negratín samples (Fig. 3A) displays the typical features of the Guadix Fm red-beds (see details and rock magnetism in Oms *et al*. 1999 and Hüsing *et al*. 2010), with a low-temperature component that was fully unblocked around 300 ºC and a higher one carried out by hematite that is fully unblocked at temperatures higher than 600 ºC. The general stability of samples permits to assign a robust reverse polarity for the Negratín section (Fig. 2A, 3A). Regarding the Gorafe section and complementary sites (Fig. 2C), they display the paleomagnetic features already described to the Gorafe and Baza lacustrine formations (Arribas *et al*. 2009; Oms *et al*. 1994; respectively). Both normal and reverse polarities have been identified (Fig. 3B and C, respectively). Reverse polarities show a low and high temperature component (Figs 3C–D), unblocked around 250 and 400 ºC, respectively. A basal sample with reverse normal polarities (Fig. 2C) is observed. An unsampled interval (due to thick regolith covering the section) follows, plus a short reverse interval (around metre 20). From metre 30 to 55 a long normal polarity interval is observed. The rest of the section is entirely reverse.

From the Botardo section (Fig. 2B), paleomagnetic results are very limited due to the low intensity of samples and its relatively unstable behavior. It is not possible to obtain a magnetostratigraphy of the whole section, but for the Botardo-C and D palaeontological sites, a reverse polarity is observed (Fig. 3E).

BIOZONATION OF THE LATE MIOCENE TO PLIOCENE

The Apodemus gudrunae – Apocricetus alberti *Zone*

Definition. Concurrent-range Zone defined by the simultaneous occurrence of *A. gudrunae* (Muridae, Rodentia) and *A. alberti* (Cricetidae, Rodentia). The lower boundary is marked by the first joint presence of the latter species, whereas the upper boundary is marked by the First Ocurrence Datum (FOD) of *Apocricetus barrierei*.

Reference section and level. Section of Negratín, level Negratín-1 (Fig. 2A; Minwer-Barakat *et al*. 2009*a*).

Other included sites in Guadix-Baza Basin. Rambla de Chimeneas-3 (Minwer-Barakat *et al*. 2009*b*), Dehesas de Guadix (Hüsing *et al*. 2010), Pino Mojón and Bacochas-1 (Sesé 1989). The site of Colorado-1 (Guerra-Merchán *et al*. 1991) could be included in this biozone. This site was assigned to the MN13 unit according to the presence of *Stephanomys* aff. *ramblensis*. Unfortunately, no measurements, descriptions or discussion of the taxa was presented, making it difficult to confirm the biostratigraphic position of this locality.

Chronostratigraphy. The reverse polarity observed in the Negratín section is correlated with C3r (ranging from 5.23 to 6.03 Ma) on the basis of the presence of African elements in Negratín-1 such as the cricetid *Myocricetodon jaegeri* and the gerbil *Debruijnimys almenarensis*. According to Agustí *et al*. (2006) these groups entered in Europe during the Messinian Salinity Crisis (C3r, late Turolian, MN13). The lower boundary of this biozone can be established at 6.03 Ma (Figs 4–5).

Associated fauna. In addition to *M. jaegeri* and *D. almenarensis*, elements associated with *A. gudrunae* and *A. alberti* in Negratín-1 are the murids *Occitanomys alcalai*, *Stephanomys dubari* and *Paraethomys meini*, as well as the cricetid *Ruscinomys schaubi*. The glirid *Eliomys truci* is present at Pino Mojón, whereas the lagomorph *Prolagus michauxi* and the sciurid *Atlantoxerus adroveri* are present in Bacochas-1 (Sesé 1989). The insectivores are represented by *Parasorex ibericus* in Negratín-1 (Minwer-Barakat *et al*. 2009*a*) and Erinaceidae indet. in Bacochas-1 (Sesé 1989) and Rambla de Chimeneas-3 (Minwer-Barakat *et al*. 2009*b*).

Biostratigraphic correlations. The presence of *M. jaegeri* and *D. almenarensis* indicates that this biozone belongs to the MN13 unit (late Turolian; Agustí *et al*. 2006). It can be equivalent with the *Apodemus gudrunae* Assemblage Zone proposed by Minwer-Barakat *et al*. (2012*a*) for the Guadix sub-basin (Fig. 6). Outside the Guadix-Baza Basin, the sites of Salobreña (Aguilar *et al*. 1984), Almenara-Casablanca M (Agustí 1990; Agustí *et al*. 2011), Zorreras (Martín-Suárez *et al*. 2000) and Gafares 2B (García-Alix *et al*. 2016) have yielded a similar association with elements of African origin. The localities attributed to this biozone are close in age to Arquillo-4 and Celadas-2 from the upper part of the *Stephanomys ramblensis* Zone from the Teruel Basin (Mein *et al*. 1990). A contemporaneous locality in the neighbour Granada Basin is Purcal-3 from the upper part of the *Paraethomys meini* Zone (García-Alix *et al*. 2008*a*). The *Paraethomys* Zone from the Crevillente Basin can be correlated with this biozone, with sites like Crevillente-6 (Martín Suárez & Freudenthal 1998). The *Paraethomys meini* Zone from the Alcoy Basin can be also correlated to the proposed biozone (Mansino *et al*. 2017).

The* Apocricetus barrierei *Zone

Definition. Interval Zone covering the biostratigraphic range of the species *Apocricetus barrierei* (Cricetidae, Rodentia) until the FOD of *Paraethomys* aff. *abaigari* (Muridae, Rodentia) in the Guadix-Baza Basin. The lower boundary of this zone is defined by the FOD of *Apocricetus barrierei*.

Reference section and level. Section of Botardo-1, level Botardo-D (Fig. 2B).

Other included sites in Guadix-Baza Basin. Botardo-A, B, C, 2 and 3 (Martín Suárez 1988), Colorado-2 (Guerra-Merchán *et al*. 1991), Cuzo-1, 2 and 3 (Guerra-Merchán & Ruiz Bustos 1991).

Chronostratigraphy. The section (see Agustí & Oms 2002) provided reverse polarities, at least for Botardo-C and D sites. This reverse interval is referred to C3n.2r (Fig. 4) based on the following criteria: Botardo-C and D are close in age to Sifón-P, from the neighbour Fortuna Basin (Garcés *et al*. 2001; Agustí *et al*. 2006). They share taxa such as *Stephanomys cordii*, *Castillomys gracilis*, *Eliomys truci* and *Eliomys intermedius*. Garcés *et al*. (2001) indicated that Sifón-P is located at the base of C3n.2n (4.63 – 4.49 Ma). However, the absence of a clear large-sized *Paraethomys* in the Botardo-1 section suggests a slightly older age for the sites in this section. The association from the Botardo-1 localities is also similar to that from Puerto de la Cadena, a site assigned to the C3n.4n (4.99 – 4.89 Ma) by Piñero *et al*. (2017). The presence in Puerto de la Cadena of *Stephanomys* cf. *dubari*, instead of its descendant *Stephanomys cordii*, suggests a somewhat older age than Botardo-1. Therefore, we place the whole Botardo-1 section in C3n.2r (between 4.79 and 4.63 Ma). Regarding the FOD of *Apocricetus barrierei*, out of the Guadix-Baza Basin it has been established at the level of Purcal-4, in the neighbour Granada Basin (García-Alix *et al*. 2008*b*). This locality was correlated with the uppermost part of C3r, roughly coinciding with the Miocene–Pliocene boundary (Martín-Suárez *et al*. 1998). Therefore, a minimum age of at around 5.3 Ma can be established for the *Apocricetus barrierei* Zone (Fig. 5).

Associated fauna. The small mammal list from Botardo-D is provided for the first time in this paper, being composed of the cricetid *Apocricetus barrierei*, the murids *Paraethomys meini*, *Apodemus gorafensis*, *Stephanomys cordii* and *Castillomys gracilis*, the gerbil *Debruijnimys* sp., the glirid *Eliomys truci* and the lagomorph *Prolagus* sp. (see Fig. 7). In this biozone, the murids *Occitanomys alcalai* and *Apodemus gudrunae* are still present. The murid *Occitanomys* cf. *brailloni* and the sciurid *Atlantoxerus* cf. *adroveri* have been indentified in Cuzo-1. *Prolagus* cf. *michauxi* has been reported in Cuzo-3. This zone records the FOD of the glirid *Eliomys intermedius* at Botardo-C (Martín Suárez 1988), whereas *Eliomys truci* is still present. Among the insectivores, *Parasorex ibericus* is present in Botardo-3 and C, *Archaeodesmana dekkersi* in Botardo-C, and *Asoriculus gibberodon* in Cuzo-1.

Regarding the large mammals, Giraffidae indet. was reported from Botardo-C (Martín Suárez 1988).

Biostratigraphic correlations. This biozone is assigned to MN14 (early Ruscinian) on the basis of the presence of *Stephanomys cordii* and *Apocricetus barrierei*, considered to be characteristic species of this unit (Mein 1975; Fejfar & Heinrich 1990; Minwer-Barakat *et al*. 2012*a*). The proposed biozone corresponds to the lower interval between the *Apodemus gudrunae* Assemblage Zone and the *Trilophomys* Assemblage Zone from the Guadix sub-basin (Minwer-Barakat *et al.* 2012*a*). Outside the Guadix-Baza Basin, the *Apocricetus barrierei* Zone from the Granada Basin (García-Alix *et al.* 2008*a*) can be correlated with this zone. In the latter basin, the localities of Purcal-4, Purcal-7, Calicasas-3 and Calicasas-4 record *Stephanomys dubari*, whereas the localities from the Botardo-1 section record its descendant *Stephanomys cordii*, suggesting a slightly older age for Botardo-C and D. Similarly, the *Apocricetus barrierei* Zone from the Alcoy Basin (Mansino *et al.* 2017) can be correlated with the homonym zone in the Guadix-Baza Basin. In the Teruel Basin, the localities included in the *Celadensia* Zone (such as the reference locality of Peralejos-E) can be also coeval with the *Apocricetus barrierei* Zone (Fig. 6). The *Celadensia* Zone is characterized by the presence of *Celadensia nicolae* (see Mein *et al.* 1990), species so far not found in southern Spain. However, this biozone is placed in the Teruel Basin prior to the first occurrence of a large-sized *Paraethomys*, as it is also the case for the localities included in the *Apocricetus barrierei* Zone. The levels of Botardo-C and D share with Peralejos-E the presence of some large specimens close in size to *Paraethomys* aff. *abaigari* (Mein *et al.* 1990). However, the presence of a second large sized species of *Paraethomys* species cannot be clearly recognized in the Botardo-1 section, so a close correlation between the *Apocricetus barrierei* Zone and the *Celadensia* Zone cannot be established.

The* Paraethomys *aff.* abaigari *Zone

Definition. Interval Zone between the FOD of *Paraethomys* aff. *abaigari* and the First Regular Occurrence (FRO) of *Trilophomys* (Cricetidae, Rodentia).

Reference level. Section of Baza, level Baza-1 (Piñero *et al.* in press; Ros-Montoya *et al.* in press).

Other included sites in Guadix-Baza Basin. Aljibe-2, 3 (Guerra-Merchán *et al.* 1991), Yeguas (Soria & Ruiz Bustos 1991; Minwer-Barakat 2005).

Chronostratigraphy. Unfortunately, the site of Baza-1 was not suitable for paleomagnetic analysis. However, we can infer the range of this biozone by indirect correlations. Therefore, from a biostratigraphic point of view, Baza-1 is placed between the level of Sifón-P, in the Fortuna Basin and the sites of Gorafe-A and Gorafe-4, in the Guadix-Baza Basin. Sifón-P is situated at the base of C3n.2n (Garcés *et al.* 2001), while Gorafe-A and Gorafe 4 are correlated with C3n.1n (this work). Therefore, the site of Baza-1 can be roughly correlated with chron 3n.1r, the *Paraethomys* aff. *abaigari* Zone being younger than 4.6 Ma and older than 4.3 Ma (Fig. 5). Outside the Guadix-Baza Basin, the FOD of *Paraethomys* aff. *abaigari* was recorded at the site of La Bullana-3, in the Cabriel Basin, a site preliminarily assigned to the chron C3n.4n (5.235 – 4.997 Ma) by Mansino et al. (2015a). If this assignment is confirmed, that would imply that there is a delay in the FOD of *P.* aff. *abaigari* in the Guadix-Baza Basin with respect to the Cabriel Basin, since as we have seen this species is absent from the Botardo-1 section, which is correlated with the younger C3n.2r. This inconsistency is best explained if the normal interval identified at La Bullana-3 would correspond to the younger chron 3n.3n (4.896 – 4.799 Ma), and La Bullana-2B to chron 3n.2r (4.799 – 4.631 Ma).

Associated fauna. A great diversity of rodents has been reported from the localities assigned to this zone. Most of them are already present in the previous biozone, such as *Stephanomys cordii*, *Paraethomys meini*, *Castillomys gracilis*, *Apodemus gorafensis* and *Eliomys intermedius*. However, other species not recorded up to this biozone are included here, such as *Debruijnimys julii* at Baza-1 and *Micromys* sp. at Aljibe-3. The murid *Occitanomys* cf. *brailloni* is also present in Baza-1. *Paraethomys jaegeri* from Aljibe-2 and 3 likely corresponds to *P.* aff. *abaigari*. However, since Guerra-Merchán *et al.* (1991) did not provided measurements or descriptions, this ascription cannot be confirmed. In Baza-1 *Trilophomys* is scarcely represented (three out of 402 rodent teeth; Piñero *et al.* in press). Among lagomorphs, *Trischizolagus maritsae* and *Prolagus michauxi* are present at Baza-1. The insectivores are represented at Baza-1 by one indeterminate Desmaninae, one Erinaceidae and the soricid *Sorex* sp. The first appearance of *Paenelimnoecus pannonicus* is recorded at Yeguas (Minwer-Barakat

2005). The Baza-1 site has an abundant large mammal assemblage, including the first record of the coexistence of two proboscideans in the Iberian Peninsula, i.e. *Mammut borsoni* and *Anancus arvernensis*, the bovid *Alephis* sp., the rhinocerotid *Stephanorhinus* cf. *jeanvireti*, one indeterminate cervid, and the equid *Hipparion* sp. (Ros-Montoya *et al.* in press).

Biostratigraphic correlations. This biozone is again correlated with the MN14 (early Ruscinian) according to the presence of *Stephanomys cordii* and *Apocricetus barrierei*. In this way, the *Paraethomys* aff. *abaigari* Zone covers the upper interval between the *Apodemus gudrunae* Assemblage Zone and the *Trilophomys* Assemblage Zone proposed by Minwer-Barakat *et al.* (2012*a*) for the Guadix sub-basin (Fig. 6). Despite the rare presence of *Trilophomys* in Baza-1, we do not include this locality in the forthcoming *Trilophomys* Zone, since in this locality *Trilophomys* represents less than one per cent of the specimens (three out of 402 rodent teeth), while in other typical localities from the *Trilophomys* Zone, such as Gorafe-A, this genus reaches at least the ten per cent (eight out of 75). Such an early presence of *Trilophomys* can only be recognized in extremely rich assemblages such as Baza-1, but this genus would appear as absent in samples below the 400 teeth. In this way, the sites of Aljibe-2 and 3, which are located in the same ravine than Baza-1 at levels above this site, and which present a very similar association, lack *Trilophomys*, despite their higher stratigraphic position. We explain this anomaly because of their smaller sample size with respect to Baza-1 (Piñero *et al.* in press). This is also the case for the site of Yeguas, which does not record *Trilophomys*. This biozone can be correlated with the *Paraethomys* aff. *abaigari* Zone from the Granada Basin (García-Alix *et al.* 2008*a*). In the latter basin, *Paraethomys* aff. *abaigari* has been recorded at the sites of Calicasas-5A and Purcal-13, indicating an age close to that of Baza-1 (García-Alix *et al.* 2008*c*). This is also the case for the *Paraethomys* aff. *abaigari* Zone from the Alcoy Basin (Mansino *et al.* 2017), Baza-1 being close in age to Alcoi Cristian-0C, B, and 0 (Mansino *et al.* 2015*b*). Some localities of the Teruel Basin included in the Two *Paraethomys* + *Promimomys* Zone, such as La Gloria-4 and Celadas-9 (Mein *et al.* 1990) can be also close in age to Baza-1. However, in these localities the two *Paraethomys* species, *P. meini* and *P.* aff. *abaigari*, are associated with *Promimomys*, a genus which is so far absent from the Guadix-Baza and other southern Iberian basins.

The* Trilophomys *Zone

Definition. Interval zone covering the FRO of *Trilophomys* species until the first entry of the arvicolid *Mimomys davakosi*.

Reference section and level. Lower part of the Gorafe section, locality Gorafe-A (Fig. 2C; Ruiz Bustos *et al.* 1984).

Other included sites in Guadix-Baza Basin. Gorafe-1 and 4 (de Bruijn 1974; Martín Suárez 1988).

Chronostratigraphy. The paleomagnetic analysis carried out in the main Gorafe barranco section, includes the levels of Gorafe-1 and 2, as well as in other smaller associated sections in the Gorafe road (including Gorafe-A, 4 and 5). The two normal intervals recorded at the main Gorafe road section are correlated with chrons 3n.2n and 3n.1n (Fig. 4). The localities belonging to the *Trilophomys* Zone in the section (Gorafe-1, 4, A) are all placed within chron 3n.1n (Fig. 4). Since the site of Zújar-4 is placed just at the base of the reverse chron 2Ar (Oms *et al.* 1999; Agustí *et al.* 2001*a*), most probably the *Trilophomys* Zone is constrained to the normal chron 3n.1n, between 4.30 and 4.19 Ma, although a somewhat older lower boundary is not excluded (Fig. 5).

Associated fauna. The faunal composition of Gorafe-1, A and 4 is very similar to that of the sites included in the *Paraethomys* aff. *abaigari* Zone. However, they differ from the former ones by the regular presence of *Trilophomys*. Among the large mammals, the site of Gorafe-4 records *Gazella borbonica* (Agustí 1986) and *Sus arvernensis* (Van der Made 1989*a*, *b*).

Biostratigraphic correlations. The presence of *Trilophomys* together with *Stephanomys cordii* is characteristic for the end of the early Ruscinian (MN14). This biozone is partly equivalent to the *Trilophomys* Assemblage Zone previously defined in the Guadix sub-basin (Minwer-Barakat *et al.* 2012*a*). There are no equivalent sites in the neighbour Granada Basin, since the sediments from this time are not suitable for recovering small mammal remains (García-Alix *et al.* 2008*a*). This biozone can be correlated with the *Trilophomys* Assemblage Zone of the Alcoy Basin (Mansino *et al.* 2017), in which the reference locality of Alcoy-2D, as well as Alcoy-2C, present an association which is very similar to that of Gorafe-A and 4. Nonetheless, the presence of *Apocricetus* cf. *angustidens* (descendant of *Apocricetus barrierei*) suggests an age somewhat younger than Gorafe-A and 4. Similarly, the proposed biozone can be correlated with the biozone of the same name from the Teruel Basin (Mein *et al.* 1990). However, the reference locality of Villalba Alta Río-1, as well as the sites of Orrios-1 and Aldehuela, record the murid *Stephanomys margaritae* (descendant of *Stephanomys cordii*), indicating a slightly younger age than Gorafe-A and 4 (Fig. 6).

The* Mimomys davakosi *Zone

Definition. Interval zone covering the FOD of *Mimomys davakosi* until the FOD of *Dolomys adroveri*.

Reference section and level. Section of Zújar, level Zújar-4 (Oms *et al.* 1999; Agustí *et al.* 2001*a*).

Chronostratigraphy. The presence of *Mimomys davakosi* (Fig. 8A) has been recognized at the base of the Zújar section, in the site of Zújar-4. This locality was correlated with the base of chron 2Ar (Fig. 4; Oms *et al.* 1999; Agustí *et al.* 2001*a*). Therefore, the lower limit of this biozone is placed at approximately 4.19 Ma. The upper boundary of this biozone cannot be precisely established. The FOD of *Dolomys adroveri*, the species characterizing the forthcoming biozone, is recorded in the Guadix-Baza Basin at the sites of Gorafe-2 and 5, included in the reverse interval identified again as chron 2Ar in the Gorafe sections. Therefore, the upper boundary of this biozone is for sure younger than 4.19 Ma and older than 3.6 Ma (Fig. 5).

Associated fauna. In this biozone there is a replacement of the murid association with respect to the previous ones. Thereby, Zújar-4 records the FOD of *Paraethomys jaegeri*, *Stephanomys margaritae* and *Apodemus atavus* in the Guadix-Baza Basin. The cricetid *Apocricetus barrierei* and the glirid *Eliomys intermedius* are still present.

Biostratigraphic correlations. The FOD of the arvicolid genus *Mimomys* in this basin marks the onset of the MN15 unit (late Ruscinian). The *Mimomys davakosi* Zone can be placed in the time gap between the *Trilophomys* Assemblage Zone and the *Dolomys adroveri* Taxon-range Zone from the Guadix sub-basin (Minwer-Barakat *et al.* 2012*a*). Apart from Zújar-4, there are no more sites recording *M. davakosi* at the Guadix-Baza Basin. However, outside from that basin, this species has been found in

Teruel, at the sites of Arquillo-3, Villalba Alta-1, Sarrión-2 and El Rajo from the upper part of the Archaic *Mimomys* Zone (Fig. 6; Mein *et al.* 1990). The species *Mimomys davakosi* has also been identified in Greece, at the early Pliocene sites of Ptolemais-3 (van de Weerd 1979), Vorio-3, 3a and Komano-2 (Hordijk & de Bruijn 2009). Vorio-3 and 3a are placed in a normal chron identified as C3n.3n (between 4.9 and 4.8 Ma; Hordijk & de Bruijn 2009), older than Zújar-4. Therefore the entry of *Mimomys davakosi* in Southeastern Europe took place before than in Southeastern Spain.

The* Dolomys adroveri *Zone

Definition. Taxon-range zone covering the biostratigraphic range of the species *Dolomys adroveri*. The lower boundary of this zone is defined by the FOD of this species while the upper boundary is defined by its Last Occurrence Datum (LOD).

Reference section and level. section of Galera, level of Galera-1C (Agustí *et al.* 1997).

Other included sites in Guadix-Baza Basin. Gorafe-2, 3, 5, Tollo de Chiclana-1.

Chronostratigraphy. The FOD of *Dolomys adroveri* is recorded at the top of the section of Gorafe (levels of Gorafe-2 and 5), included in a reverse interval which is correlated to chron 2Ar (4.19 – 3.58 Ma; Fig. 4). The LOD of this species is recorded at the site of Galera-1C, which is placed at the base of the section of Galera, in a normal interval identified as C2An.3, between 3.58 – 3.33 Ma (Agustí *et al.* 1997; Garcés *et al.* 1997). Therefore, the time interval of this biozone can be established approximately between 3.3 Ma and 3.9 Ma (Fig. 5).

Associated fauna. Besides *Dolomys adroveri* (Fig. 8D–E), the association from the level of Galera-1C includes the following accompanying rodent fauna (Agustí *et al.* 1997; and this work): *Stephanomys donnezani, Apodemus atavus, Castillomys crusafonti*, *Occitanomys brailloni, Eliomys intermedius, Pliopetaurista* sp. and *Castor fiber.* Agustí *et al*. (1997) also indicated the presence of *Mimomys occitanus*. A similar association of *Dolomys adroveri* and *M. occitanus* was mentioned for the level of Gorafe-2 (de Bruijn 1973). However, the specimens assigned to *Mimomys occitanus* have proven to be worn teeth of *Dolomys adroveri* (Castillo & Agustí 1996), so the co-occurrence of an archaic *Mimomys* species with *Dolomys adroveri* has to be excluded in the Guadix-Baza Basin. This biozone records the FOD of *Castillomys crusafonti*, *Stephanomys donnezani*, *Apocricetus angustidens*, *Ruscinomys europaeus* and *Archaeodesmana elvirae*, and the LOD of the genus *Paraethomys* in the Guadix-Baza succesion. So far, *A. elvirae* has only been identified from the type locality Tollo de Chiclana-1 (Minwer-Barakat *et al.* 2008*a*). Otherwise, this biozone includes taxa already present in the previous biozones such as *Apodemus gorafensis*, *Apodemus atavus*, *Stephanomys margaritae* (Fig. 7B–E), *Paraethomys meini*, *Paraethomys jaegeri* (Fig. 7F–H), *Occitanomys brailloni*, *Eliomys intermedius*, *Trilophomys* cf. *castroi* (Fig. 7R–S), *Asoriculus gibberodon* and *Paenelimnoecus pannonicus*. There are some taxa no longer present in this biozone such as *Apocricetus barrierei*, *Castillomys gracilis* and *Stephanomys cordii*.

Biostratigraphic correlations. The *Dolomys adroveri* Zone is assigned to the upper part of MN15. This zone is equivalent to the same zone proposed by Minwer-Barakat *et al*. (2012*a*) in the Guadix sub-basin. Again in Southern Spain, a similar association with *Dolomys adroveri* is present at the site of Asta Regia-3, in levels interbeded with marine deposits of Pliocene age (Aguirre *et al.* 1995; Castillo & Agustí 1996). Outside the Guadix-Baza Basin, a *Dolomys* Zone was defined in the Teruel Basin (Mein *et al.* 1990), including the sites of Teruel-Cementerio, Villalba Alta-4, Orrios-3 and Orrios-4 (Fig. 6). The localities of Barranco de Blas-1, 5A and 6 from the *Stephanomys donnezani* Zone in the Granada Basin are probably close in age to Galera-1C (García-Alix *et al.* 2008*a*). However, the Arvicolinae from these localities could not be identified, so it is not possible to establish a reliable correlation with this biozone.

Discussion. Overlying the *Dolomys adroveri* Zone, Martín Suárez (1988) and Agustí & Martín Suárez (1994) proposed the *Apodemus Agustíi* Zone. This zone was established on the basis of the site of Cañada del Castaño-1, in the Cañada del Castaño section. This site was placed in continuity with the Galera section and was characterized by a rich rodent association including *Paraethomys jaegeri, Occitanomys brailloni, Castillomys crusafonti, Apodemus Agustíi, Stephanomys* cf. *thaleri, Apodemus atavus, Eliomys intermedius, Muscardinus* sp. and Soricini indet. (Martín Suárez 1988). The most suprising fact from this association was the absence of arvicolids, being already present in the previous biozone. Otherwise, Cañada del Castaño-1 shares some taxa with other localities from the Guadix-Baza Basin such as Galera-1C and Tollo de

Chiclana-1B. However, the exact stratigraphic position of the Cañada del Castaño section with respect to the Galera section cannot be precisely established, since this section disappeared shortly after the first samplings of the site. Even so, a lower stratigraphic position with respect to Galera-1C, as assumed by Agustí & Julià (1990), cannot be excluded, after the absence of any arvicolid species. Given the probable narrow stratigraphic range of this biozone and the difficulties in order to establish a correlation outside the Guadix-Baza Basin, Minwer-Barakat *et al*. (2012*a*) decided to include this zone in the *Mimomys haussiacus-Stephanomys donnezani* Zone from the Guadix sub-basin. Provided the stratigraphic uncertainities of the lost Cañada del Castaño section, we also discard to include this biozone in this work.

The* Mimomys hassiacus *Zone

Definition. Taxon-range zone covering the biostratigraphic range of the species *Mimomys hassiacus* (Arvicolidae, Rodentia). The lower boundary of this zone is defined by the FOD of this species while the upper boundary is defined by the FOD of *Mimomys polonicus.*

Reference section and level. Section of Tollo de Chiclana, level of Tollo de Chiclana-1B (Minwer-Barakat *et al.* 2004, 2008*b*, 2012*a*).

Other included sites in Guadix-Baza Basin. Tollo de Chiclana-1B is the only site in the Guadix-Baza Basin in which this species has been recognized (Minwer-Barakat *et al.* 2012*a*). It is also present in the neighbour fissure infilling site of Moreda-1A (Castillo 1990; Minwer-Barakat *et al.* 2012*a*).

Chronostratigraphy. Unfortunatelly, no paleomagnetic data are associated with the section of Tollo de Chiclana. However, we can reasonably constrain the time-range of this biozone. Therefore, the lower boundary should be younger than the level of Galera-1C, which still presents *Dolomys adroveri.* This level is placed in the Galera section in a normal interval identified as chron 2An.3 (Fig. 4; Garcés *et al.* 1997; Agustí *et al.* 1997). On the other hand, the upper boundary should be younger than the levels of Zújar-10, which already presents *Mimomys polonicus* (Agustí *et al.* 2001*a*). This site is placed in the Zújar section at the base of a normal interval correlated with chron 2A.2r (Fig. 4; Oms *et al.* 1999). Therefore, the range of the *Mimomys hassiacus* Zone should be roughly equivalent to the reverse chron 2An.2r, between 3.20 and 3.33 Ma (Fig. 5).

Associated fauna. This biozone records the FOD of the soricid *Myosorex meini*, and the LOD of the talpid *Archaeodesmana brailloni*, the cricetid *Blancomys meini*, the sciurid *Pliopetaurista pliocaenica*, and the murid genus *Occitanomys* (see Minwer-Barakat *et al.* 2005, 2008*a*, 2010, 2012*a*; García-Alix *et al.* 2007, 2008*b*). The species *Apodemus atavus*, *Castillomys crusafonti*, *Stephanomys donnezani*, *Eliomys truci*, *Eliomys intermedius*, *Asoriculus gibberodon* and *Paenelimnoecus pannonicus* persist in this biozone (Minwer-Barakat *et al.* 2005, 2010; García-Alix *et al.* 2008*b*). The especies *Rhagapodemus frequens* and *Trilophomys vandeweerdi* also appears at Tollo de Chiclana-1B (Minwer-Barakat 2005; Minwer-Barakat *et al.* 2005).

Biostratigraphic correlations. This zone was initially defined in the Guadix sub-basin by Minwer-Barakat *et al*. (2012*a*) as *Mimomys hassiacus* – *Stephanomys donnezani* Concurrent-range Zone. It marks the end of the MN15 in the Guadix-Baza Basin. The presence of *Stephanomys donnezani* in Huéscar-3 (Mazo *et al.* 1985), Barranco de Quebradas-1, Barranco de Cañuelas-2, 3 and 5 (Sesé 1989) and Nuca-1 (Ruiz Bustos 1991) allows their correlation to the late Ruscinian. However, it is impossible to include these localities to any biozone from this work, given the confusion in the ascription of their arvicolids (Minwer-Barakat *et al.* 2008*b*, 2012*a*). Outside the Guadix-Baza Basin, the *Mimomys hassiacus* Zone is most probably correlated with the *Mimomys gracilis* + *Mimomys hajnackensis* Zone from the Teruel Basin (Fig. 6; Mein *et al.* 1990), *Mimomys hajnackensis* being a junior synonym of *M. hassiacus*.

The* Mimomys polonicus *Zone

Definition. Taxon-range zone covering the biostratigraphic range of the species *Mimomys polonicus.*

Reference section and level. Section of Zújar, level of Zújar-10 (Oms *et al.* 1999; Agustí *et al.* 2001*a*).

Other included sites in Guadix-Baza Basin. So far, Zújar-10 is the only locality having delivered *Mimomys polonicus* in the Guadix-Baza Basin.

Chronostratigraphy. In the Zújar section, the level of of Zújar-10 is placed at the base of the normal chron 2An.2n, between 3.11 and 3.20 Ma (Fig. 4; Oms *et al.* 1999).

The FOD of *Kislangia ischus*, which marks the upper limit of this biozone, is recorded at Zújar-11. This site was correlated with the base of chron 2An.1n (at approximately 3.03 Ma; Oms *et al.* 1999; Agustí *et al.* 2001). Therefore, the chronostratigraphic range of this biozone is established between 3.03 and 3.30 Ma (Fig. 5).

Associated fauna. *Mimomys polonicus* (Fig. 8B) is associated in Zújar-10 with *Stephanomys donnezani*, *Castillomys crusafonti*, *Apodemus atavus* and *Eliomys intermedius*. This biozone records the LOD of *Stephanomys donnezani*.

Biostratigraphic correlations. This zone is assigned to the MN16 because of the presence of *Mimomys polonicus*. Previously, this species has never been reported in other Iberian basins. The presence of members of the lineage *Mimomys hajnackensis–polonicus* have been mentioned in the *Kislangia* Zone from the Teruel Basin without a specific assignament (Mein *et al.* 1990). In previous biozonations from the Guadix-Baza Basin (Agustí 1986; Martín-Suárez 1988; Agustí & Martín-Suarez 1994), a *Mimomys* (later *Kislangia*) *cappettai* Zone was defined for a number of sites from the basin, being correlated with the MN16. However, an accurate analysis of the specimens originally assigned to *Kislangia cappettai* led to the conclusion that they actually belonged to *Kislangia ischus*, a more advanced species of the genus *Kislangia* which characterizes the following biozone (Adrover *et al.* 1988; Agustí *et al.* 1993). Therefore, most of the localities formerly included in the *Kislangia cappettai* Zone are younger than Zújar-10.

The* Kislangia ischus *Zone

Definition. Taxon-range zone covering the range of the species *Kislangia ischus*. The lower boundary of this zone is defined by the FOD of this species while the upper boundary is defined by the FOD of *Kislangia gusii.*

Reference section and level. Section of Zújar, level of Zújar-11 (Agustí *et al.* 2001*a*).

Other included fossil sites in Guadix-Baza Basin. Tollo de Chiclana-3 and 13 (Minwer-Barakat *et al*. 2005, 2007, 2008*b, c*).

Chronostratigraphy. In the Guadix-Baza Basin, the presence of *Kislangia ischus* has been recognized at Zújar-11, placed at the base of chron 2An.1n, at about 3.03 Ma (Fig. 4; Oms *et al.* 1999; Agustí *et al.* 2001*a*). The upper boundary of this biozone is defined by the FOD of *Kislangia gusii*. In the Guadix-Baza Basin, the latter species has been recorded in the Zújar section at Zújar-14, a level which is placed at the basal part of chron 2r (Matuyama), already in the Pleistocene. Therefore, we assume that the upper boundary of the *Kislangia ischus* Zone is close to the chron 2An.2r (Gauss–Matuyama boundary), at about 2.6 Ma, almost coincident with the Pliocene–Pleistocene and Neogene–Quaternary boundaries (Fig. 5; Agustí *et al.* 2015).

Associated fauna. Associated with *Kislangia ischus* at Zújar-11 (Fig. 8C) are the murids *Stephanomys minor* and *Stephanomys thaleri*. In addition, the faunal association from Zújar-11 includes the rodents *Castillomys crusafonti*, *Apodemus atavus*, *Eliomys intermedius*, *Castor fiber* and the insectivore *Galemys* sp. Lagomorphs are represented by *Prolagus michauxi* and *Oryctolagus* sp. (De Marfà 2009). Among the large mammals, the presence of *Anancus arvernensis* should be noticed (Agustí *et al.* 2001*a*). The two lineages of *Sthephanomys* found in Zújar-11 have also been recognized at Tollo de Chiclana-3 and 13 (Minwer-Barakat *et al.* 2005). However, these latter levels include another arvicolid, the especies *Mimomys stehlini* (Minwer-Barakat *et al.* 2008*b*). Tollo de Chiclana-13 represents the type locality of the murid *Micromys caesaris* (Minwer-Barakat *et al.* 2008*c*), whereas the soricid *Blarinoides aliciae* was described for the first time at Tollo de Chiclana-3 (Minwer-Barakat *et al.* 2007). Further, this biozone records the glirids *Eliomys truci* and *Eliomys intermedius*, the soricids *Asoriculus gibberodon*, *Paenelimnoecus pannonicus*, *Myosorex meini* and *Petenyia hungarica*, and the talpids *Archaeodesmana* sp. and Desmaninae indet.

Biostratigraphic correlations. The presence of *Stephanomys minor* at Zújar-11 suggests that this biozone is equivalent to the *Stephanomys minor* Zone proposed by Minwer-Barakat *et al*. (2012*a*) for the Guadix sub-basin. The presence of a similar association with *Stephanomys minor* at the neighbour fissure infilling of Moreda-1B indicates that this site can be also correlated with Zújar-11 (Castillo 1990). In the Teruel Basin, part of the localities assigned to the *Kislangia* Zone (Mein *et al.* 1990) contains most probably *Kislangia ischus*, so the *Kislangia ischus* Zone from Guadix-Baza can be correlated with the upper part of the *Kislangia* Zone from Teruel (Fig. 6). *Kislangia ischus* is also present at the site of Villarroya, at the westernmost end of the Ebro Basin, in a magnetostratigraphic position which is very close to that of Zújar-11 (base of chron 2An.1n; Agustí & Oms 2001).

CONCLUSIONS

In the late Neogene of the Guadix-Baza Basin it has been possible to recognize up to nine biozones, ranging from the latest Miocene to the latest Pliocene, between 6.03 and 2.58 Ma. One biozone (*Apodemus gudrunae* – *Apocricetus alberti* Zone) is placed in the latest Miocene (from 6.03 to 5.33 Ma) while the remaining eight belong to the Pliocene (from 5.3 to 2.6 Ma). The oldest biozones, the *Apodemus gudrunae* – *Apocricetus alberti* and *Apocricetus barrierei* zones, are those with longer durations, at about 0.7 Myr, which is indicative of a lower level of resolution for this time-span. However, the event represented at the Negratín section, with the entry of African rodent species most probably lasted much less, about 0.3 Myr, as recorded in the neighbour Fortuna Basin. In the case of the *Apocricetus barrierei* Zone, if we only take into account the FOD of this species in the Guadix-Baza Basin at the Botardo section, the duration of the biozone is reduced to about 0.3 Myr. The duration of the late early Pliocene *Paraethomys* aff. *abaigari* and *Trilophomys* zones is much shorter, roughly 0.2 Myr, which is also the case for the *Mimomys davakosi* Zone. In contrast, the time-span of the *Dolomys adroveri* Zone is much longer, at about 0.6 Myr, due to the difficulties to constrain the duration of this biozone within the long 2Ar chron. The shorter biozones and the highest resolution level are attained at the beginning of the late Pliocene, with the *Mimomys haussiacus* and *Mimomys polonicus* zones, with durations at about 0.1 and 0.15 Myr, respectively. The time-span of the latest Pliocene *Kislangia ischus* Zone is of about 0.45 Myr.

According to the magnetobiostratigraphic correlation here established, we can conclude that the *Apodemus gudrunae* – *Apocricetus alberti* Zone corresponds to the late Messinian. The *Apocricetus barrierei*, *Paraethomys* aff. *abaigari*, *Trilophomys* and *Mimomys davakosi* zones are included in the Zanclean marine stage. The lower part of the *Dolomys adroveri* Zone also belong to this stage, while the upper part (Galera-1C, placed at the base of chron 2An.3) is already Piazencian. The *Mimomys hassiacus*, *Mimomys polonicus* and *Kislangia ischus* zones are definitively Piazencian. Therefore, most of the MN14 mammal unit (including the *Apodemus gudrunae* – *Apocricetus alberti*, *Paraethomys* aff. *abaigari* and *Trilophomys* zones) can be correlated with the early Zanclean. Most of the MN15 (including the *Mimomys davakosi* and *Dolomys adroveri* zones) can be correlated with the late Zanclean. However, the uppermost part of this unit already belongs to the Piazencian, as is the case of the above mentioned level of Galera-1C. Finally, the MN16 can be correlated with the Piazencian, the MN16–MN17 boundary being roughly coincident with the Pliocene–Pleistocene and Neogene–Quaternary boundaries.

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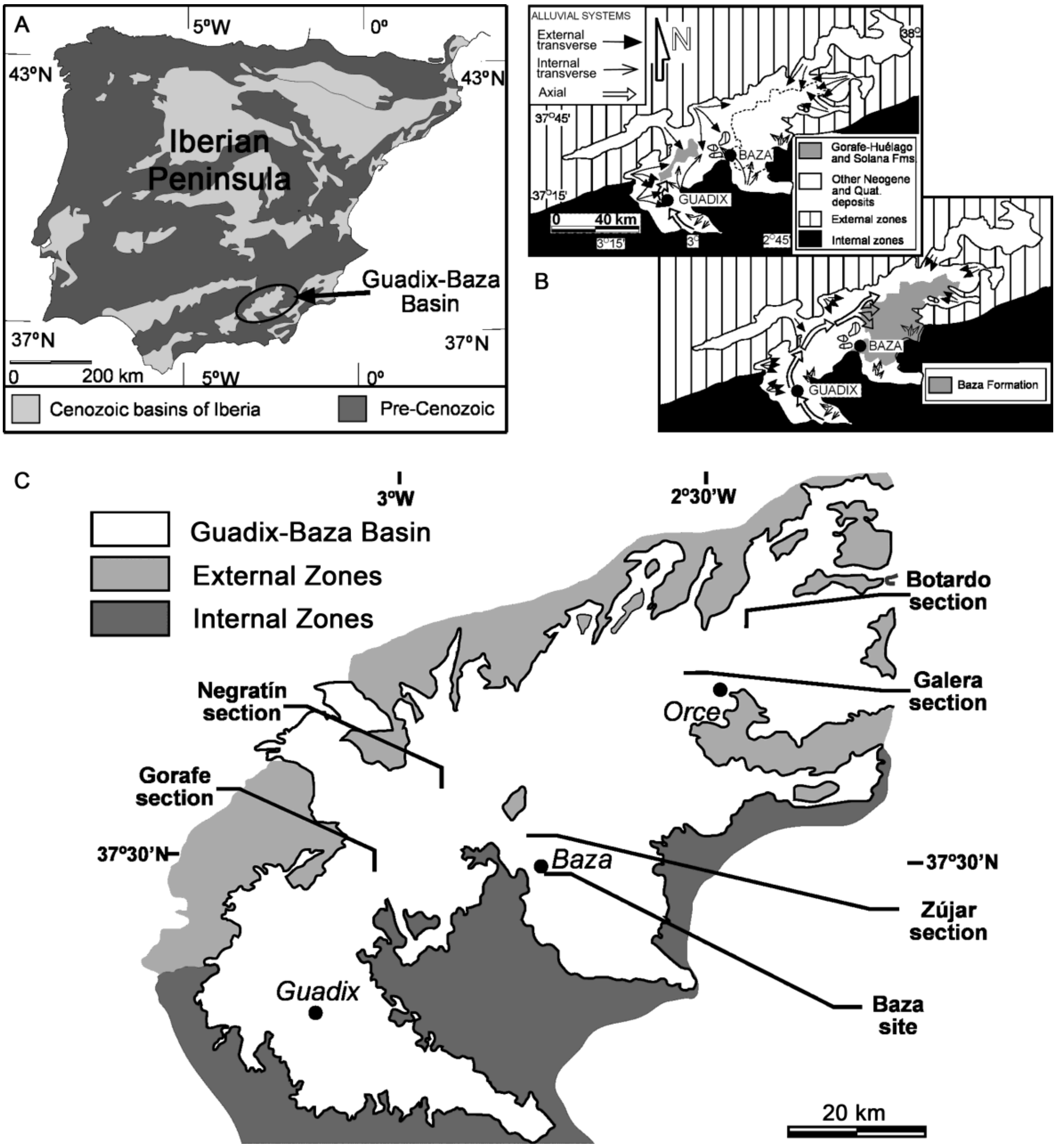


FIG. 1. Geological setting. A, The Guadix-Baza Basin in the context of the Cenozoic basins of the Iberian Peninsula. B, Paleogeographic distribution of the lacustrine-palustrine formations in the Guadix-Baza Basin (after Viseras 1991). C, Guadix-Baza Basin with location of the sections and sites here discussed.

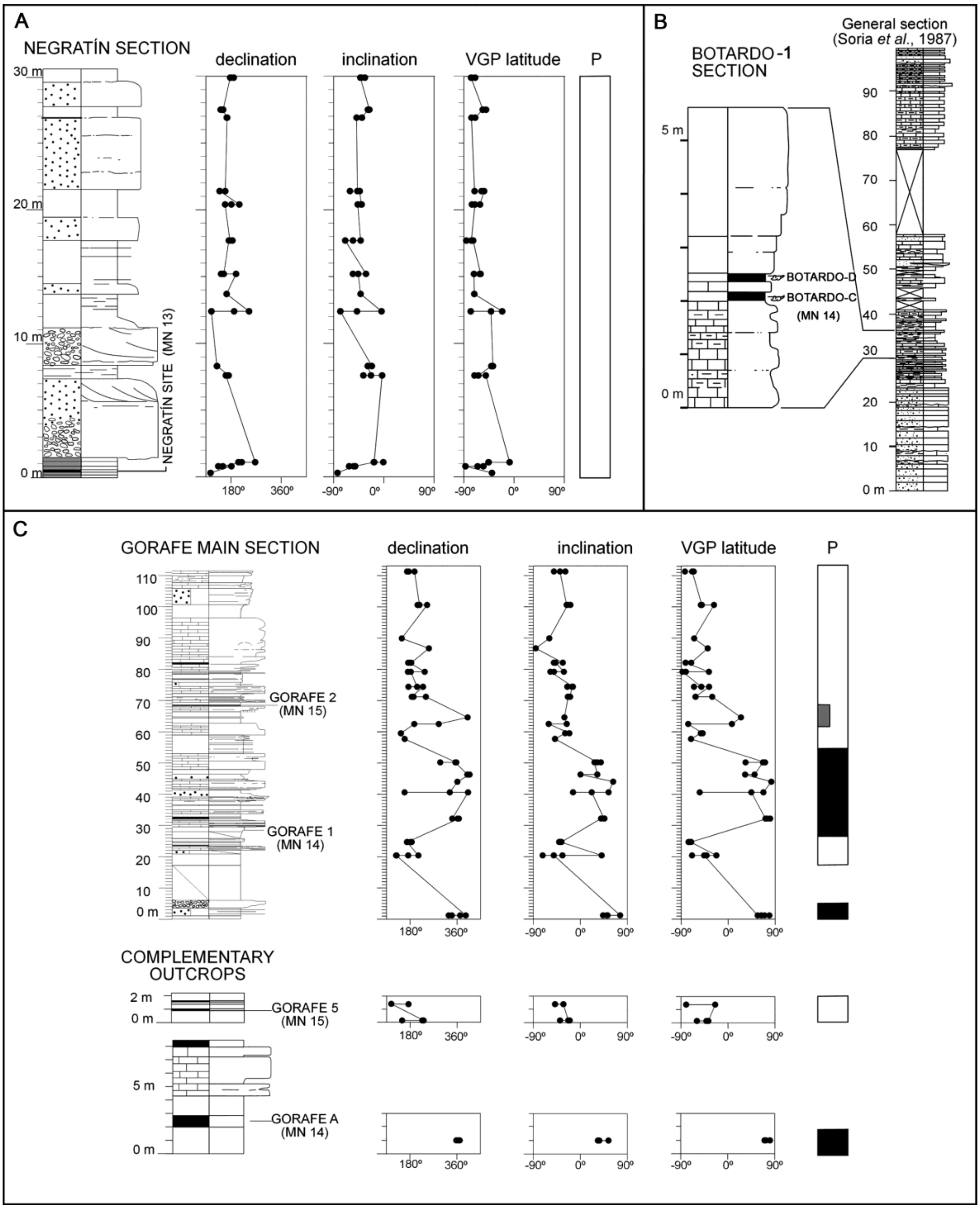


FIG. 2. Magnetostratigraphic and lithological data. A, Magnetostratigraphic data from the Negratín section. B, Lithological location of the Botardo-C and D sites. C, Magnetostratigraphic data from the Gorafe section.

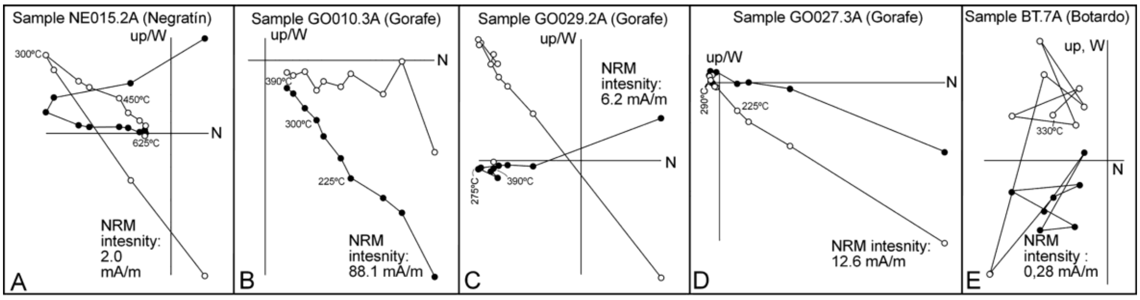


FIG. 3. Demagnetization plots from the studied sections. A, Negratín section. B–D, Gorafe section. E, Botardo section.

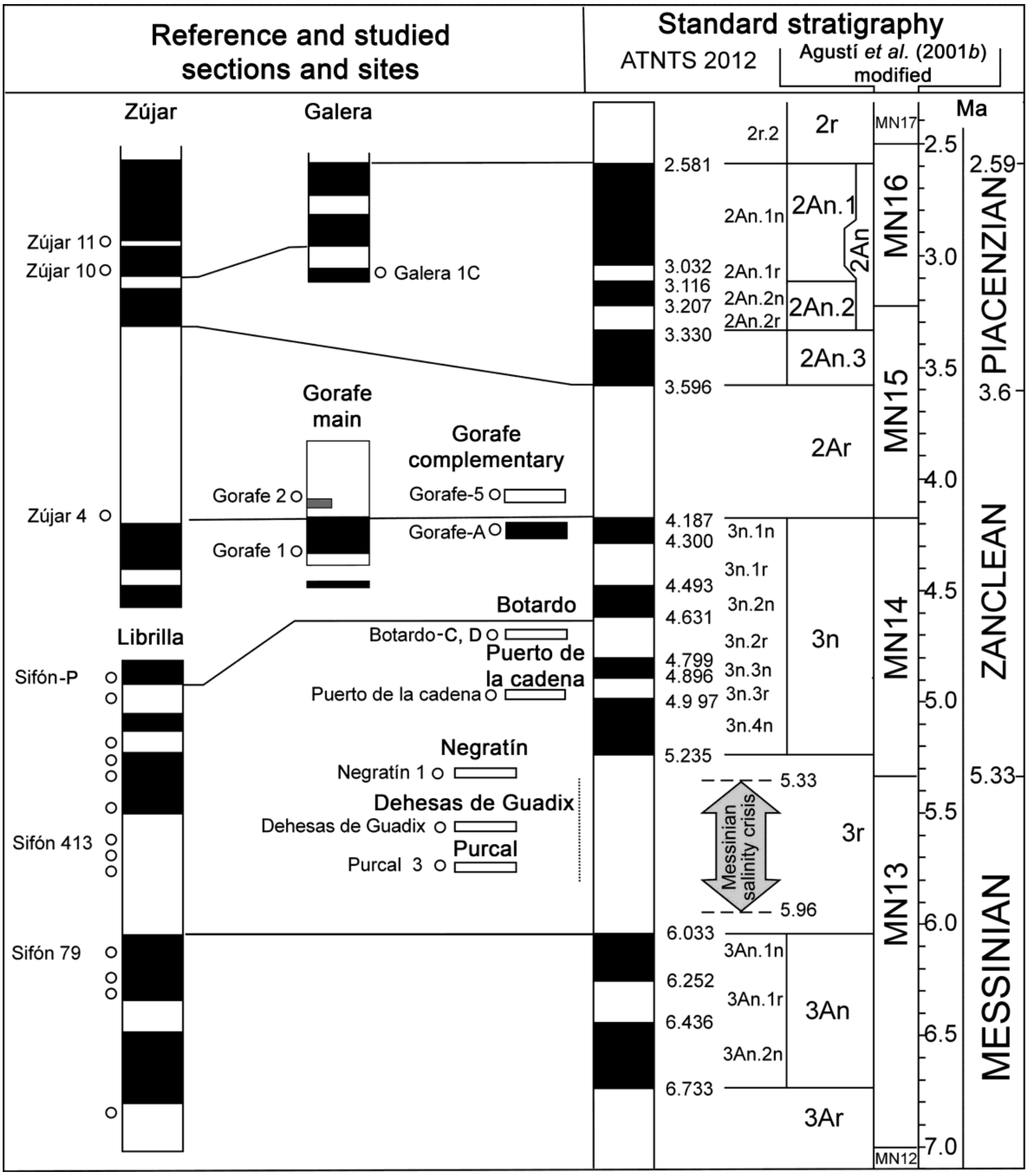


FIG. 4. General magnetobiostratigraphic correlation of the sections and sites here studied. It also includes other localities supporting the correlation scheme (according to Garcés *et al.* 1997, 2001; Martín-Suárez *et al.* 1998; Oms *et al.* 1999; Hüsing *et al.* 2010; Piñero *et al.* 2017).

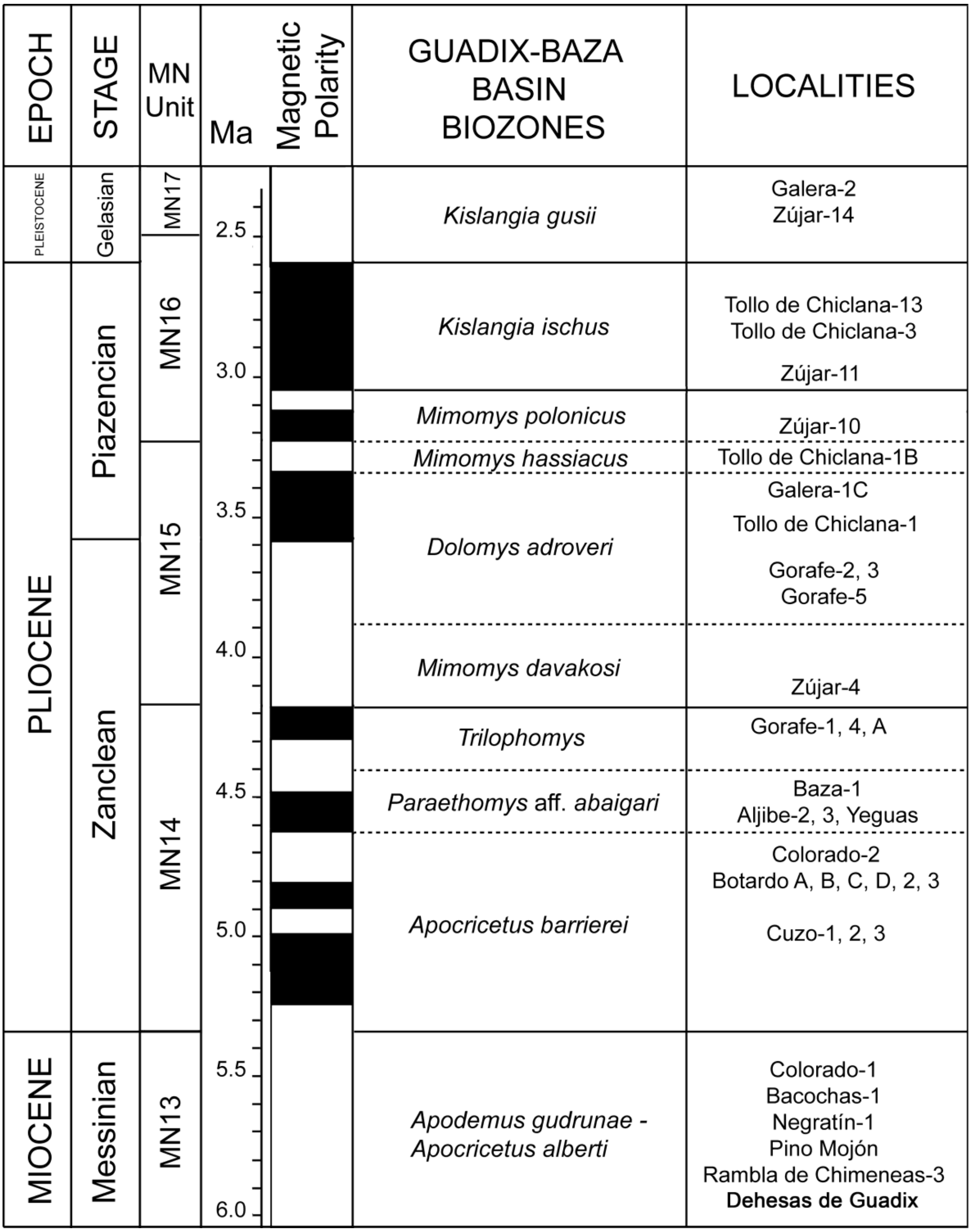
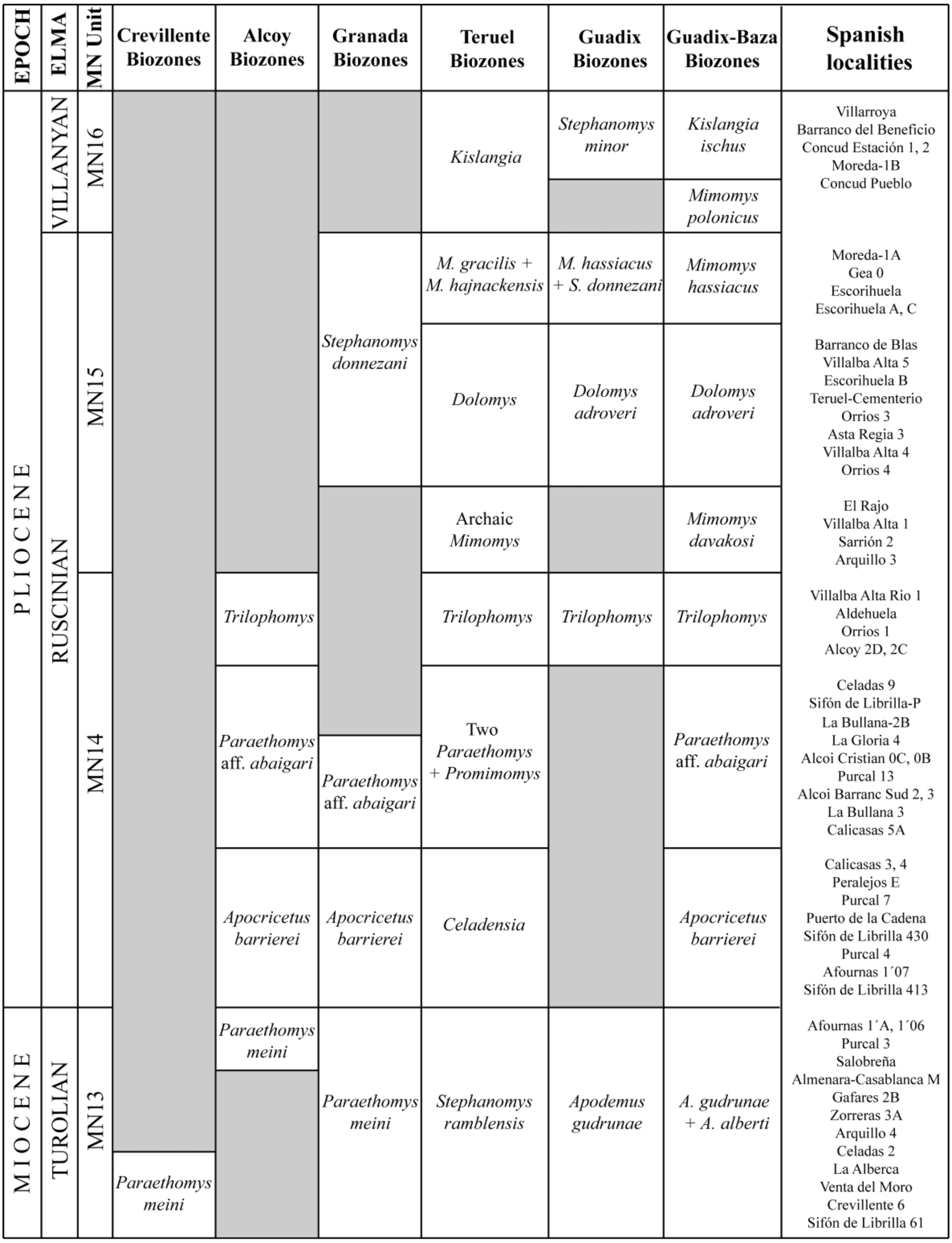


FIG. 5. Succession of rodent biozones in the late Neogene of the Guadix-Baza Basin, and correlation with the geomagnetic polarity time-scale.



<table>
<tr><th>EPOCH</th><th>ELMA</th><th>MN Unit</th><th>Crevillente Biozones</th><th>Alcoy Biozones</th><th>Granada Biozones</th><th>Teruel Biozones</th><th>Guadix Biozones</th><th>Guadix-Baza Biozones</th><th>Spanish localities</th></tr>
<tr><td rowspan="9">PLIOCENE</td><td rowspan="2">VILLANYAN</td><td rowspan="2">MN16</td><td rowspan="11">▨</td><td rowspan="5">▨</td><td rowspan="2">▨</td><td rowspan="2"><i>Kislangia</i></td><td><i>Stephanomys minor</i></td><td><i>Kislangia ischus</i></td><td rowspan="2">Villarroya
Barranco del Beneficio
Concud Estación 1, 2
Moreda-1B
Concud Pueblo</td></tr>
<tr><td>▨</td><td><i>Mimomys polonicus</i></td></tr>
<tr><td rowspan="7">RUSCINIAN</td><td rowspan="3">MN15</td><td rowspan="2"><i>Stephanomys donnezani</i></td><td><i>M. gracilis</i> + <i>M. hajnackensis</i></td><td><i>M. hassiacus</i> + <i>S. donnezani</i></td><td><i>Mimomys hassiacus</i></td><td>Moreda-1A
Gea 0
Escorihuela
Escorihuela A, C</td></tr>
<tr><td><i>Dolomys</i></td><td><i>Dolomys adroveri</i></td><td><i>Dolomys adroveri</i></td><td>Barranco de Blas
Villalba Alta 5
Escorihuela B
Teruel-Cementerio
Orrios 3
Asta Regia 3
Villalba Alta 4
Orrios 4</td></tr>
<tr><td rowspan="3">▨</td><td>Archaic <i>Mimomys</i></td><td>▨</td><td><i>Mimomys davakosi</i></td><td>El Rajo
Villalba Alta 1
Sarrión 2
Arquillo 3</td></tr>
<tr><td rowspan="4">MN14</td><td><i>Trilophomys</i></td><td><i>Trilophomys</i></td><td><i>Trilophomys</i></td><td><i>Trilophomys</i></td><td>Villalba Alta Rio 1
Aldehuela
Orrios 1
Alcoy 2D, 2C</td></tr>
<tr><td rowspan="2"><i>Paraethomys</i> aff. <i>abaigari</i></td><td rowspan="2">Two <i>Paraethomys</i> + <i>Promimomys</i></td><td rowspan="3">▨</td><td rowspan="2"><i>Paraethomys</i> aff. <i>abaigari</i></td><td rowspan="2">Celadas 9
Sifón de Librilla-P
La Bullana-2B
La Gloria 4
Alcoi Cristian 0C, 0B
Purcal 13
Alcoi Barranc Sud 2, 3
La Bullana 3
Calicasas 5A</td></tr>
<tr><td><i>Paraethomys</i> aff. <i>abaigari</i></td></tr>
<tr><td><i>Apocricetus barrierei</i></td><td><i>Apocricetus barrierei</i></td><td><i>Celadensia</i></td><td><i>Apocricetus barrierei</i></td><td>Calicasas 3, 4
Peralejos E
Purcal 7
Puerto de la Cadena
Sifón de Librilla 430
Purcal 4
Afournas 1´07
Sifón de Librilla 413</td></tr>
<tr><td rowspan="3">MIOCENE</td><td rowspan="3">TUROLIAN</td><td rowspan="3">MN13</td><td><i>Paraethomys meini</i></td><td rowspan="3"><i>Paraethomys meini</i></td><td rowspan="3"><i>Stephanomys ramblensis</i></td><td rowspan="3"><i>Apodemus gudrunae</i></td><td rowspan="3"><i>A. gudrunae</i> + <i>A. alberti</i></td><td rowspan="3">Afournas 1´A, 1´06
Purcal 3
Salobreña
Almenara-Casablanca M
Gafares 2B
Zorreras 3A
Arquillo 4
Celadas 2
La Alberca
Venta del Moro
Crevillente 6
Sifón de Librilla 61</td></tr>
<tr><td rowspan="2">▨</td></tr>
<tr><td><i>Paraethomys meini</i></td></tr>
</table>

FIG. 6. Proposed correlation between local biozones in the Guadix-Baza (this work), Crevillente (Martín Suárez & Freudenthal, 1998), Alcoy (Mansino *et al.* 2017), Granada (García-Alix *et al.* 2008*a*), Teruel (Mein *et al.* 1990) and Guadix basins (Minwer-Barakat *et al.* 2012*b*), and other contemporaneous Spanish localities.

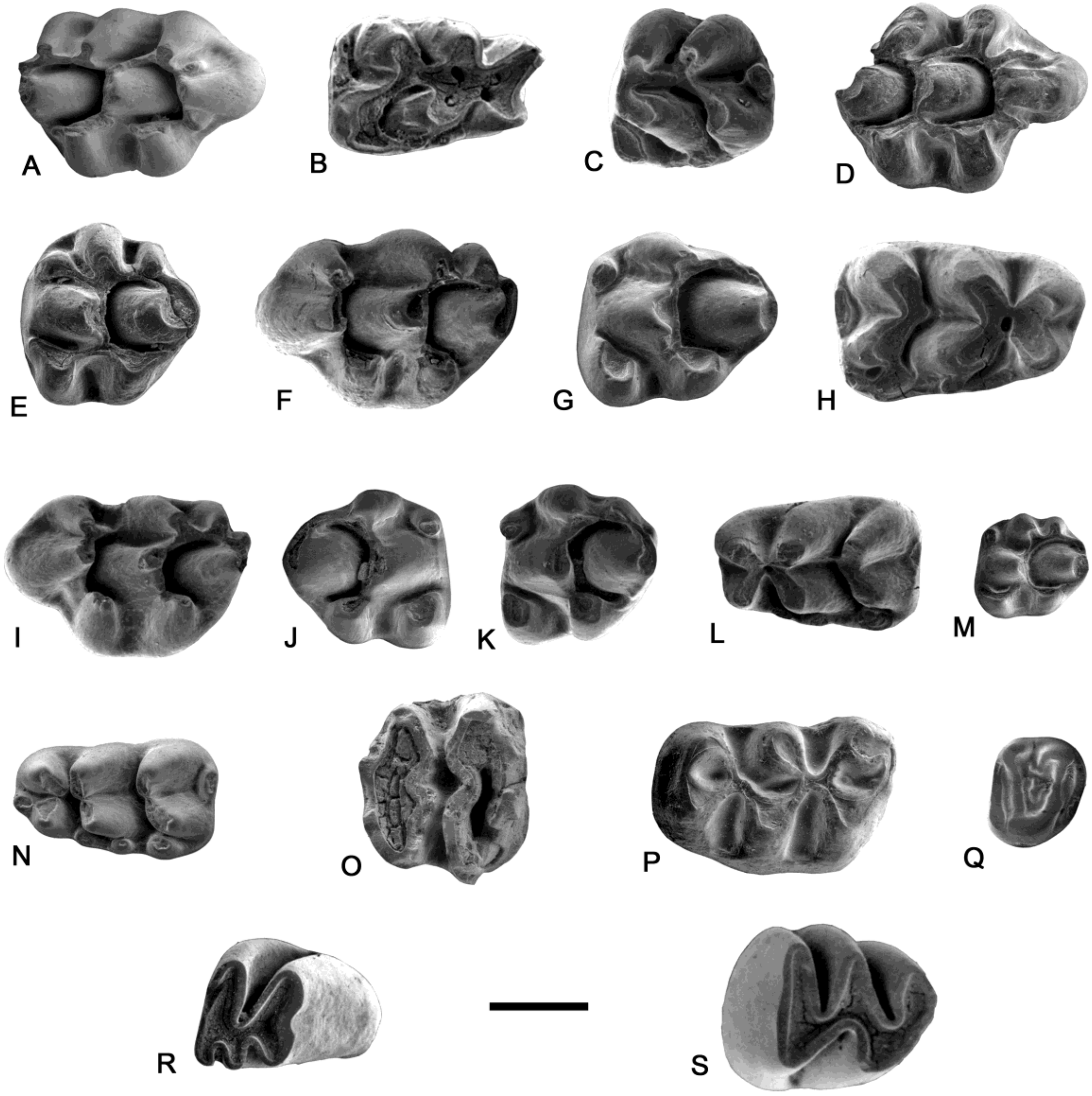


FIG. 7. Some rodent teeth from the Botardo and Gorafe sections. *Stephanomys cordii*: A, right M^1, Botardo-D. *Stephanomys margaritae*: B, right M_1, Gorafe-3; C, left M_2, Gorafe-2; D, right M^1, Gorafe-5; E, left M^2, Gorafe-5. *Paraethomys jaegeri*: F, left M^1, Gorafe-5; G, left M^2, Gorafe-5; H, right M_1, Gorafe-5. *Paraethomys meini*: I, left M^1, Botardo-C; J, right M^2, Botardo-D; K, left M^2, Botardo-2; L, left M_1, Botardo-3. *Castillomys gracilis*: M, left M^2, Botardo-D. *Apodemus gorafensis*: N, left M_1, Botardo-D. *Debruijnimys* sp.: O, right M^2, Botardo-D. *Apocricetus barrierei*: P, left M^1, Botardo-D. *Eliomys truci*: Q, right M^1, Botardo-D. *Trilophomys* cf. *castroi*: R, right M_2, Gorafe-3; S, left M^2, Gorafe-3. All the figured specimens are deposited at the *Institut Català de Paleontologia Miquel Crusafont* (ICP; Sabadell, Barcelona, Spain). Scale bar represents 1 mm.

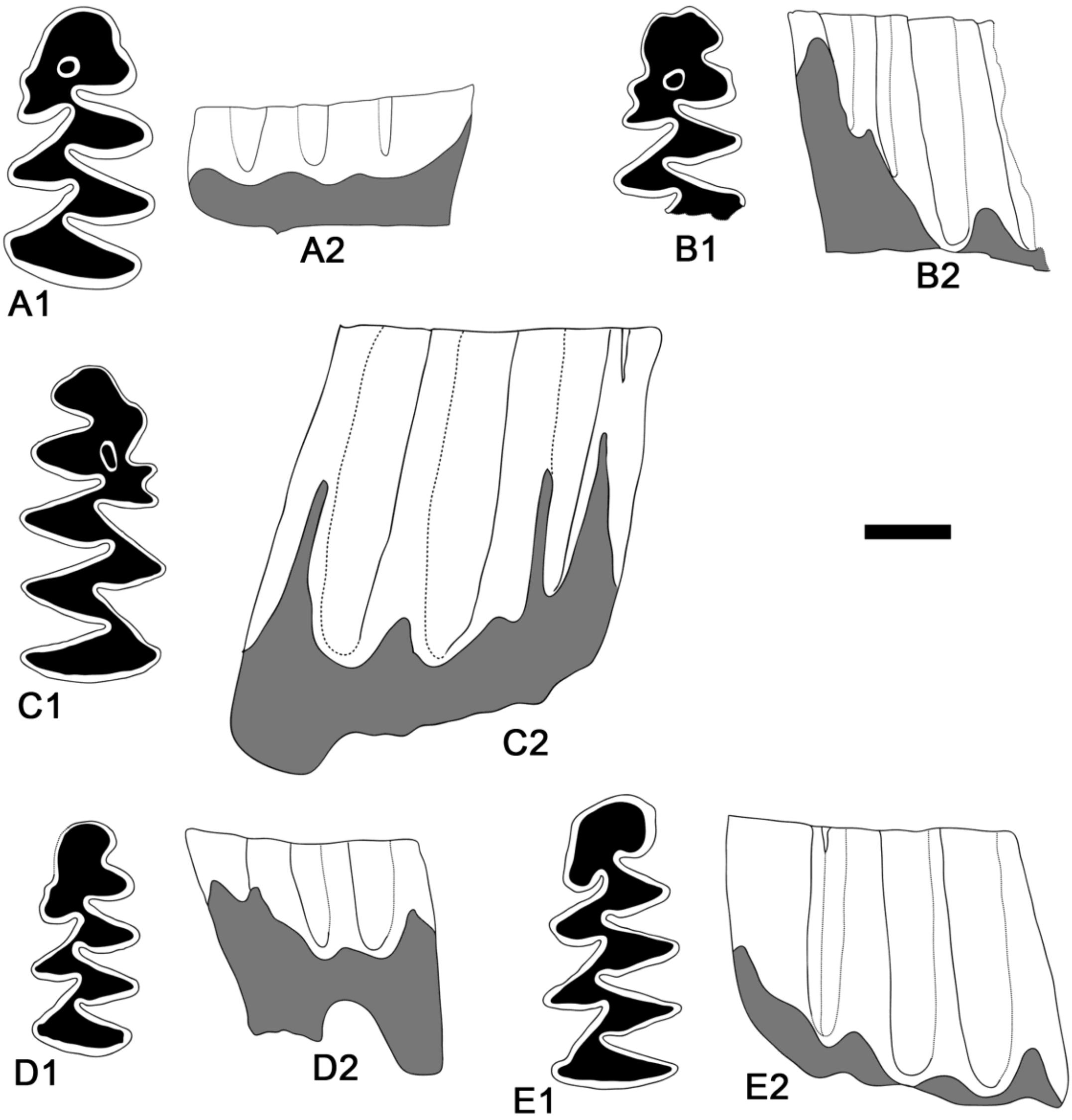


FIG. 8. Some significant arvicolid M_1s recognized in the described biozones. *Mimomys davakosi* from Zújar-4: A1, occlusal view; A2, lingual view. *Mimomys polonicus* from Zújar-10: B1, occlusal view; B2, labial view. *Kislangia ischus* from Zújar-11: C1, occlusal view; C2, labial view. *Dolomys adroveri* from Galera-1C: D1, occlusal view; D2, labial view; E1, occlusal view; E2, labial view. The figured specimens are deposited at the *Institut Català de Paleontologia Miquel Crusafont* (ICP; Sabadell, Barcelona, Spain). Scale bar represents 1 mm.

X. DATOS BIOCRONOLÓGICOS DEL YACIMIENTO DEL PLEISTOCENO INFERIOR DE QUIBAS (SE ESPAÑA) A TRAVÉS DE LA ASOCIACIÓN DE ROEDORES

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Biochronological data for the Early Pleistocene site of Quibas (SE Spain) inferred from rodent assemblage

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ABSTRACT

In this paper, the rodent fauna from the Early Pleistocene of Gruta1 (Quibas karstic complex, Murcia, SE Spain) is described. The assemblage includes one arvicoline (*Allophaiomys* sp.), two murines (*Apodemus* ex gr. *mystacinus-epimelas*, *Castillomys rivas*) and one glirid (*Eliomys quercinus*). The rodent assemblage indicates an age very close to the age of Fuente Nueva 3 and Barranco León 5 in the Guadix-Baza Basin, and Sima del Elefante in the Atapuerca karstic complex, between ca. 1.2-1.4My.

KEYWORDS Biochronology. Rodentia. Early Pleistocene. Iberian Peninsula.

INTRODUCTION

The karstic paleontological site of Quibas (Abanilla, Murcia) is situated on the SE slope of the Sierra de Quibas, in an area called Collado del Rey, in an abandoned limestone quarry at an altitude of 669m AMSL (Fig. 1A). The coordinates correspond to 38° 18’ 51”N, 1° 4’ 42”W. The fossil record provides both vertebrates and invertebrates from the Early Pleistocene. Previous faunal lists were published in Montoya *et al*. (1999, 2001). The sample studied in the present work was collected in 2009 by A. Cuadros in order to complete her M.D. thesis (on the taphonomy of micromammals; Cuadros, 2010). This paper includes part of the M.D. thesis of P. Piñero (Piñero, 2012). As for the macrofauna from this palaeontological site, several taxonomic studies have been carried out by Carlos-Calero *et al*., 2004, 2006a, b; Made *et al*., 2007; Alba *et al*., 2011. Finally, the agamid lizards have been studied by Blain *et al*. (2014).

The stratigraphic and sedimentological features of the basal part of the palaeontological site have been established in Montoya *et al.* (1999). The main interest of this site is the abundance and diversity of the faunal association identified, as well as its age (Rodríguez-Estrella *et al.*, 2004). The studied sample was collected from Gruta 1, a different point from the earlier work (Fig. 1B) because the former section is currently covered by debris.

The aim of the present paper is to identify the rodent fauna from Quibas/Gruta1 and to stablish its age through the correlation with other Early Pleistocene sites from the Iberian Peninsula.

GEOLOGICAL SETTING

The Sierra de Quibas is a 6km long and 2.5km wide carbonate massif that extends in a NE-SE direction in the Middle Subbetic region. It is mainly composed of Jurassic limestone and dolomites (Rodríguez-Estrella *et al.*, 2004), which were largely affected by karstic processes during the Plio-Pleistocene, leading to numerous exokarstic and endokarstic structures. Many of these structures are infilled by chemical precipitates and/or by mixed detritic sediments. In one of these karstic structures the Quibas palaeontological site is located (Durán *et al.*, 2004).

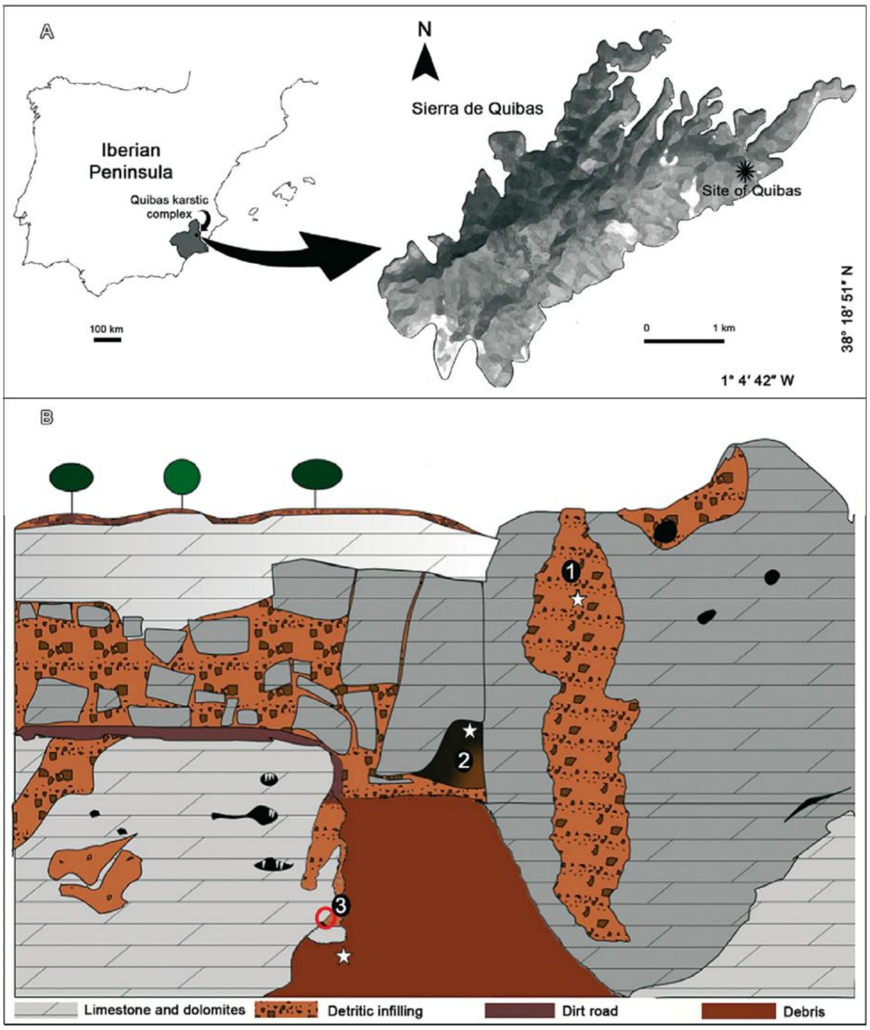

FIGURE 1. A) Geographic location of the site of Quibas (Murcia, Spain). B) Wide-angle sketch from Quibas site. 1: Sima; 2: Entrada Cueva; 3: Gruta 1; Circle: sample extraction area (modified from Cuadros, 2010).

The Quibas outcrop is mainly formed by a 5m wide and 9m high gallery (known as "Entrada Cueva"=EC on maps of the cave system) that extends laterally for more than 30m, and displays several collateral branches separated by calcitic speleothems (1 in Fig. 1B); and a 20m deep and 2m wide chasm (known as "Sima"; 2 in Fig. 1B). Although the two karstic structures are separated by 3m thick calcitic speleothems, they are likely connected (in Montoya *et al*., 1999). Six detritic layers have been distinguished in the basal part of the site, and these are mainly composed of clays, silts, and partially cemented breccias. The studied sample is located in a detritic layer formed by limestone clasts which range between 10 and 20cm in size, and reddish silty clay matrix with carbonate crusts.

MATERIALS AND METHODS

The small mammal remains were collected from the small karst grotto known as Gruta 1 (Fig. 1B; the extraction area is marked with a red circle). All the sediment was screen-washed using superimposed 4, 1 and 0.5mm mesh screens. The specimens described are currently stored at the Institut de Paleoecologia Humana i Evolució Social (IPHES; Tarragona, Spain).

The Quibas/Gruta1 assemblage includes 199 identified rodent teeth corresponding to a minimum number of 32 individuals, representing at least four taxa. 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.

In describing and measuring the teeth of *Apodemus* and *Castillomys*, we have followed van de Weerd (1976) and, Martín Suárez and Freudenthal (1993), respectively (Fig. 2). The terminology employed for the description of the teeth of *Eliomys* is that of Daams (1981); length and width have been measured as defined by Freudenthal (2004). The nomenclature used in the descriptions of the arvicoline teeth (only lower first molars (m1) and upper third molars (M3) have been considered) is that of van der Meulen and Zagwijn (1974). To measure the different parameters of the first lower molar and the third upper molar, we have followed the criteria proposed by Agustí (1991) and Nadachowski (1991), respectively (Fig. 2). Moreover, we have carried out a principal component analysis on arvicolines in order to decrease the variables and represent them in a scatter plot. The aim is to compare the measurements of arvicoline m1s from Quibas/Gruta1 with other values from other localities (Agustí, 1991; Agustí *et al*., 1993, 2010). The values used for the analysis are: i) ACC (anteroconid relative length) (A–A'/L–L'); ii) AC2 (anterior complex) isolation degree in relation to the rest of the tooth (B–B'/W–W'); and iii) isolation degree between T4 and T5 (C–C'/W–W') (see Fig. 2).

Institutional Abbreviations. IPHES, Institut Català de Paleoecologia Humana i Evolució Social; QB, Quibas; G1, Gruta1.

Anatomical Abbreviations. ACC, anteroconid complex; AC2, anterior complex; AL, anterior lobe; BRA, buccal re-entrant angle; BSA, buccal salient angle; LRA, lingual re-entrant angle; LSA, lingual salient angle; PC, posterior cap; PL, posterior lobe; T1–T7, triangles 1–7; A-A', ACC length; B-B', shortest distance between BRA3 and LRA4; C-C', shortest distance between LRA3 and BRA3; L, length; L-L', occlusal surface length; W, width; W-W', distance between LSA4 and BSA3.

SYSTEMATIC PALEONTOLOGY

Family: Muridae ILLIGER, 1811
Subfamily: Arvicolinae GRAY, 1821

GENUS ***Allophaiomys*** (Kormos, 1932)
Allophaiomys sp. (Figure 3 A–D)

Material and measurements. Two complete m1s (IPHES QB-10-G1-R/19a, IPHES QB-10-G1-R/19b), and one partial m1 (IPHES QB-10-G1-R/19c), one complete M3 (IPHES QB-10-G1-R/20a) (Table 1).

Description. The studied m1 of *Allophaiomys* sp. has a very simple dental pattern, with three closed angles (T1–T3), and is rootless. The ACC is simple. The amount of cement in the re-entrant angles is always abundant. The AC2 is round and its leading edge does not have any enamel. The neck of AC2 is relatively wide. The lingual edge in LSA3, and particularly in LSA4, is round and slightly angular. T4 and T5 are in an alternate position but are widely confluent. The enamel differentiation of the triangles is *Mimomys*-like: the enamel is wider on the posterior face than on the anterior side. In M3 the AL is continued by three angles (T2, T3 and T4). T2 is narrowly connected to AL and T3. T4 has a small size and is widely connected to PC. LSA4 is absent. The BRA3 is shallow.

Discussion. The shape of both m1 and M3 of *Allophaiomys* from Quibas/Gruta1 is in perfect accordance with *Allophaiomys* sp. from Fuente Nueva 3 and Barranco León 5 (Agustí and Madurell, 2003; Agustí *et al*., 2010). The morphology of m1 recalls that of *Victoriamys chalinei*, which was first recognized in the Cueva Victoria site (Alcalde *et al*., 1981) and subsequently in other Early Pleistocene karstic sites from the Iberian Peninsula (Agustí, 1982; Laplana, 1999; Cuenca-Bescós *et al*., 2001; Minwer-

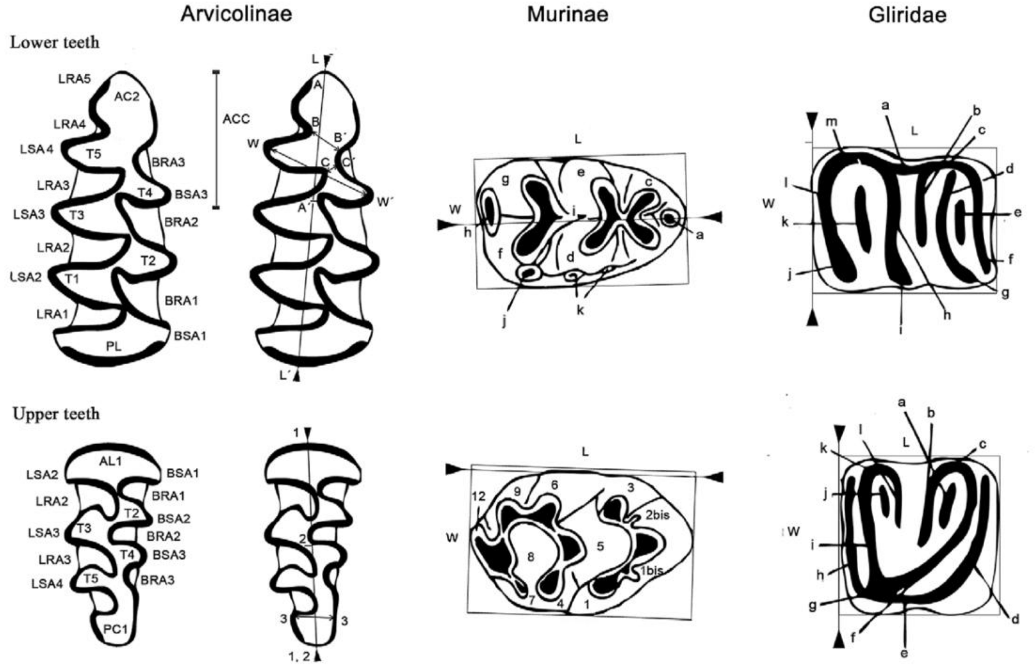

FIGURE 2. Nomenclature and measurements used in the descriptions of dental elements from the studied taxa. Arvicolinae (modified from Agustí, 1991 and Nadachowski, 1991). General abbreviations: BRA, buccal re-entrant angle; BSA, buccal salient angle; LRA, lingual re-entrant angle; LSA, lingual salient angle; T (1-5), triangle (1-5). Lower teeth: AC2, anterior complex; ACC, anteroconid complex; PL, posterior lobe. Upper teeth: AL, anterior lobe; PC, posterior complex. Murinae (modified from van de Weerd, 1976). Lower teeth: a, anterocentral cusp (=tma); b, anterolabial cusp; c, anterolingual cusp; d, protoconid; e, metaconid; f, hypoconid; g, entoconid; h, terminal heel; i, longitudinal spur; j, posterior accessory cusp (=c1); k, accessory cusps on the labial cingulum. Upper teeth: t (1-12), tubercle (1-12). Gliridae (modified from Daams, 1981). Lower teeth: a, endolophid; b, centrolophid; c, metaconid; d, metalophid; e, anterior extra ridge; f, anterolophid; g, protoconid; h, mesolophid; i, mesoconid; j, hypoconid; k, posterior extra ridge; l, posterolophid; m, entoconid. Upper teeth: a, anterior extra ridge; b, anterior centroloph; c, paracone; d, anteroloph; e, endoloph; f, protoloph; g, protocone; h, posteroloph; i, metaloph; j, posterior extra ridge; k, metacone; l, posterior centroloph. Measurement abbreviations: L, length; W, width. Arvicolinae. Lower teeth: L-L', occlusal surface length; W-W', distance between LSA4 and BSA3; A-A', ACC length; B-B', shortest distance between BRA3 and LRA4; C-C', shortest distance between LRA3 and BRA3. Upper teeth: 1, occlusal surface length; 2, PC length; 3, PC posterior part width.

Barakat *et al.*, 2011). Nevertheless, some specimens do not closely resemble the morphology of *V. chalinei*, but rather look like *Mimomys oswaldoreigi*, which has been identified in the Early Pleistocene levels of the Guadix-Baza basin (Agusti *et al.*, 1993). Thus, the morphology of M3 is clearly of mimomyan type, and different from that of *V. chalinei* from the Cueva Victoria site. However, the specimens from Quibas/Gruta1 do not belong to *Mimomys* because roots are absent. Even so, the relatively short length of ACC indicates that this is a primitive form of *Allophaiomys*.

Allophaiomys sp. from Quibas/Gruta1 was compared with species of arvicolines from other localities (Agustí, 1991; Agustí *et al.*, 1993, 2010), using principal component analysis performed on the values of A–A'/L–L', B–B'/W–W', and C–C'/W–W'. The cumulative amount of variance explained by the first two components reaches 94.47%. The resulting scatter plot (Fig. 4) indicates that the greatest similarity with respect to size is between the sample from Quibas/Gruta1 and *Allophaiomys ruffoi* from Venta Micena 1, followed closely by *Allophaiomys* sp. from Fuente Nueva 3, *A. pliocaenicus* from Betfia 2, and *Allophaiomys* sp. from Barranco León 5. It is concluded that the species from Quibas/Gruta1 resembles the more archaic species of *Allophaiomys* (*A. pliocaenicus, A. ruffoi, Allophaiomys* sp.), diverging from the more derived forms (*A. vandermeuleni, A. burgondiae, A. nutiensis*). Although biometrically closer to *Allophaiomys ruffoi*, morphologically *Allophaiomys* sp. from Quibas/Gruta1 is closer to *Allophaiomys* sp. from Fuente Nueva 3 and Barranco León. In the species from Quibas/Gruta1 some derived features typical of *A. ruffoi*, such as the frequent presence of a well developed BSA 3 (*sensu* Meulen, 1973) are lacking. This is also the case of *Allophaiomys* sp. from Fuente Nueva 3 and Barranco León. This is why we consider *Allophaiomys* sp. from Quibas/Gruta1 closer to the latter species, rather than to *A. ruffoi*. According to Agustí *et al*. (2010), the presence of an archaic *Allophaiomys* can be successfully explained by the evolution of *Mimomys oswaldoreigi* (derived *Mimomys* with a tendency to develop hypsodont molars, according to Agustí *et al*. (1993)). Furthermore, Agustí and Madurell (2003) suggested that *Allophaiomys* sp. from Fuente Nueva 3 could possibly be an ancestor of *Victoriamys chalinei*. However, this hypothesis can be refuted in the light of both biometric and enamel differences (see Fig.

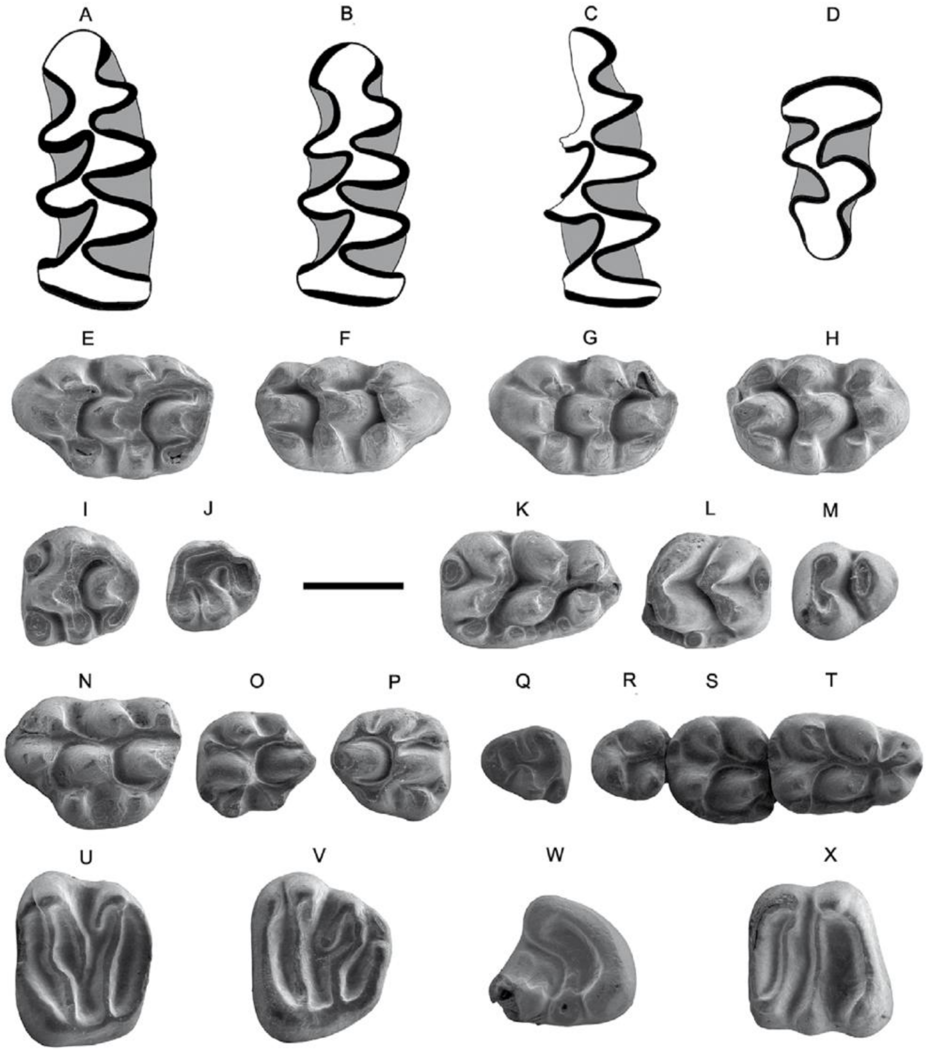

FIGURE 3. *Allophaiomys* sp. from Quibas/Gruta1: A) m1, left, QB-10-G1-R/19a; B) m1, left, QB-10-G1-R/19b; C) partial m1, left, QB-10-G1-R/19c; D) M3, right, QB-10-G1-R/20a. *Apodemus* ex gr. *mystacinus* (Danford and Alston, 1877)–*epimelas* (Nehring, 1902) from Quibas/Gruta1: E) M1 left, QB-10-G1-R/2d; F) M1, right, QB-10-G1-R/1k; G) M1, left, QB-10-G1-R/2g; H) M1, right, QB-10-G1-R/1d; I) M2, left, QB-10-G1-R/3n; J) M3, left, QB-10-G1-R/4i; K) m1, right, QB-10-G1-R/6m; L) m2, left, QB-10-G1-R/8p; M) m3, left, QB-10-G1-R/9u. *Castillomys rivas* Martín Suárez and Mein, 1991 from Quibas/Gruta1: N) M1, left, QB-10-G1-R/11a; O) M2, left, QB-10-G1-R/11e; P) M2, right, QB-10-G1-R/11g; Q) m3, left, QB-10-G1-R/11i; R) m3, right, QB-10-G1-R/11k3; S) m2, right, QB-10-G1-R/11k2; T) m1, right, QB-10-G1-R/11k1. *Eliomys quercinus* (Linnaeus, 1766) from Quibas/Gruta1: U) M1–2, left, QB-10-G1-R/13i; V) M3, right, QB-10-G1-R/14e; W) p4, left, QB-10-G1-R/15a; X) m1–2, left, QB-10-G1-R/16k. Scale bar equals 1mm.

TABLE 1. Measurements (mm) of the teeth of *Allophaiomys* sp. from Quibas Gruta1

Element	L-L´	W-W´	A-A´	B-B´	C-C´	Element	1	2	3
m1	2.825	0.974	1.068	0.236	0.201	M3	1.812	0.946	0.412
m1	2.655	1.117	1.129	0.295	0.237				

4, where *V. chalinei* and *Allophaiomys* sp. can be seen to be biometrically dissimilar). The arvicoline species from Quibas/Gruta1 probably represents a new species close to *A. ruffoi* from Fuente Nueva 3, but it is assigned as *Allophaiomys* sp. because only four teeth of *Allophaiomys* of taxonomic value have been recovered.

Subfamily: Murinae ILLIGER, 1811

GENUS ***Apodemus*** Kaup, 1829
Apodemus ex gr. ***mystacinus*** (Danford and Alston, 1877)–***epimelas*** (Nehring, 1902). (Figure 3 E–M)

Material and measurements. 28 M1s (IPHES QB-10-G1-R/1a–1m, 2a–2n, 5a1), 17 M2s (IPHES QB-10-G1-R/3a–3p, 5a2), 9 M3s (IPHES QB-10-G1-R/4a–4i); 37 m1s (IPHES QB-10-G1-R/6a–6o, 7a–7n, 10a1, 10c1, 10d1, 10e1, 10f1, 10g1, 10h1, 10i1), 28 m2s (IPHES QB-10-G1-R/8a–8u, 10a2, 10b2, 10c2, 10d2, 10e2, 10g2, 10h2,), 28 m3s (IPHES QB-10-G1-R/9a–9z, 9aa, 10d3) (Table 2).

Description. The m1s have a round and well-developed anterocentral cuspid, which is isolated in 35% of cases. The anterolabial and anterolingual cusps are symmetric. The protoconid is slightly larger than the metaconid. The hypoconid-entoconid complex is isolated. The labial cingulum is well developed (with a large and isolated c1 and up to three accessory cusps). The terminal heel is oval, large and isolated (except IPHES QB–10–G1–R/6c, 7b, 7i). The m2s usually present an oval and isolated anterolabial cuspid. The protoconid and the metaconid are not connected to the hypoconid and the entoconid. The c1 is absent (in ten specimens). When it is present, it is round and reduced, with one to no accessory cusp. IPHES QB–10–G1–R/8l has a reduced round tuber attached to the labial edge of the terminal heel. In m3, the anterolabial cusp is weakly represented in four specimens (IPHES QB–10–G1–R/9m, 9n, 9d, 9e). The c1 is absent. The lower molars have no longitudinal crests. In M1, t1 is round and separated from t5. Only IPHES QB–10–G1–R/1a has t2bis. In 18 out of 28 recovered specimens, t1 is connected to t2 forming a ridge to t3 (in the other specimens t1 is isolated). The t3 has a spur in a posterior direction that does not contact t5 or t6. The anterior tubercles (t1, t2 and t3) are not connected to the middle tubercles (t4, t5 and t6), but the latter do connect with t9. The t4 is completely separated from t7 (except in four out of 28 specimens in an advanced stage of wear). In most specimens, t12 is laterally compressed, forming a curved lamellar structure toward t9, which may present a t12 connection both with t8 and t9 (38% of the studied M1; see Fig. 3E, F), or a t12 connection just with t8, excluding the t12-t9 connection (62% of the studied M1; see Fig. 3G, H). In M2, t1 and t3 are round and isolated, t1 being larger than t3. The t4 is oval and generally smaller than t6. The t4, t5, t6, t9 and t8 are connected to form a single ridge, even reaching t7 (in 70% of cases). The t7 is oval and separated from t4. The t6 is larger than t9, and they are connected. The t9 is well developed in 60% of the sample. The t12 is absent or weak. The M3s have a large and oval t1. The t3 is absent. The t4 is fused to t5, t6 and t8 to form a continuous ridge.

Discussion. The morphology of the studied teeth agrees with that of *A.* ex gr. *mystacinus–epimelas*. The species from Quibas/Gruta1 differs from *A. sylvaticus* because the latter is smaller and characterized by great development of t7 in M1 (Arrizabalaga *et al*., 1999) and a frequent t7–t4 connection (Nores, 1988), while none of the teeth from Quibas/Gruta1 have those features (except four specimens in an advanced stage of wear). Moreover, 60% of the teeth studied have the t9 in M2 poorly developed or absent, a lack of connection between hypoconid-entoconid and protoconid-metaconid, tma in m2 is attached to only one of the anteroconids, and the t12 in M1 laterally compressed toward t9. All these characteristics allow *A.* ex gr. *mystacinus–epimelas* to be distinguished also from *A. flavicollis* which is morphologically more similar to *A. sylvaticus* (Agustí *et al*., 2010).

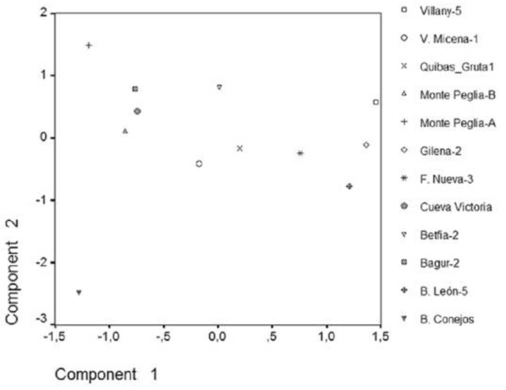

FIGURE 4. Scatter plot with the two principal components (Component 1 = 0.316xL + 0.243xA/L + 0.322xB/W + 0.358xC/W; Component 2 = 0.090xL + 0.877xA/L – 0.605xB/W – 0.132xC/W) for A-A’/L-L’, B-B’/W-W’ and C-C’/W-W’ values of m1 from Gruta1, and different arvicolines from other localities previously studied: *Allophaiomys* sp. (Fuente Nueva 3 and Barranco León 5), *Mimomys oswaldoreigi* (Gilena 2), *Allophaiomys deucalion* (Villany-5), *A. pliocaenicus* (Betfia-2, Bagur-2), *A. ruffoi* (Venta Micena-1), *A. vandermeuleni* (Barranco de los Conejos), *V. chalinei* (Cueva Victoria), *A. nutiensis* (Monte Peglia-A), *A. burgondiae* (Monte Peglia-B).

TABLE 2. Measurements (mm) of the teeth of *Apodemus* ex gr. *mystacinus-epimelas* from Quibas Gruta1

	Length				Width			
Element	N	min	mean	max	N	min	mean	max
M1	28	1.94	2.05	2.22	26	1.21	1.30	1.39
M2	17	1.22	1.35	1.50	17	1.18	1.28	1.34
M3	9	0.87	0.97	1.13	9	0.87	0.93	0.97
m1	33	1.67	1.90	2.09	35	0.88	1.14	1.25
m2	28	1.19	1.29	1.36	28	1.01	1.16	1.27
m3	28	0.88	1.08	1.19	27	0.78	0.96	1.04

The mean length and width of the sample from Quibas/Gruta1 was compared with *A. mystacinus* from Cueva Victoria (Agustí, 1982), *A. mystacinus* from Orce-7 (Agustí *et al.*, 1987a), *A. atavus* from Tollo de Chiclana (Minwer-Barakat, 2005), *A. flavicollis* from Fuente Nueva 3 (Agustí *et al.*, 2010) and *Apodemus sylvaticus* from Torrent de Vallparadís (Minwer-Barakat *et al.*, 2011). In all cases, the species from Quibas/Gruta1 is larger than *A. atavus* and *A. flavicollis*, being more similar to *A. mystacinus* from Orce-7 and Cueva Victoria. The mean values of *A.* ex gr. *mystacinus–epimelas* from Quibas/Gruta1 are slightly smaller than *A. mystacinus* from Cueva Victoria, but larger than those from Fuente Nueva 3 (Agustí *et al.*, 2010), and very close to those from Orce-7 (Agustí *et al.*, 1987a). Besides, the values fit the range of *A. mystacinus* from Fuente Nueva 3 (Agustí *et al.*, 2010), Orce-2, and Barranco León 2-3 (Agustí *et al.*, 1987a).

Until recently, *A. mystacinus* included two subspecies: *A. mystacinus mystacinus* and *A. mystacinus epimelas*. Nowadays these subspecies are ranked as separate species, *A. mystacinus* and *A. epimelas* (Krystufek and Vohralik, 2009; Wilson and Reeder, 2005). Hitherto *A. epimelas* has not been identified in Early Pleistocene sites from the Iberian Peninsula. However, this species is likely to be present but recorded as *A. mystacinus*. Thus a revision of all specimens of *A. mystacinus* from the Iberian Peninsula is required. In this context, 62% of the M1 from Quibas/Gruta1, according to Storch (1977), have features typical of *A. epimelas* (t12 is only connected to t8, the t12–t9 connection is absent, see Fig. 3G, H and Fig. 5B), while the remaining 38% present features of *A. mystacinus* (t12 is usually connected directly both with t8 and t9, see Fig. 3E, F and Fig. 5C). Accordingly, the species from Gruta1 is identified as *A.* ex gr. *mystacinus–epimelas*.

Apodemus mystacinus has been identified at many Early Pleistocene sites in southwestern Europe such as Mas Rambault, Bourgade, Le Vallonet or Bagur-2 (Agustí, 1982). In these localities, the molars are slightly smaller than the specimens from Gruta1 (López-Martínez *et al.*, 1976). Measurements of *A. mystacinus* from eastern Europe are larger than the ones of *A. mystacinus* from Quibas/Gruta1. The smaller size of western representatives of *A. mystacinus* in relation to the eastern populations is a constant in all sites from southwestern Europe (Agustí, 1982). Today, *A. mystacinus* and *A. epimelas* (recorded as *A. mystacinus*) are found in areas with a relatively warm climate in the Balkan Peninsula and Middle East. They are associated with dry forest and shrub land in rocky areas. Their presence in fossil sites can be related to the occurrence of rocky environments in the vicinity of the locality (Agustí, 1982; Storch, 2004; Minwer-Barakat, 2005; Mitchell-Jones *et al.*, 1999).

GENUS ***Castillomys*** Michaux, 1969
Castillomys rivas Martín Suárez and Mein, 1991. (Figure 3 N–T)

Material and measurements. 3 M1s (IPHES QB-10-G1-R/11a–11c), 4 M2s (IPHES QB-10-G1-R/11d–11g), 4 m1s (IPHES QB-10-G1-R/11k1, 11l1, 11h, 11j1), 3 m2s (IPHES QB-10-G1-R/11k2, 11l2, 11j2), 2 m3s (IPHES QB-10-G1-R/11i, 11k3). Table 3.

Description. The lower molars have a well-developed longitudinal crest which connects the hypoconid-entoconid with the protoconid-metaconid. In m1, the anterolingual and anterolabial cusps are connected with the metaconid through a ridge. The labial cingulum is very broad and is separated from the protoconid by a valley. The c1 is

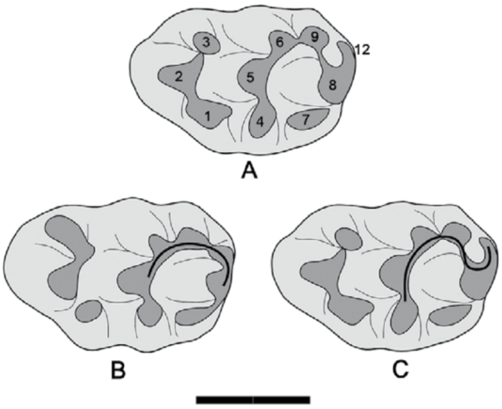

FIGURE 5. Occlusal pattern of the first upper molar of *A. mystacinus* and *A. epimelas*. A) numbering of cusps; B) QB-10-G1-R/2g, left, cusp connections typical of *Apodemus epimelas*; C) QB-10-G1-R/2i, left, cusp connections typical of *Apodemus mystacinus*. Scale bar equals 1mm. Modified from Storch, 1977.

either oval or round and it is connected to the hypoconid. Accessory cusps are absent. The anterocentral cusp is weak. The terminal heel is oval, large and isolated. The m2s have a large and oval or subtriangular anterolabial cusp, which is connected to the protoconid by a ridge in two of the three specimens (IPHES QB-10-G1-R/11j2, 11l2). The labial cingulum is wide and forms a valley with the protoconid. The c1 is small, round, and it is connected to the hypoconid. The terminal heel is oval. In m3, the anterolabial cusp may be either oval, large and connected to the protoconid (IPHES QB-10-G1-R/11i), or absent (QB-10-G1-R/k3). The upper molars have well-developed longitudinal crests. Even t4 is connected to t8 by a ridge, completing the join of the crown. Moreover, both the labial longitudinal crest (t3–t5 connection) and the lingual longitudinal crest (t1–t5 connection, except in IPHES QB-10-G1-R/11g) are present. The M1s and M2s have a small and round t1bis. In M1, the t2bis and t12 are well developed. In M2, t12 appears as a thickening from the crest that connects t8 and t9.

Discussion. The morphology of the studied molars agrees with that of *C. rivas*. To differentiate *C. rivas* from *C. crusafonti*, Martín Suárez and Mein (1991) established a set of criteria, some of them based on the percentage of appearance of certain features. *C. rivas* differs from *C. crusafonti* in that its cusps are completely connected by ridges. In the studied specimens, both upper and lower molars have well-developed longitudinal crests, completing the crown connection. Other differences between *C. rivas* and *C. crusafonti* are discernible, such as the presence in the lower molars of a very broad labial cingulum and its separation from the protoconid by a valley. Another difference is the general presence in the upper molars of t1bis and t2bis, and the large size in *C. rivas* (Martín Suárez and Mein, 1991).

The measurements of *Castillomys* from Quibas/Gruta1 were compared with the mean values of *C. crusafonti* and *C. rivas* from Tollo de Chiclana reported by Minwer-Barakat (2005). The result was a great similarity of the studied sample with *C. rivas, C. crusafonti* being smaller. Additionally, the size values fit the range of *C. rivas* from Venta Micena (Agustí *et al*., 1987b), Fuente Nueva 3 and Barranco León 5 (Agustí *et al*., 2010), Orce-2, Orce-3, Orce-7 and Barranco León 2-3 (Agustí *et al*., 1987a). Populations of *C. rivas* from Fuente Nueva 3 and Barranco León 5 are slightly smaller than those of Quibas/Gruta1. *C. rivas* has also been recognized in other Early Pleistocene sites such as the lower unit of Sima del Elefante (Cuenca-Bescós *et al*., 2001) and Loma Quemada-1 (Martín Suárez, 1988). The mean values from the latter are comparable with those from Quibas/Gruta1.

TABLE 3. Measurements (mm) of the teeth of *Castillomys rivas* from Quibas Gruta1

	Length				Width			
Element	N	min	mean	max	N	min	mean	max
M1	1		1.95		1		1.39	
M2	4	1.14	1.21	1.24	4	1.14	1.18	1.22
M3								
m1	3	1.57	1.58	1.59	4	0.96	1.00	1.04
m2	3	1.08	1.12	1.17	3	0.99	1.03	1.09
m3	2	0.87	0.91	0.96	2	0.76	0.80	0.96

Castillomys rivas is an extinct rodent. It is interpreted as an eurytopic species, *i.e*. it does not provide information about specific ecological conditions (Minwer-Barakat, 2005). Nevertheless, the development of wall-shaped ridges on the teeth suggests a diet based on grains, so open meadows should be expected as a preferred habitat (Montoya *et al*., 1999).

Family: Gliridae THOMAS, 1897

GENUS ***Eliomys*** Wagner, 1840
Eliomys quercinus (Linnaeus, 1766). (Figure 3 U–X)

Material and measurements. 5 P4s (IPHES QB-10-G1-R/12a–12e), 9 M1–2s (IPHES QB-10-G1-R/13a–13i), 5 M3s (IPHES QB-10-G1-R/14a–14e), 2 d4s (IPHES QB-10-G1-R/18a, 18b), 4 p4s (IPHES QB-10-G1-R/15a–15d), 11 m1–2s (IPHES QB-10-G1-R/16a–16k), 1 m3 (IPHES QB-10-G1-R/17a). Table 4.

Description. The p4 has a triangular outline. The protoconid and metaconid are fused at the anterior end of the tooth, forming a high and robust cusp. The mesoconid and the entoconid are connected by a continuous mesolophid (but in IPHES QB-10-G1-R/15d this is interrupted). The hypoconid and the entoconid are connected by a high, curved and continuous posterolophid. There is no posterior extra ridge. The lower molars have a simple dental pattern. The m1 and m2 have five main cusps: protoconid and metaconid on the lingual border, and mesoconid, hypoconid and entoconid on the labial border. These cusps are connected by continuous crests: anterolophid, metalophid, mesolophid and posterolophid. The endolophid and accessory ridges are absent. The centrolophid may be weak or absent. The entoconid and the metaconid are separated by a wide and deep valley. In P4, the paracone and the metacone are stronger than the protocone, but this is higher than the metacone. The anteroloph is poorly developed (except in IPHES QB-10-G1/R12c). The protoloph is long and continuous, and is connected with the endoloph. The posterior and anterior

TABLE 4. Measurements (mm) of the teeth of *Eliomys quercinus* from Quibas Gruta1

	Length				Width			
Element	N	min	mean	max	N	Min	mean	max
P4	5	0.94	1.03	1,13	5	1.43	1.55	1.64
M1-2	9	1.12	1.29	1.39	9	1.56	1.76	1.99
M3	4	1.33	1.44	1.50	4	1.46	1.57	1.67
D4	2	1.04	1.045	1.05	2	0.85	0.93	1.02
p4	4	1.34	1.44	1.51	4	1.17	1.23	1.29
m1-2	11	1.25	1.38	1.53	11	1.46	1.65	1.75
m3	1		1.24		1		1.53	

centrolophs are weak or absent. The paracone and the metacone are separated by a wide and deep valley. The metaloph is continuous. The posteroloph is curved at its lingual edge and is connected to the protocone. The M1 and M2 have continuous anterolophs, protolophs, metalophs and posterolophs. There are no accessory ridges. The paracone is larger than the metacone. The anterior and posterior centrolophs are well developed. The metaloph and posteroloph are straight. In M3, the metaloph, posteroloph, anteroloph and protoloph are continuous, and the latter two are separated by a wide and deep valley. The paracone is the highest cusp. Accessory ridges are absent. The posterior centroloph is more developed than the anterior centroloph. The metacone is lower than the paracone and they are separated by a deep furrow.

Discussion. *Eliomys quercinus* is considered a descendant of the Pliocene *E. intermedius*, from which it differs in its more simple dental pattern, with accessory ridges absent in both upper and lower teeth, and reduced centrolophids in the lower teeth (García-Alix *et al.*, 2009). All the elements described in this paper fit the morphology of *E. quercinus*. Although *E. intermedius* was quoted in the faunal list of Montoya *et al.* (1999; 2001), the sample from Gruta1 shows no morphological evidence of the presence of this species.

The measures are similar to those of *E. quercinus* from other Early Pleistocene sites such as Torrent de Vallparadís (Minwer-Barakat *et al.*, 2011), Cueva Victoria (Agustí, 1982) and Huétor-Tájar and Tojaire (García-Alix *et al.*, 2009). This species is also described in Sima del Elefante (Cuenca-Bescós and Laplana, 1997), Gran Dolina (Cuenca-Bescós *et al.*, 2011) and Almenara-Casablanca-1 and Almenara-Casablanca-3 (Agustí and Galobart, 1986). Overall, *E. quercinus* from Quibas/Gruta1 shows great biometric variability. The centrolophids of the lower molars are present but poorly developed (as in the specimens from Cueva Victoria), which indicates a more archaic morphology than the specimens from layers EVT7 and EVT12 of Torrent de Vallparadís (Minwer-Barakat *et al.*, 2011).

Eliomys quercinus underwent a great expansion throughout Europe during the entire Pleistocene. Nowadays, it is generally found in deciduous and conifer forests, and also in stony or rocky areas with some vegetation, from Spain to the Ural Mountains. Its presence in fossil sites has been considered indicative of forest areas and a temperate climate (Chaline, 1972; Sesé and Villa, 2008).

DISCUSSION AND CONCLUSIONS

The rodent assemblage from Quibas/Gruta1 includes *Allophaiomys* sp., *Apodemus* ex gr. *mystacinus–epimelas*, *Castillomys rivas* and *Eliomys quercinus*. This association is comparable to that described by Montoya *et al.* (1999): *Allophaiomys* sp. (=*Arvicola deucalion* according to Montoya *et al.* (1999)), *Apodemus* sp., *Castillomys rivas*, *Eliomys intermedius* and *Hystrix refossa*. The presence of an archaic representative of *Allophaiomys* places both sites in the Biharian mammal age (Early Pleistocene).

The association from Quibas/Gruta1 is very similar to those from Fuente Nueva 3 and Barranco León 5 (Guadix-Baza Basin, SE Spain), with a number of common species such as *Allophaiomys* sp., *Castillomys rivas* (Agustí and Madurell, 2003; Agustí *et al.*, 2010) and *Apodemus mystacinus*. According to Duval *et al.* (2013) Fuente Nueva 3 and Barranco León 5 are dated *ca.* 1.2My and according to Toro-Moyano *et al.* (2013) *ca.* 1.4My. Assuming a trend in this species to increase its size during the Early Pleistocene, as suggested by Agustí (1982) and Martín-Suárez and Mein (1991) the morphometric data of *Castillomys rivas* could be taken to suggest a younger age for Quibas/Gruta1 than Barranco León 5 and older than Fuente Nueva 3. However, Laplana and Blain (2008) established by data analysis that this trend may not exist; rather, there is a size gap between the populations of *C. crusafonti* and *C. rivas*, and the size within each population is stable with fluctuations. Due to the present of *Allophaiomys* sp., an age close to the Barranco León and Fuente Nueva 3 is proposed for Quibas/Gruta1, between *ca.* 1.2–1.4My.

The rodent association from Quibas can also be compared with that from Sima del Elefante (Atapuerca karstic complex), in which *Castillomys rivas* and *Eliomys quercinus* are also present (Cuenca-Bescós *et al.*, 2001; 2013) and the LAD of *Castillomys rivas* has been established at 1.1My (Cuenca Bescós *et al.*, 2010). However, the presence in Sima del Elefante of more derived forms of *Allophaiomys* than *Allophaiomys* sp. of Quibas/Gruta1 such as *A. lavocati* suggests an older age for the latter site.

Another site close in age to Quibas in the same region (Murcia) is Cueva Victoria. This locality shares with Quibas/Gruta1 *Castillomys rivas* and *Eliomys quercinus* (Agustí, 1982), and perhaps *Apodemus mystacinus* (a review is required). However, the presence in Cueva Victoria of a species more derived such as *V. chalinei* indicates an older age for Quibas/Gruta1.

The sites of Barranco León 5, Fuente Nueva 3 and Sima del Elefante are characterized by the first occurrence of a human presence in the Iberian Peninsula (Carbonell *et al.*, 2008; Oms *et al.*, 2000; Toro-Moyano *et al.*, 2013). Thus the site of Quibas, although without human evidences, coincides in time and space with the first human occupation in Iberia, as recorded in the Guadix-Baza Basin and the Atapuerca karstic complex (Fig. 6).

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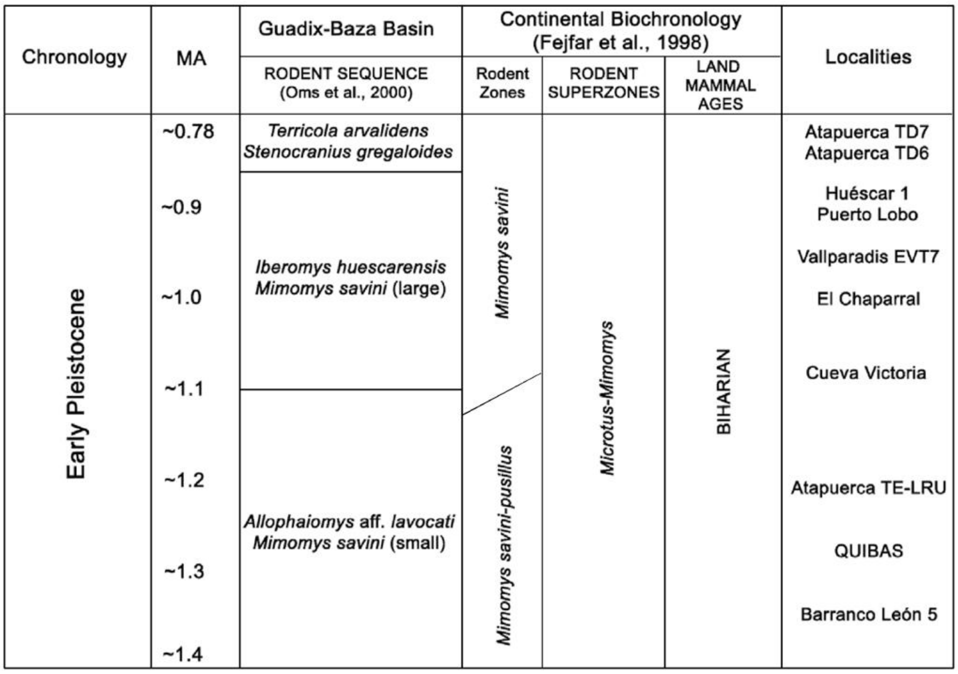

FIGURE 6. Correlation of the European chronology with the principal early Pleistocene archaeo-paleontological sites in the Iberian Peninsula, placing the Quibas site in its context. Atapuerca TE-LRU refers to Lower Red Unit of the Sima del Elefante; Atapuerca TD refers to Gran Dolina.

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XI. RECONSTRUCCIÓN PALEOAMBIENTAL DEL YACIMIENTO DEL PLEISTOCENO INFERIOR DE QUIBAS (SE ESPAÑA) POR MEDIO DEL USO DE LA ASOCIACIÓN DE ROEDORES

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General Palaeontology, Systematics and Evolution (Palaeoenvironment)

Paleoenvironmental reconstruction of the Early Pleistocene site of Quibas (SE Spain) using a rodent assemblage

Reconstruction paléoenvironnementale du site Pléistocène inférieur de Quibas (Sud-Est de l'Espagne) à partir d'un assemblage de rongeurs

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ABSTRACT

In this paper we analyze the rodent assemblage from the Early Pleistocene site of Gruta1 (Quibas karstic complex, Murcia, SE Spain), providing taphonomic comments and paleoecological and paleoclimatic data. The studied assemblage includes 209 identified rodent teeth corresponding to at least four taxa. The karstic source of the site and the low presence of digested remains suggest that the accumulation is scatological in origin, with the influence of predators such as owls; the accumulation also shows certain evidence of slight hydrodynamic sorting. For the area around Quibas/Gruta1 the paleoecological study indicates a predominance of rocky areas (31.7%), forested environments (31.7%) and open dry meadows or shrublands (29.7%), which would indicate a mosaic forest environment, and to a lesser extent the presence of open humid land (5.4%) and areas along streams or ponds (1.5%). The distribution of the bioclimatic spectra yields the highest percentage for a Mediterranean climate (37.5%), while the climatic parameters calculated (MAT = 15 °C, MTW = 25.7 °C, MTC = 4.3 °C, MAP = 390 mm) suggest colder and slightly more humid conditions than today at the time of the deposition of the remains. The data also point to a relative decrease in temperature within the phase in which the site was produced, which possibly occurred during a relative cold period between MIS 36 and MIS 40 according to the age.

RÉSUMÉ

Dans cet article, nous analysons l'assemblage de rongeurs du Pléistocène inférieur de Gruta1 (complexe karstique de Quibas, Murcie, Sud-Est de l'Espagne), en ajoutant une remarque taphonomique et en fournissant des données paléoécologiques et paléoclimatiques. L'assemblage étudié comprend 209 dents de rongeurs correspondant au minimum à quatre taxons. L'origine karstique du site et le faible pourcentage de restes digérés suggèrent

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Pléistocène inférieur
Péninsule Ibérique

que l'accumulation est d'origine scatologique, avec l'influence de prédateurs comme les rapaces nocturnes ; l'accumulation montre aussi une certaine évidence d'un léger tri hydrodynamique. Pour l'environnement autour de Quibas/Gruta1, l'étude paléoécologique montre une prédominance de zones rocheuses (31,5 %), d'environnements forestiers (31,5 %) et de prairies ouvertes et sèches ou de zones broussailleuses (30,3 %), qui indiquerait un environnement forestier en mosaïque et, dans une moindre mesure, la présence de territoires ouverts et humides (5,8 %) et d'aires riveraines (1 %). La distribution des spectres bioclimatiques fournit le plus haut pourcentage pour le climat méditerranéen (37,5 %), alors que les paramètres climatiques calculés (MAT = 15 °C, MTW = 25,7 °C, MTC = 4,3 °C, MAP = 390 mm) suggèrent des conditions plus froides et légèrement plus humides que l'actuel lors du dépôt des restes. Les données montrent aussi une certaine baisse des températures, suggérant que le site s'est formé probablement au cours d'une période froide, entre le SIM 36 et le SIM 40, d'après la chronologie du site.

1. Introduction

The Early Pleistocene site of Quibas (Abanilla, Murcia) is situated in an area called Collado del Rey, on the southeastern slope of the Sierra de Quibas, in an abandoned limestone quarry at an altitude of 669 meters AMSL (Fig. 1A). The location coordinates are 38° 18′ 51″ N, 1° 4′ 42″ W. The Sierra de Quibas is a 6-km-long and 2.5-km-wide calcareous massif (mainly Jurassic limestone and dolomites) that runs in a NE-SE direction in the Middle Subbetic region (Rodríguez-Estrella et al., 2004). This complex was affected by great karstic activity during the Plio-Pleistocene, resulting in many karstic structures. Some of these structures are infilled by mixed detritic sediments and/or chemical precipitates, and in one of them the Quibas site is located (Durán et al., 2004). Thus, the Quibas outcrop is formed by Pleistocene karstic infilling of several cavities situated within the dolomites of the Lower Lias (Jurassic). The main karstic structures are a gallery known as "Entrada Cueva" (5 m wide, 9 m high and more than 30 m in length; 2 on Fig. 1B) and a chasm known as "Sima" (20 m deep and 2 m wide; 1 on Fig. 1B). These two cavities are separated by 3-m-thick calcitic speleothems but are probably connected internally (Montoya et al., 1999). The stratigraphic and sedimentological features of the basal part of the Quibas site have been established by Fumanal and Blázquez in Montoya et al. (1999); nowadays they are covered by debris ("debris" on Fig. 1B). The sample was collected in 2009 (Cuadros, 2010) from Gruta1, a small karstic cavity located in the basal part of the Quibas site profile (3 on Fig. 1B). It is a detritic cavity formed by limestone clasts, which range between 10 and 20 cm in size, and a reddish silty clay matrix with carbonate crusts.

The main interest of this site lies in its chronology and the abundance and diversity of the faunal association identified (Rodríguez-Estrella et al., 2004). The fossil record provides both vertebrates and invertebrates from the Early Pleistocene. Preliminary faunal lists were published in Montoya et al. (1999, 2001), including both the vertebrate and invertebrate fossil record. As for the macrofauna, several taxonomic works have studied *Macaca sylvanus*, *Vulpes praeglacialis*, *Capra alba*, *Equus altidens* and *Equus suessenbornensis* (Alba et al., 2011; Carlos-Calero et al., 2004, 2006a, 2006b; Made van der et al., 2007; Piñero and Alberdi, 2015). Regarding the microfauna, Montoya et al. (1999, 2001) included a preliminary identification of the micromammal association; Piñero (2012); Piñero et al. (2015) described the rodent assemblage from Quibas/Gruta1; Cuadros (2010) carried out a taphonomic approach of the micromammals; and Blain et al. (2014) ascertained the latest occurrence of agamid lizards from western Europe.

Piñero (2012) and Piñero et al. (2015) identified the rodent faunal list from Quibas/Gruta1 as comprising *Allophaiomys* sp., *Apodemus* ex gr. *mystacinus-epimelas*, *Castillomys rivas*, and *Eliomys quercinus* (Fig. 2). Until recently, *A. mystacinus* included two subspecies: *A. mystacinus mystacinus* and *A. mystacinus-epimelas*. Nowadays these subspecies are ranked as separate species, *A. mystacinus* and *A. epimelas* (Krystufek and Vohralik, 2009; Wilson and Reeder, 2005). However, *A. epimelas* is likely to be present but recorded as *A. mystacinus*. Therefore Piñero (2012) and Piñero et al. (2015) classified *Apodemus* species as *A.* ex gr. *mystacinus-epimelas*. Based on the comparison with other Early Pleistocene sites, and although the arvicoline was not identified at species level, the shape of both m1 and M3 of *Allophaiomys* sp. from Quibas/Gruta1 was perfectly in accordance with *Allophaiomys* sp. from Fuente Nueva 3 and Barranco León 5 (Guadix-Baza Basin). Further comparison using principal component analysis (performed on different measurements), also indicated a great similarity with respect to the sample from Fuente Nueva 3 and Barranco León 5. Thus the chronology of Quibas/Gruta1 can be estimated as between ca. 1.2–1.4 Ma. This result is congruent with the age established for Quibas by Montoya et al. (1999, 2001) according to the faunal association (not only micromammals), which includes species that indicates an Early Pleistocene age.

The aim of the present paper is to complement the information about the rodent assemblage from Quibas/Gruta1 offered by Piñero et al. (2015), adding taphonomic information and providing paleoecological and paleoclimatic data on the "Sierra de Quibas" during the Early Pleistocene.

2. Materials and methods

The small-mammal sample was collected from the small karst cave known as Gruta1 (Piñero et al., 2015). All the sediment (around 10 kg.) was water-screening using superimposed 4, 1 and 0.5 mm mesh screens. The

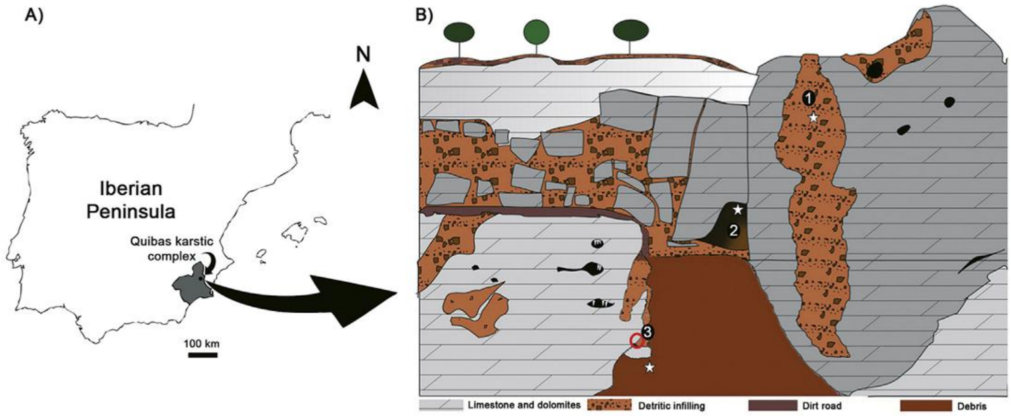

Fig. 1. (Color online.) **A.** Geographic location of the site of Quibas (Murcia, Spain). **B.** Wide-angle sketch of Quibas site. **1**, Sima; **2**, Entrada Cueva; **3**, Gruta1; **Circle**, sample extraction area.

Fig. 1. (Couleur en ligne.) **A.** Localisation géographique du site de Quibas (Murcie, Espagne). **B.** Schéma grand-angle du site de Quibas. **1**, Sima ; **2**, Entrada Cueva ; **3**, Gruta1 ; **Cercle**, zone d'extraction de l'échantillonnage.

Quibas/Gruta1 assemblage includes 209 identified rodent teeth corresponding to at least four taxa (a minimum number of 32 individuals). The specimens studied are currently stored at the Institut de Paleoecologia Humana i Evolució Social (IPHES; Tarragona, Spain).

To analyze the evidence of hydrodynamic transport, the relative abundance of each type of tooth was expressed as a percentage of the recovered teeth with respect to the expected number according to the minimum number of individuals (based on the most abundant element present in the fossil sample) (Andrews, 1990; Wolff, 1973).

In order to reconstruct the ecological conditions that prevailed in the vicinity of Quibas/Gruta1, we used the Habitat Weightings Method (Blain et al., 2008; Cuenca-Bescós et al., 2005, 2009; López-García et al., 2014; among others), based on the distribution of each rodent taxon in the habitat(s) where they are found today (for extant species) or where they are assumed to have lived in the past (for extinct species). The habitats were classified into five main types: open dry meadows, open humid meadows, woodland and woodland-margin areas, water-edges, and rocky areas (Blain et al., 2008). Each taxon was rated to a maximum score of 1.00, which was divided up proportionally to its habitat preferences if the species dwelled in more than one habitat type.

To implement the Habitat Weightings Method, it was necessary to calculate the proportions of each taxon in the assemblage. There are different methods of making this calculation, one of them being the minimum number of individuals (MNI), which is normally applied to fossil assemblages without evidence of hydrodynamic transport (Avery, 2003; Chaline et al., 1995). Our sample did show

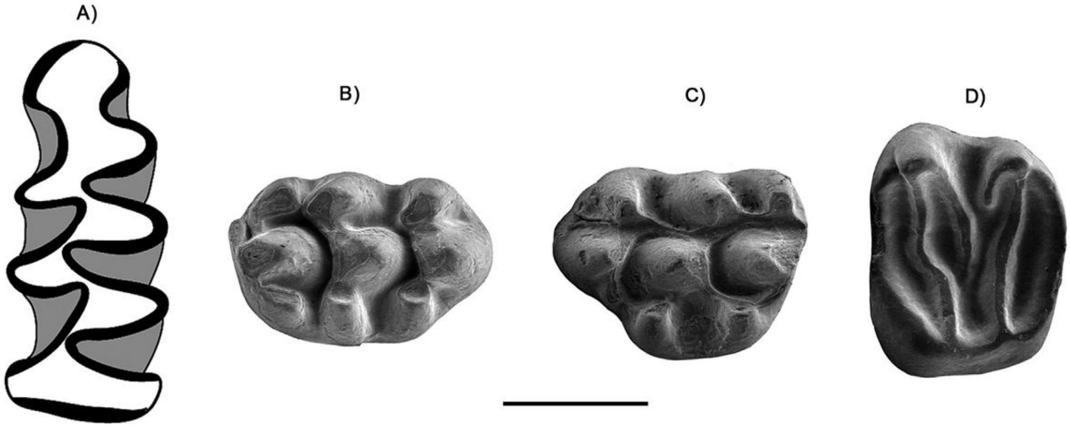

Fig. 2. Rodent species from Quibas/Gruta1. **A.** Left m1 of *Allophaiomys* sp., QB-10-G1-R/19b. **B.** Right M1 of *Apodemus* ex gr. *mystacinus–epimelas*, QB-10-G1-R/1d. **C.** Left M1 of *Castillomys rivas*, QB-10-G1-R/11a. **D.** Left M1–2 of *Eliomys quercinus*, QB-10-G1-R/13i. Scale bar equals 1 mm.

Fig. 2. Espèces de rongeurs de Quibas/Gruta1. **A.** m1 gauche d'*Allophaiomys* sp., QB-10-G1-R/19b. **B.** M1 droite d'*Apodemus* ex gr. *mystacinus–epimelas*, QB-10-G1-R/1d. **C.** M1 gauche d'*Castillomys rivas*, QB-10-G1-R/11a. **D.** M1–2 gauche d'*Eliomys quercinus*, QB-10-G1-R/13i. Échelle = 1 mm.

Modified from *Piñero et al. (2015).*

certain evidence of hydrodynamic sorting, so we calculated the quantitative composition on the basis of the relative abundance of each taxon (following Castillo, 1990; García-Alix et al., 2008, 2009; Martín-Suárez, 1988; Martín-Suárez et al., 2001; Minwer-Barakat, 2005). To avoid the over-representation of a taxon, we used the total number of teeth of each taxon, divided by its number of diagnostic elements (Murinae and Arvicolinae: 12 molars; Gliridae: 16 molars). Daams et al. (1999) proposed using rodent associations with 100 or more m1 + m2 + M1 + M2 for paleoecological studies based on micromammals. Hadly (1999) suggested that reconstructing the local mammalian community requires only a minimum sampling effort (200–250 specimens). Minwer-Barakat (2005) reduced this number to 100 because he only considered Rodentia and Insectivora. Our sample consists of 209 specimens, of which 151 are m1 + m2 + M1 + M2.

Paleoclimatic reconstruction was carried out following the qualitative bioclimatic method proposed by Hernández Fernández (2001). This analysis is made on the supposition of a significant correlation between climate and mammal community composition, applying multivariate discriminant analysis to modern mammal faunas and climates from throughout the world (Hernández Fernández and Peláez-Campomanes, 2003a). The approach to the past climatic conditions at Quibas/Gruta1 was based on the bioclimatic components from the rodent fauna (Hernández Fernández and Peláez-Campomanes, 2005). We used the rodent assemblage identified by Piñero et al. (2015) to apply this method. The bioclimatic characterization of the extinct rodent species and living species from Quibas/Gruta1 that was required for calculation of the bioclimatic spectra was taken from Hernández Fernández et al. (2007) and Hernández Fernández (2001), respectively.

3. Taphonomy

3.1. Scatological origin

The percentages of specimens digested, exemplified by the progressive reduction of enamel on the teeth (Fig. 3), are low (9 pieces, 4.3% of the rodent teeth). This suggests the influence of what Andrews (1990) designated a category 1 predator, such as owls, in the accumulation of the rodent assemblage in Quibas/Gruta1. Most authors consider that small-mammal remains in karstic sites are accumulated by the action of nocturnal avian predators (owls) through the rejection of pellets rich in skeletal material after digestion (Dauphin et al., 1996; Saavedra and Simonetti, 1998; Terry, 2004). Agustí and Martín-Suárez (1986) pointed out that nocturnal birds of prey are the major accumulators of micromammal remains at sites of scatological origin, above all those that are active near their nesting and roosting sites, such as current barn owls.

The faunal list of the Quibas site published in Montoya et al. (1999, 2001) includes three species of nocturnal birds of prey (which are potential predators): *Athene noctua*, *Otus scops* and *Strix aluco*. *Athene noctua* is a small predator that nests in cavities and feeds mainly on small mammals and invertebrates (Tomé et al., 2008), so it may be an important accumulator of small mammals in our karstic site. In this case, the biological bias would be reduced because *A. noctua* shows opportunistic feeding behaviour that does not reflect prey selection (Goutner and Alivizatos, 2003). *Otus scops* can incorporate small vertebrates into its diet, but it is mainly insectivorous (Latková et al., 2012). *Strix aluco* is an opportunistic bird of prey that can collect and accumulate a significant representation of the small-mammal fauna from a given area (Cuenca-Bescós et al., 2005; Pokines, 1998). These owl species are usually generalist feeders, but they are limited by their small body size and take a restricted range of prey, though one that is representative of their hunting range area (Fernandez-Jalvo et al., 1998). The opportunistic behaviour of the potential predators point out to a reduced biological bias. To a lesser degree, diurnal birds of prey and mammalian carnivores may also be involved in the scatological accumulation, but these show opportunistic behaviour (Fernandez-Jalvo et al., 1998).

3.2. Evidence of slight hydrodynamic transport

In karstic systems, fluvial activity is usually a short-lived process because transport ranges tend to be short in contrast to those of open-air sites (Gillieson, 1996; Kos, 2003a). Taking into account the rodent cranial fossils (mandibles, maxillaries and teeth), our sample shows a certain degree of evidence of slight hydrodynamic sorting:

- the number of isolated molars is ten times greater than the number of empty alveolar spaces in the maxillae

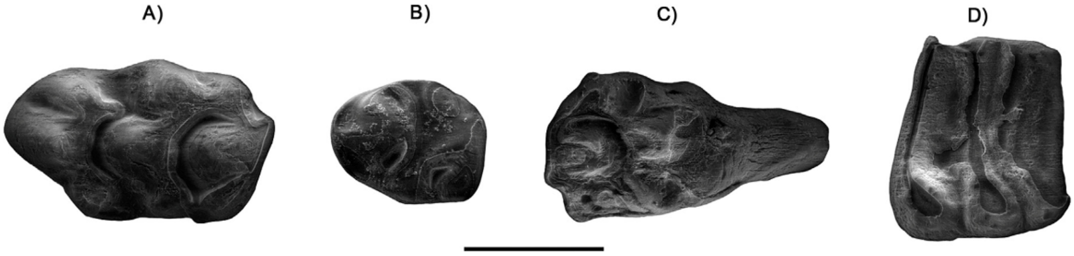

Fig. 3. Digested teeth from Quibas/Gruta1. **A.** Left M1 of *A.* ex gr. *mystacinus-epimelas*, QB-10-G1-R/2k. **B.** Right M3 of *A.* ex gr. *mystacinus-epimelas*, QB-10-G1-R/4d. **C.** Left M1 of *C. rivas*, QB-10-G1-R/11c. **D.** Right m2 of *E. quercinus*, QB-10-G1-R/16a. Scale bar equals 1 mm.
Fig. 3. Dents digérées de Quibas/Gruta1. **A.** M1 gauche d'*A.* ex gr. *mystacinus-epimelas*, QB-10-G1-R/2k. **B.** M3 droite d'*A.* ex gr. *mystacinus-epimelas*, QB-10-G1-R/4d. **C.** M1 gauche de *C. rivas*, QB-10-G1-R/11c. **D.** m2 droite d'*E. quercinus*, QB-10-G1-R/16a. Échelle = 1 mm.

Table 1
Percentage of each type of tooth for each rodent species recovered from Quibas/Gruta1 relative to the expected number according to the MNI (100% correspond to a recovery of all teeth expected in accordance with the MNI).
Tableau 1
Pourcentage de chaque type de dent pour chaque espèce de rongeurs récoltés à Quibas/Gruta1 en fonction du nombre attendu selon le NMI (100 % correspond à la récolte de toutes les dents attendues dans le gisement en accord avec le NMI).

Species	*Apodemus* ex gr. *mystacinus-epimelas*	*Castillomys rivas*	*Allophaiomys* sp.	*Eliomys quercinus*
P^4				35.7
M^1	73.7	50	0	32.2
M^2	44.8	66.6	16.7	
M^3	23.7	0	16.7	35.7
Total upper teeth	47.4	38.9	11.1	33
P_4				21.5
M_1	97.4	66.6	50	39.3
M_2	73.7	50	50	
M_3	73.7	33.3	16.7	14.3
Total lower teeth	81.6	50	38.8	28.6
Total population	64.5	44.5	25	31.3

MNI: minimum number of individuals.

and mandibles (only 26 out of 209 teeth are inserted in 14 bones, which present in total 17 empty alveolar spaces), indicating destruction either of mandibles or skulls (Andrews, 1990; Kos, 2003a);

- lower teeth are over-represented with respect to upper teeth (see Table 1). Maxillae are more fragile than jaws (Castillo et al., 2001), so during transport activity the former tend to be lost faster. In this context, element abundances indicate that more than half of the expected pieces based on the MNI are absent from the upper teeth; and only one fractured maxilla is preserved as opposed to 13 mandibles (*A.* ex gr. *mystacinus*: nine mandibles and one maxilla; *C. rivas*: three mandibles; *Allophaiomys* sp.: one mandible; *E. quercinus*: no mandible or maxilla);
- the frequency of preservation and the size of the murine teeth (*Apodemus* and *Castillomys*) decrease overall in the order: M1, M2, M3 (see Table 1). A predominance of the same type of tooth is evidence of the dispersion of the remains due to hydrodynamic sorting (Wolff, 1973). A lower 0.5 mm screen has been used in order to recover all the fossils and so avoid possible bias during the collecting process (Minwer-Barakat, 2005);
- different numbers of left and right teeth occur within the same species. Lateral selection indicates separation of the pellets before their burial (Minwer-Barakat, 2005).

Montoya et al. (1999) detected infilling of the cavities at the Quibas site by mudflow and mass displacement. Pellets produced by owls could have been transported into the cave via the entrance or moved inside the cavities. If material was regurgitated within the vicinity of the cave or even inside the cave, it could have been displaced with minimal damage (Andrews, 1990; Kos, 2003b), since most of the teeth retain their roots and show no signs of abrasion (rounding).

4. Paleoecology

Micromammals are more effective than macromammals when it comes to making paleoenvironmental inferences, since they have more specific ecological requirements, the energetic and physiological restrictions create a high degree of specialization in small species, and micromammal species are more abundant than macromammal species (Hernández Fernández, 2001). In this sense, micromammals have widely been used as paleoclimatical and paleoecological indicators; studies of rodent assemblages in particular provide useful information on paleoenvironments and paleoclimates (García-Alix et al., 2008; Martín-Suárez et al., 2001; Minwer-Barakat et al., 2005; Montuire et al., 2006, among others). The rodent association may be influenced by the ability of predators to select their prey. However, as pointed out in the previous section, the owl species in question can collect and accumulate a significant representation of the small-mammal fauna, and also in this case potential predators do not seem to have led to a significant biological bias. In this context, we attempt to analyze the environment in the vicinity of Quibas/Gruta1 at the moment of its deposition.

The main criterion used to establish the habitat(s) of an extant species is based on actualism, whereas the habitat of an extinct taxon is based on its phylogenetic relationships with extant species, on its association with taxa whose ecological requirements are known, or on biogeographical criteria (García-Alix et al., 2008; López Antoñanzas and Cuenca-Bescós, 2002). Dental patterns can also be used (Gómez Cano et al., 2013; Hernández Fernández and Peláez-Campomanes, 2003b), but this method should be taken with caution, at least in reconstructing the humidity preferences of fossil rodents (Freudenthal et al., 2014). Martín-Suárez et al. (2001) indicated that taxa within the same anagenetic evolutionary lineage have the same preferences. Nevertheless, when the speciation occurs due to a change in the physical environment (vicariant speciation) ancestor and descendant may have opposite ecological preferences. These authors also suggested that taxa with opposite frequency peaks have opposite ecological preferences, and that immigrants replacing taxa with highly similar dental patterns may have opposite preferences.

4.1. *Ecological preferences*

Allophaiomys is an extinct microtine genus and represents the earliest evolutionary grade of voles with

Table 2
Relative abundances of each rodent taxon from the Early Pleistocene of Quibas/Gruta1, with the distribution of their potential habitats.
Tableau 2
Abondances relatives pour chaque taxon de rongeur du Pléistocène inférieur de Quibas/Gruta1, avec leur distribution selon les habitats potentiels.

Species	Relative abundance (%)	Habitat				
		W	R	OD	OH	WE
Allophaiomys sp.	4.6	–	–	0.33	0.33	0.33
Apodemus ex gr. *mystacinus-epimelas*	73.0	0.33	0.33	0.33	–	–
Castillomys rivas	7.6	–	–	0.5	0.5	–
Eliomys quercinus	14.8	0.5	0.5	–	–	–

W: woodland and woodland-margin areas; R: rocky areas; OD: open dry meadows or shrublands; OH: open humid meadows; WE: water-edges.

rootless lower teeth and cementum in the reentrant angles. According to Cuenca-Bescós et al. (2005), the fact that *Allophaiomys* has no roots and has continuously growing molars indicates open grassland or tundra dwellers. *Allophaiomys* is believed to have been ancestral to European *Microtus* (Chaline, 1966; Martin, 1975). Nowadays *Microtus* generally prefers open meadows, but there are also species inhabiting water-edge areas. Voles in general are animals adapted to fibrous grasslands, as shown by their hypsodont molars (Cuenca-Bescós et al., 2005). During the Plio-Pleistocene, different lines of arvicolids increased their molar hypsodonty with the appearance of cementum, an evolutionary trend which is usually interpreted as an adaptation to a diet rich in abrasive food such as grasses, and therefore as indicating a spread of open meadow areas (Fejfar and Heinrich, 1990; Fejfar and Repenning, 1992; Minwer-Barakat, 2005). On the basis of this information we assume that the environment inhabited by *Allophaiomys* sp. was open dry meadows (0.33), open humid meadows (0.33) and water-edge areas (0.33).

Today, *A. mystacinus* and *A. epimelas* (recorded as *A. mystacinus*) are found in areas with a relatively warm climate in the Balkan Peninsula and Middle East. They are associated with dry forest and shrubland in rocky areas. Their presence in fossil sites may be connected with the presence of rocky environments in the vicinity of the locality (Agustí, 1982; Minwer-Barakat, 2005; Mitchell-Jones et al., 1999; Storch, 2004). Therefore, we distribute this taxon into three habitat types: open dry meadows (0.33), woodland (0.33) and rocky areas (0.33).

Castillomys rivas is an extinct rodent. It is interpreted as a eurytopic species, i.e. it does not provide information about specific ecological conditions (García-Alix et al., 2009; Minwer-Barakat, 2005). Nevertheless, given the presence of morphological features in the dental pattern associated with stephanodonty (the development of longitudinal ridges between molar cusps), it may indicate a diet based on grass (van Dam and Weltje, 1999; Gómez Cano et al., 2013; Montoya et al., 1999; Renaud et al., 2005), so open meadows should be expected as its preferred habitat (0.5 open dry; 0.5 open humid).

Eliomys quercinus underwent a great expansion throughout Europe during the entire Pleistocene. Nowadays, it is generally found in low-density deciduous and conifer woodland (0.5), and also in stony or rocky areas (0.5) with some vegetation at forest edges from Spain to the Ural Mountains. Areas with abundant herbaceous vegetation seem to be a limiting factor on its presence (López-García et al., 2011). Its identification in fossil sites has been considered indicative of forest areas and a temperate climate (Chaline, 1972; López-García et al., 2011; Sesé and Villa, 2008).

4.2. Paleoecological reconstruction

The rodent assemblage from Quibas/Gruta1 is clearly dominated by *Apodemus* ex gr. *mystacinus-epimelas*, with a relative abundance of 73%, followed by *Eliomys quercinus* with a prevalence of 14.8%, *Castillomys rivas* with 7.6% and *Allophaiomys* sp. with 4.6% (Table 2). The distribution of the relative abundances of rodent taxa and their habitat preferences (Table 2; Fig. 4) indicates a dominance of rocky habitats (31.7%), woodland and woodland-margin areas (31.7%), and open dry meadows (29.7%). The mixture of inhabitants of dry meadows or shrublands and forested environments is consistent with a mosaic forest scenario in the vicinity of Quibas/Gruta1, while rocky areas probably reflect the proximity of the cave. The existence of open habitats with a predominance of shrublands and rocky environments is supported by the appearance of certain macromammal taxa in Quibas, such as *Lynx pardinus* and *Capra alba*, and gastropods such as *Pomatias sulcatus* and *Chondrina farinesii*, while the presence of cervids (Cervidae indet.) suggests the occurrence of forested areas (Montoya et al., 1999, 2001). Our rodent assemblage also indicates open herbaceous habitats with some humidity requirements (5.4%) and areas surrounding water such as

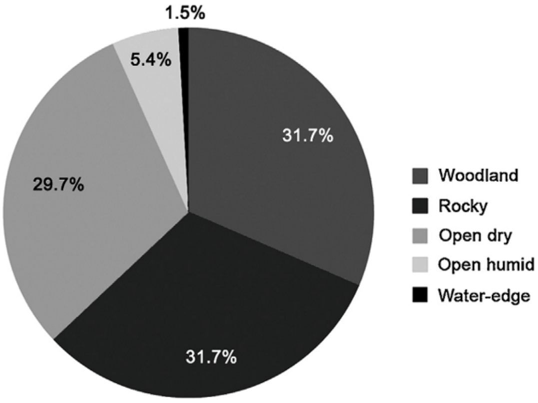

Fig. 4. Distribution of the habitats at Quibas/Gruta1 according to the ecological preferences of the rodent species.
Fig. 4. Distribution des rongeurs de Quibas/Gruta1 par habitat, en accord avec leurs préférences écologiques.

Table 3
Climatic parameters for Quibas/Gruta1 calculated according to the bioclimatic analysis based on rodent associations proposed by Hernández Fernández (2001), present climate data from Abanilla (Rivas-Martínez and Rivas-Sáenz, 1996–2009), and climatic parameters from Quibas obtained by Agustí et al. (2009) and Hernández Fernández et al. (2007).
Tableau 3
Paramètres climatiques pour Quibas/Gruta1, calculés selon l'analyse bioclimatique basée sur les associations de rongeurs proposée par Hernández Fernández (2001), les données climatiques actuelles d'Abanilla (Rivas-Martínez et Rivas-Sáenz, 1996–2009) et les paramètres climatiques de Quibas obtenus par Agustí et al. (2009) et Hernández Fernández et al. (2007).

	Quibas/Gruta1			Current data in Abanilla	Difference between results and current data	Agustí et al. (2009)	Hernández Fernández et al. (2007)
	Results	r^2	ES				
MAT	15.1	0.930	3.6	19.6	−4.5	15.0 ± 2.3	15.378
MTW	25.7	0.746	4.7	33.6	−7.9	24.2 ± 1.5	26.074
MTC	4.3	0.932	5.1	8.8	−4.5	7.0 ± 2.9	4.307
MATA	21.4	0.779	6.4	24.8	−3.4	–	21.76
MAP	390.6	0.746	470.6	303	+87.6	723 ± 233	417.217
AD	4.5	0.926	1.3	5	−0.5	–	4.94

MAT: mean annual temperature (in °C); MTW: mean temperature of the warmest month (in °C); MTC: mean temperature of the coldest month (in °C); MATA: mean annual thermal amplitude (in °C); MAP: mean annual precipitation (in mm); AD: aridity duration (months); ES: standard error for the estimation; r^2: coefficient of determination.

areas along streams, lakes or ponds (1.5%). The presence of humid areas at Quibas is well supported by the occurrence of *Anthus pratensis*, *Geronticus eremita* and *Saxicola torquata* (Montoya et al., 1999, 2001), avian species that dwell in wet meadows and at pond edges. Large herbivores such as *Praeovibos mediterraneus* as well as *Equus altidens* and *Equus suessenbornensis* (Piñero and Alberdi, in press) also provide evidence of the presence of wet and open meadows.

5. Paleoclimatology

Nowadays, the climate around the Sierra de Quibas is characterized by a strong tendency towards aridity due to the low and irregular rainfall distribution shared by all Mediterranean basins. The great variability of rainfall together with elevated temperatures results in high evapotranspiration, reaching a maximum in the months of extreme drought, i.e. June, July and August. Abanilla has a mean annual precipitation (MAP) that ranges between 250–300 mm and a mean annual temperature (MAT) of 19.6 °C (Manzano Garro, 1987; Rivas-Martínez and Rivas-Sáenz, 1996–2009).

On the basis of the rodent association from Quibas/Gruta1 we have calculated climatic parameters (Table 3) following the bioclimatic model proposed by Hernández Fernández (2001) for rodent assemblages. The distribution of the bioclimatic spectra yields the highest percentage for a Mediterranean climate (37.5%), followed by tropical with summer rains (25%), typical temperate (12.5%), arid-temperate (12.5%), and cold-temperate (12.5%). The Mediterranean climate at Quibas/Gruta1 is supported by the resulting climatic parameters, such as low mean annual precipitation ($MAP_{Quibas/Gruta1} = 390$ mm) and the aridity duration ($AD_{Quibas/Gruta1} = 4.5$ months). Our results indicate a colder and slightly more humid climate than today in the Sierra de Quibas. The mean annual temperature ($MAT_{Quibas/Gruta1} = 15.1$ °C) was 4.5 °C lower, and the mean annual precipitation 87 mm higher than current values. The mean temperature of the coldest month (MTC) was 4.3 °C, and the mean temperature of the warmest month (MTW) was 25.7 °C, whereas today in Abanilla MTC = 8.8 °C and MTW = 33.6 °C.

Previous paleoclimatic inferences from Quibas have been drawn using both the bioclimatic model proposed by Hernández Fernández (2001) for rodent assemblages (Hernández Fernández and Peláez-Campomanes, 2003a; Hernández Fernández et al., 2007) and the Mutual Climate Range method (Blain et al., 2009) for amphibian and squamate reptile assemblages (Agustí et al., 2009). Both studies are based on the faunal list of Quibas published in Montoya et al. (1999, 2001). The data published by Agustí et al. (2009) (Table 3) resemble ours but with differences in the MTC (7 °C) and MAP (723 mm), Quibas/Gruta1 being colder and dryer. Otherwise, the climatic parameters proposed by Hernández Fernández et al. (2007) (Table 3) fit very well with the results of this work. In any case, all of them corroborate the prevalence of colder and wetter conditions than at present.

Agustí et al. (2009) recognize five alternating climatic phases in the Early Pleistocene. Phase 3 includes the sites of Barranco León 5, Fuente Nueva 3, Sima del Elefante, Cueva Victoria and Quibas, and is characterized by a sharp increase in temperature and precipitation in relation to the previous phase, which explains the early human occupation at that time (Agustí et al., 2009). However, within this context the site of Quibas represents a moment of relative decline in temperature, particularly the mean temperature of the coldest month (Agustí et al., 2009), which also occurs in Quibas/Gruta1. García-Alix et al. (2009) indicated relative cold and wet conditions for Huétor Tájar and Tojaire sections (Granada Basin), which are coeval of Quibas/Gruta1. These localities would be included into the same phase according to the time interval and the climatic interpretation.

In conclusion, the data obtained in this work suggest a colder and slightly wetter climate than today during the formation of Quibas/Gruta1 between ca. 1.4 and 1.2 Ma (Piñero et al., 2015). This interpretation is concordant with the progressive general cooling detected by Shackleton (1995) during the Early Pleistocene. One of the characteristics of the latest Early Pleistocene of the southeast of the Iberian Peninsula was the slightly colder climate than nowadays and the change in the rainfall regime with more rainy winters and slightly drier summers, as is displayed at Barranco León and Fuente Nueva 3 (Blain et al., 2011) and Cueva Victoria (Blain, 2015). As shown by Lisiecki and Raymo (2005) using the benthic $\delta^{18}O$ record, the period between 1.2 and 1.4 Ma manifested various cold stages, which include Marine Isotope Stages (MIS) 36, 38, and 40. The accumulation of remains at Quibas/Gruta1 could have occurred during a relative cold period between MIS 36 and MIS 40.

6. Conclusions

The analysis of the rodent assemblage from the Early Pleistocene of Gruta1 establishes the following conclusions:

- the very low percentage of digested teeth in the rodent assemblage from Quibas/Gruta1 and the karstic origin of the site suggest that the sample was accumulated by the action of nocturnal avian predators. The main accumulators are likely to have been generalist feeders, whose accumulations would represent the rodent association from their hunting area;
- the remains display evidence of a certain degree of hydrodynamic transport, such as a great abundance of isolated molars, distinct proportions of lower and upper teeth, different numbers of left and right teeth within the same species, and a decrease in the preservation of murine teeth by size in the order M1, M2, M3;
- the distribution of the species according to their potential habitat(s) indicates a mixture of dry meadows or shrublands, woodland and woodland-margin zones and rocky habitats with the presence of open herbaceous meadows and water-edges, which is consistent with a mosaic forest scenario in the vicinity of Quibas/Gruta1 during the formation of the site;
- paleoclimatic data suggest a Mediterranean climate for the Sierra de Quibas during the Early Pleistocene, with colder temperatures and slightly higher rainfall than today. They also point to a relative decrease in temperature within the phase in which it was produced. The accumulation of remains may have occurred during a relative cold period between MIS 36 and MIS 40 according to the age of the site.

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XII. CONCLUSIONES

En este último capítulo se exponen las principales conclusiones que se obtienen de este trabajo, y que ya han sido adelantadas en los capítulos anteriores:

1. Se han descrito e identificado un total de 2084 dientes de pequeños mamíferos procedentes de 14 niveles paleontológicos diferentes localizados en el sureste de la Península Ibérica (cuenca de Guadix-Baza, cuenca de Fortuna, cuenca de Murcia-Carrascoy, Sierra de Quibas). En conjunto se han identificado 51 especies de micromamíferos, de las cuales 19 se incluyen en la familia Muridae. Las poblaciones de esta familia suponen un 65,74% del total de restos analizados, con 1370 dientes:

   - El nivel de SIF-1 ha proporcionado 139 dientes de roedores pertenecientes a siete especies, de las cuales cuatro son múridos: *Stephanomys ramblensis*, *Apodemus gudrunae*, *Occitanomys alcalai* y *Occitanomys adroveri*.

   - La localidad de SIF-3 contiene 104 molares asignados a ocho especies de roedores diferentes, entre las cuales cinco corresponden a múridos: *Stephanomys ramblensis*, *Apodemus gudrunae*, *Apodemus gorafensis*, *Occitanomys alcalai* y *Occitanomys adroveri*.

   - El nivel de ROM-2B ha cedido 131 piezas de roedores e insectívoros asignadas a nueve especies diferentes, de las que cuatro son múridos: *Occitanomys alcalai*, *Occitanomys* aff. *adroveri*, *Apodemus gudrunae* y *Stephanomys ramblensis*.

   - La asociación de roedores e insectívoros de ROM-2C está formada por 414 piezas dentarias atribuidas a 11 especies, siendo cuatro de ellas múridos: *Occitanomys alcalai*, *Occitanomys* aff. *adroveri*, *Apodemus gudrunae* y *Stephanomys ramblensis*.

   - ROM-3A es el nivel más pobre de los estudiados, con sólo cuatro molares pertenecientes a dos múridos: *Stephanomys ramblensis* y *Occitanomys alcalai*.

   - Se han obtenido 55 dientes de roedores del yacimiento de SIF-52, identificándose cinco especies distintas, entre las que hay tres múridos: *Stephanomys ramblensis*, *Apodemus gorafensis* y *Occitanomys alcalai*.

- La lista de roedores de SIF-61 con 158 dientes incluye nueve especies, siendo seis de ellas múridos: *Stephanomys ramblensis*, *Occitanomys alcalai*, *Paraethomys meini*, *Apodemus gudrunae*, *Apodemus gorafensis* y *Castromys* cf. *littoralis*.

- Entre las 28 piezas dentarias que ha librado SIF-79, se han identificado cinco especies, de las que tres son múridos: *Stephanomys ramblensis*, *Occitanomys alcalai* y *Paraethomys meini*.

- El nivel de SIF-413 contiene 157 dientes de roedores atribuidos a nueve especies diferentes, contando con cinco múridos: *Stephanomys dubari*, *Paraethomys meini*, *Apodemus* cf. *gudrunae*, *Occitanomys alcalai* y *Occitanomys brailloni*.

- SIF-430 ha proporcionado solamente nueve molares pertenecientes a tres especies, de las cuales dos son múridos: *Stephanomys dubari* y *Paraethomys meini*.

- Se han recuperado 155 molares de roedores de la localidad de SIF-P pertenecientes a ocho especies distintas, incluyendo cuatro múridos: *Stephanomys cordii*, *Paraethomys* aff. *abaigari*, *Castillomys gracilis* y *Occitanomys brailloni*.

- El yacimiento del Puerto de la Cadena incluye más de un centenar de dientes de roedores y lagomorfos asignados a siete especies, pero sólo dos son múridos: *Stephanomys* cf. *dubari* y *Paraethomys* cf. *meini*.

- La localidad de Baza-1 ha ofrecido una colección de 447 fósiles pertenecientes a 16 taxones de pequeños mamíferos, siendo seis de ellos múridos: *Stephanomys cordii*, *Apodemus gorafensis*, *Castillomys gracilis*, *Paraethomys meini*, *Paraethomys* aff. *abaigari*, *Occitanomys* cf. *brailloni*.

- La Gruta-1 del yacimiento de Quibas ha librado 204 restos de roedores asignados a cuatro especies distintas, entre las que hay dos especies de múridos: *Apodemus* ex gr. *mystacinus-epimelas* y *Castillomys rivas*.

- Se ha revisado además la fauna de múridos de las secciones de Botardo-1, Gorafe, Zújar y Galera.

2. Los yacimientos estudiados se extienden a lo largo de 6 Ma, registrando una sucesión casi completa de las paleocomunidades de múridos desde el Turoliense superior (Mioceno superior) hasta el Bihariense (Pleistoceno inferior).

3. La buena preservación de los fósiles ha permitido realizar inferencias bioestratigráficas fiables, permitiendo la correlación con las principales localidades de micromamíferos de la Península Ibérica. De esta forma se ha podido determinar la edad relativa de los yacimientos:

- Los niveles de SIF-1, SIF-3, ROM-2B, ROM-2C y ROM-3A son comparables con las asociaciones más antiguas asignadas al Turoliense superior (base de MN13). El nivel de SIF-52 se correlaciona con el Turoliense superior (MN13) poco antes de la llegada de *Paraethomys* a la Península Ibérica.

- Las localidades de SIF-61 y SIF-79 corresponden al Turoliense superior (MN13) tras la llegada de *Paraethomys*.

- Los yacimientos de SIF-413, SIF-430, SIF-P, Puerto de la Cadena y Baza-1 se asignan al Rusciniense inferior (MN14).

- La Gruta-1 del yacimiento de Quibas corresponde al Bihariense (Pleistoceno inferior). A través de la asociación de roedores se ha podido determinar que esta localidad es algo más reciente que Barranco León-5 y Fuente Nueva-3, y ligeramente más antigua que Sima del Elefante. De acuerdo a las edades establecidas en estos últimos yacimientos, la Gruta-1 de Quibas tiene una edad comprendida entre 1,2 y 1,4 Ma.

4. El registro de más de 2 Ma de sedimentos continentales en la sección de Sifón de Librilla, con localidades ricas en micromamíferos, ha favorecido la redefinición de relaciones filogenéticas para algunos géneros de múridos:

- Se confirma la línea de evolución anagenética *S. ramblensis* – *S. dubari* – *S. cordii* en base al material procedente de Sifón de Librilla. Además, no se observa una tendencia clara hacia el aumento de tamaño dentro de las poblaciones de *Stephanomys ramblensis* a lo largo del tiempo.

- La coexistencia de *Apodemus gudrunae* y *Apodemus gorafensis* en SIF-3 (base del Turoliense superior), así como la ausencia de poblaciones transicionales, sugiere que *Apodemus gorafensis* es o bien un inmigrante en la Península Ibérica, o bien el resultado de un proceso cladogenético rápido, descartando un origen anagenético desde *Apodemus gudrunae*, tal y como se indica en trabajos previos.

- Se propone que *Paraethomys* aff. *abaigari* deriva de *Paraethomys meini* como resultado de un proceso anagenético marcado por un aumento de tamaño y un incremento en el desarrollo de los espolones posteriores del t1 y t3 del M^1 y M^2 durante el Plioceno inferior.

5. La localidad de SIF-413 se formó durante el Plioceno más basal, tras la Crisis de Salinidad del Messiniense. El estudio detallado de su fauna ha permitido confirmar la equivalencia entre los límites Mioceno-Plioceno y MN13-MN14.

6. Se han analizado las implicaciones bioestratigráficas del conjunto de roedores de SIF-413 para detectar el inicio del Plioceno en depósitos continentales. Se ha establecido así que *Occitanomys brailloni* es el elemento clave para reconocer el inicio del Plioceno en los niveles continentales de Europa Occidental con asociaciones de roedores, así como para diferenciar la MN13 de la MN14.

7. El yacimiento de Baza-1 contiene el registro más abundante y diverso de micromamíferos del Rusciniense inferior de la cuenca de Guadix-Baza, mejorando el conocimiento sobre este intervalo de tiempo hasta ahora poco conocido. De esta forma se contribuye a la continuidad del registro bioestratigráfico de la Cordillera Bética.

8. La conjunción de bioestratigrafía y magnetoestratigrafía establece las siguientes correlaciones magnetoestratigráficas:

- La parte alta de la sección del Cigarrón, donde se localiza el yacimiento del Puerto de la Cadena, presenta una polaridad inversa que se correlaciona con el subcrón 3n.3r (4,997 – 4,896 Ma).

- Toda la sección de Negratín registra una polaridad inversa, asignándose al cron 3r (6,033 – 5,235 Ma).

- La sección de Botardo-1 (Bo-C y Bo-D) ha ofrecido una polaridad inversa, correlacionándose con el subcrón 3n.2r (4,799 – 4,631 Ma).

- La parte baja de la sección de Gorafe, donde se localizan los yacimientos de Go-1 y Go-4, registra una polaridad normal que se correlaciona con el subcrón 3n.1n (4,300 – 4,187 Ma). La parte alta de esta misma sección, donde se sitúan los yacimientos de Go-5 y Go-2, presenta una polaridad inversa y se correlaciona con el cron 2Ar (4,187 – 3,596 Ma).

9. La disposición de una sección larga y continua como es Sifón de Librilla ligada a un estudio magnetoestratigráfico fiable, ha permitido calibrar las primeras y últimas apariciones de muchas especies de roedores, e incluso se ha establecido el rango cronológico completo de algunas de ellas. A continuación se exponen las relativas a múridos:

- La primera aparición de *Apodemus gudrunae*, *Occitanomys alcalai* y *Stephanomys ramblensis* se correlaciona con el techo del cron 3Ar, ligeramente anterior a 6,7 Ma.

- La primera aparición de *Apodemus gorafensis* y la última aparición de *Occitanomys adroveri* se establecen ligeramente por encima de la base del cron 3An2n, algo posterior a 6,7 Ma.

- La transición de *Stephanomys ramblensis* a *Stephanomys dubari*, y la primera aparición de *Paraethomys meini* se correlacionan con el cron 3An.1n, entre 6,033 y 6,252 Ma.

- La primera aparición de *Occitanomys brailloni* se asigna a la parte más alta del cron 3r, en torno al límite Mioceno-Plioceno (5,33 Ma).

- La primera aparición de *Paraethomys* aff. *abaigari* se establece en el subcrón 3n.4n (5,235 – 4,997 Ma).

- La transición de *Stephanomys dubari* a *Stephanomys cordii* tuvo lugar en algún momento entre la base del subcrón 3n.3n y el techo del subcrón 3n.2r (4,896 – 4,631 Ma). La última aparición de *Apodemus gudrunae* se correlaciona con el subcrón 3n.2r (4,799 – 4,631 Ma).

10. Se ha propuesto la primera escala magnetobioestratigráfica para el Mioceno superior y Plioceno de la cuenca de Guadix-Baza. Esto ha permitido correlacionar la MN13 con el Messiniense superior, la MN14 con el Zancliense inferior, la mayor parte de la MN15 con el Zancliense superior, y la parte más alta de la MN15 y la MN16 con el Piacenziense. Se han definido un total de nueve biozonas en base a las asociaciones de roedores:

- Biozona de Extensión Coincidente de *Apodemus gudrunae* y *Apocricetus alberti*. Su límite inferior se correlaciona con la base del subcrón 3r (6,03 Ma).

- Biozona de Intervalo de *Apocricetus barrierei*. La base de esta biozona se establece en la parte alta del cron 3r, coincidiendo aproximadamente con el límite Mioceno-Plioceno (5,33 Ma).

- Biozona de Intervalo de *Paraethomys* aff. *abaigari*. El límite inferior de esta biozona se correlaciona aproximadamente con la base del subcrón 3n.2n (4,63 Ma).

- Biozona de Intervalo de *Trilophomys*. Probablemente la extensión de esta biozona se ajusta al subcrón 3n.1n (4,30 – 4,19 Ma), aunque su límite inferior podría ser algo más bajo.

- Biozona de Intervalo de *Mimomys davakosi*. Esta biozona tiene una edad máxima de 4,19 Ma (base del cron 2Ar), y una edad mínima de 3,60 Ma (techo del cron 2Ar).

- Biozona de Extensión de *Dolomys adroveri*. El intervalo de esta biozona se puede establecer aproximadamente entre 3,3 y 3,9 Ma.

- Biozona de Extensión de *Mimomys hassiacus*. El rango cronológico de esta biozona parece ser equivalente al del subcrón 2An.2r (3,33 – 3,21 Ma).

- Biozona de Extensión de *Mimomys polonicus*. La base de esta biozona se establece en el subcrón 2An.2n (3,21 – 3,12 Ma), mientras que el techo se correlaciona con la base del subcrón 2An.1n (3,03 Ma).

- Biozona de Extensión de *Kislangia ischus*. Esta biozona tiene una edad máxima de 3,03 Ma, mientras que su límite superior parece ser anterior a la base del cron 2r, por lo que coincide prácticamente con el límite Plioceno-Pleistoceno (2,58 Ma).

11. Se ha realizado una interpretación de las condiciones ambientales dominantes en el entorno de algunos de los niveles estudiados en el momento de su formación, en base a las proporciones de las distintas especies de micromamíferos en relación con sus preferencias ecológicas:

- Las proporciones relativas de los roedores e insectívoros de ROM-2B y ROM-2C apuntan hacia el dominio de un espacio abierto herbáceo relativamente homogéneo durante la formación de estos niveles, con la presencia de parches boscosos en ROM-2C. Probablemente las condiciones reinantes fuesen templadas. Se detecta un ligero descenso de temperatura y humedad desde ROM-2B hacia ROM-2C. El bajo valor del índice de diversidad específica tanto de ROM-2B como de ROM-2C y la proporción de los taxones sugieren la presencia de ambientes herbáceos abiertos y homogéneos, permitiendo inferir el dominio de unas condiciones climáticas inestables durante la base del Turoliense superior en la cuenca de Fortuna.

- La asociación de micromamíferos de Baza-1 indica que este yacimiento se depositó en un entorno dominado por un hábitat herbáceo abierto con presencia ocasional de manchas forestales y desarrollo de cursos de agua estables. Es probable que las condiciones climáticas fueran cálidas y secas, correspondiéndose al período cálido que sucedió al enfriamiento de hace 4,5 Ma, y previo al máximo de aridez de hace 3,95 Ma.

- La distribución de las especies de la Gruta-1 de Quibas en relación a sus hábitats potenciales indica una mezcla de praderas o matorrales, bosques y zonas marginales boscosas y hábitats rocosos, con presencia de praderas herbáceas abiertas y zonas acuíferas. Todo esto es coherente con la presencia de un escenario boscoso en mosaico en los alrededores del yacimiento de Quibas durante la formación de la Gruta-1.

12. El análisis tafonómico llevado a cabo sobre la muestra de roedores de la Gruta-1 de Quibas indica lo siguiente:

- El bajo porcentaje de dientes digeridos y el origen kárstico del yacimiento sugieren que la muestra se acumuló como resultado de la acción predadora de aves rapaces nocturnas. Lo más probable es que los principales predadores fuesen generalistas en su alimentación, de forma que sus eyecciones estarían representando la asociación de roedores de su área de caza.

- Los restos muestran evidencias de un cierto grado de transporte hidrodinámico: gran abundancia de dientes aislados, distintas proporciones entre los molares inferiores y superiores, diferente número de dientes izquierdos y derechos dentro de una misma especie, y selección decreciente en los múridos desde los primeros molares hacia los terceros.

13. El estudio paleoambiental realizado sobre los restos de roedores de la Gruta-1 de Quibas ha incluido un análisis bioclimático cualitativo. Los datos resultantes sugieren un clima Mediterráneo para la Sierra de Quibas durante el Pleistoceno inferior, con unas temperaturas más frías que las actuales y unas precipitaciones ligeramente superiores. Los resultados apuntan también hacia una ligera disminución de las temperaturas dentro de la fase en la que se encuentra. De acuerdo a la edad de este yacimiento, la acumulación de los restos podría haber tenido lugar durante un período relativamente frío entre el MIS 36 y el MIS 40.

PERSPECTIVAS DE FUTURO

Las publicaciones que se presentan en esta tesis abren un campo de posibles trabajos ligados a la temática tratada. Los trabajos más inmediatos se pueden resumir en los siguientes puntos:

- Realizar un análisis sobre la evolución ambiental en la sección de Sifón de Librilla por medio de las proporciones relativas y requerimientos ecológicos de los taxones que integran las paleocomunidades de micromamíferos.

- Realizar un estudio sistemático de las poblaciones de roedores del resto de secciones de la cuenca de Fortuna (El Chorrico/Autovía, Barranco de la Salada).

- Proponer una biozonación calibrada para el Mioceno superior y Plioceno inferior de la cuenca de Fortuna basada en las sucesiones de roedores.

- Análisis sistemático de los roedores de la sección de Zújar, permitiendo una mayor continuidad estratigráfica para el estudio de la evolución de las paleocomunidades de múridos en el sureste ibérico.

- Análisis sistemático de las asociaciones de roedores del noreste de la Península Ibérica.

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APÉNDICE

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Early to Middle Pleistocene rodent biostratigraphy of the Guadix-Baza Basin (SE Spain)

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Guadix-Baza Basin

ABSTRACT

In this paper, a biozonation of the Pleistocene continental record of the Guadix-Baza Basin is proposed. This biozonation is based on the small mammal succession, which ranges from the earliest Pleistocene (ca. 2.6 Ma) to the Middle Pleistocene (ca. 0.3 Ma). A total of 9 biozones have been recognized, all based on the range or concurrent-range of arvicolid species. Therefore, seven biozones have been defined for the Early Pleistocene: *Kislangia gusii* Zone, *Mimomys* cf. *reidi* Zone, *Mimomys (Tcharinomy)s oswaldoreigi* Zone, *Allophaiomys ruffoi* Zone, *Allophaiomys* aff. *lavocati* Zone, *Iberomys huescarensis* Zone and *Terricola arvalidens* Zone. In the Middle Pleistocene of the basin two biozones have been recognized: *Iberomys brecciensis*–*Arvicola mosbachensis* Zone and *Iberomys brecciensis-Arvicola* aff. *sapidus* Zone. According to different dating methods, the duration of each Early Pleistocene biozone ranges between 0.4 and 0.1 My, with increasing resolution from the Earliest Pleistocene to the late Early Pleistocene. The small mammal succession reveals a high degree of endemism and a persistent Eastern Mediterranean influence, as opposed to Central and Eastern Europe. However, correlation with other Iberian and European sites has been possible on the basis of each biozone associated fauna.

1. Introduction: the Guadix-Baza Basin

Guadix-Baza is an intramontane Neogene and Quaternary basin (Fig. 1) of approximately 3000 km^2 which is located in the Betic chain. This chain is an Alpine fold and thrust belt that mainly originated during the Miocene. At the contact area between the basement units or Internal areas (located to the south and mainly of Paleozoic age) and the cover units or External areas (located to the north and of Mesozoic age) the Guadix Baza basin was developed. This basin was part of the corridors connecting the Atlantic and Mediterranean seas during part of Miocene (see general sedimentary schemes by Fernández et al., 1996; Soria et al., 1998). Towards the end of the Miocene the basin was disconnected from the sea and continental successions were deposited (Minwer-Barakat et al., 2009a, 2009b, 2012a, 2012b; Hüsing et al., 2010, 2012; Martín-Suárez et al., 2012). Thus, these successions provide an almost continuous continental record for the last 6 Ma. This unparalleled succession is recorded in several different paleogeographic settings.

The Guadix-Baza Basin is split into two sub-basins: Guadix to the east and Baza to the west. The sub-basins are separated by the Jabalcón threshold, a prominent relief of the External Zones. These two sub-basins underwent several connections and disconnections as a function of both tectonics and the varying development of the alluvial and fluvial network, forming the Guadix Formation (see Viseras, 1991). This formation is build up of a main basin-axis aligned deposits (east–west) known as the longitudinal system (see Fig. 1b). Other supplies were derived from the basin margins to

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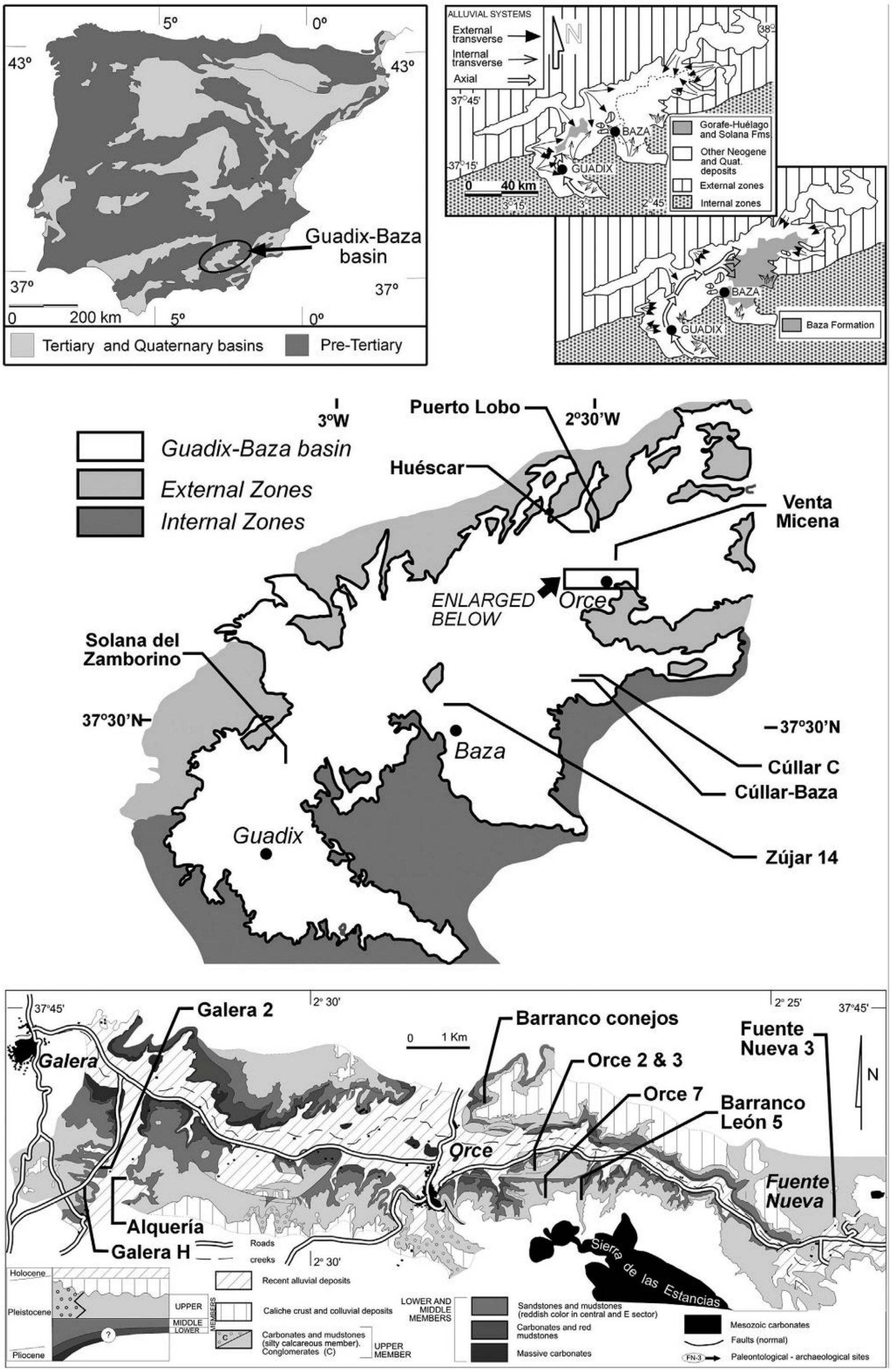


Fig. 1. A: Location of the Guadix-Baza in the context of the Cenozoic basins of Iberia. B and C: Extension of the lacustrine sedimentation (Gorafe-Huélago, Solana and Baza formations) according to the dominant alluvial system (after Viseras, 1991; Viseras et al., 1998).

the north and south, known as the transversal systems. The alternating development of these systems created confined lacustrine systems in different places of the basin. The distal lacustrine facies of the Guadix Formation are the Baza and Gorafe-Huélago Formations (Vera, 1970). Thus, when the longitudinal system was more active, lacustrine systems were mainly developed in the Baza sub-basin, those of the Baza Formation. When transversal systems were more active, the main fluvial network was blocked and minor lacustrine systems formed in the Guadix sub-basin, known as Gorafe-Huélago and Solana formations, restricted to the Guadix sub-basin (Vera, 1970). The transversal systems from the north and south are known as the External transverse system and Internal transverse system, respectively (see Fig. 1b).

The paleontological sites considered in this study, in general terms belong to the lacustrine–palustrine systems of the basins, but with some variations and specific details. Ten of these sites are located in the Galera-Orce-Fuente nueva area. This area in the northeast part of the basin displays three different members in the Baza Formation (Vera et al., 1985; Oms et al., 2000a,b, 2011): Lower calcareous, Middle red detrital, and Upper calcareous (or silty calcareous) member. The Middle member contains the sites of Alquería, Galera H and Galera 2, which are found in dark mudstones intercalated in a succession of pale colours clastics and some carbonates. The upper member contains the sites of Barranco León D (conglomerate level), Fuente Nueva 3 (both mudstones and sandstones), Venta Micena (limestones) and Orce 2, 3, and 7 (dark mudstones).

Huéscar and Puerto Lobo sites are found in the northwestern most edge of the basin and are mainly found in a succession of mudstones, sandstones, conglomerates, and limestones. Similarly, Cúllar Baza 1 and Cúllar C are found in mudstones of the western edge of the basin. The Zújar 14 site (Oms et al., 1999) and Solana del Zamborino (Martín-Penela, 1988) are the only representatives in the Guadix sub-basin, and belong to lacustrine palustrine intervals found among the reddish sedimentary successions of the Guadix Formation.

As a result, a complete Early to Middle Pleistocene succession of vertebrate sites has been sampled over the last 30 years, with more than 60 fossiliferous levels. This succession includes the first evidence of hominin presence in Western Europe (Toro et al., 2013). Independent dating of this biostratigraphic record has been possible throughout the use of different methodologies (cyclostratigraphy, magnetostratigraphy, Electron Spin Resonance). With its paleontological richness and stratigraphic continuity, the succession in the Guadix-Baza Basin represents a unique case in Western Europe and a reference for correlation with other areas.

2. Biozonation of the Early to Middle Pleistocene

2.1. *Kislangia gusii zone (Earliest Pleistocene)*

2.1.1. *Definition*

Interval zone covering the biostratigraphic range of the species *Kislangia gusii* (Arvicolidae, Rodentia). The lower boundary of this zone is defined by the First Occurrence Datum (FO) of this species while the upper boundary is defined by the FO of *Mimomys* cf. *reidi*.

2.1.2. *Chronostratigraphy*

In the Guadix-Baza Basin, the presence of *K. gusii* has been recognized in two long sections, Galera and Zújar (Garcés et al., 1997; Oms et al., 1999). In the Galera section it is present at the site of Galera 2, while in Zújar it is present at the localitity of Zújar 14. Galera 2 is placed about the middle part of the lower Matuyama chron (Agustí et al., 1997), while Zújar 14 is placed towards the basal part of this chron, at the base of the cycle 17 from this latter section (Agustí et al., 2001). The top of this cycle has been correlated with the Eccentricity Maxima cycle at 2.2 Ma. Since typical Gauss levels both at Galera and Zújar present a more archaic representative of *Kislangia* (*K. ischus*; Agustí et al., 2001; Agustí and Oms, 2001) we assume that the lower boundary of the *K. gusii* Zone is close to the Gauss-Matuyama boundary at around 2.6 Ma.

2.1.3. *Associated fauna*

Elements commonly associated with *K. gusii* are the arvicolid *Mimomys medasensis* and the murids *Castillomys rivas* and *Stephanomys progressus*. At the level of Galera 2, the insectivores are represented by the desmanine *Desmana inflata* and the soricids *Myosorex meini* and *Sorex minutus*. Among the large mammals, at Zújar 14 *K. gusii* is associated with teeth remains of *Mammuthus meridionalis*, a datum which is consistent with a post-Gauss age for this biozone. The common association of *K. gusii* and *M. medasensis* suggests that this biozone can be equivalent with the *M. medasensis* biozone proposed by Minwer-Barakat et al. (2012b) in his Late Miocene–earliest Pleistocene biozonation. However, given the scarce representation of the species *M. medasensis* in the basin, we prefer to use the more abundant *K. gusii* as a marker for the earliest Pleistocene.

2.1.4. *Correlation with other sites*

Kislangia gusii was originally defined at the karst site of Almenara-Casablanca 1 (Castellón, Eastern Spain; Agustí et al., 1993a,b). The *K. capettai*–*K. gusii* group is an endemic lineage covering Spain and Southern France, which makes it difficult the correlation with other earliest Pleistocene sites of Europe (such as the Tegelen succession in the Netherlands). However, the association of *K. gusii* with *Mimomys tornensis* suggests the correlation of this zone with the *Mimomys pliocaenicus* Zone from Central and Northern Europe, in which *M. tornensis* is also present.

2.2. *Mimomys cf. reidi zone (Earliest Pleistocene)*

2.2.1. *Definition*

Interval zone covering the biostratigraphic range of the species *M.* cf. *reidi* (Arvicolidae, Rodentia). The lower boundary of this zone is defined by the FO of this species while the upper boundary is defined by the FO of *Mimomys (Tcharinomys) oswaldoreigi*. This biozone is equivalent to the *M.* cf. *reidi* Zone of Oms et al., 2000a,b and Gibert et al. (2007), as shown in Fig. 3.

2.2.2. *Chronostratigraphy*

In the Guadix-Baza Basin, the presence of *M.* cf. *reidi* has been recognized in the section of Galera, at the sites of Galera H and Alquería (Baza Formation), as well as at the site of Huélago-carretera (Gorafe-Huélago Formation; Sesé, 1989). The site of Galera H is placed immediately below a normal event which was correlated with the Olduvai subchron by Garcés et al. (1997). However, doubts have risen about the identification of this chron in the Galera section (Gibert et al., 2006, 2007). The Olduvai subchron has been clearly identified at the top of the Zújar section, although unfortunately it is not associated with a fossiliferous level. In any case, what is clear is that both Galera H and Alquería are placed at the top of the Galera section, and certainly below the Olduvai chron. We can assume, therefore, that the range of the *M.* cf. *reidi* Zone includes the upper part of the lower Matuyama chron, between 2.2 Ma (inferred upper boundary of the *K. gusii* Zone) and 1.8 Ma (upper boundary of the Olduvai geomagnetic chron).

2.2.3. *Associated fauna*

A common element associated with *M.* cf. *reidi* is again the murid *C. rivas*. The murid *S. progressus* is still present but much

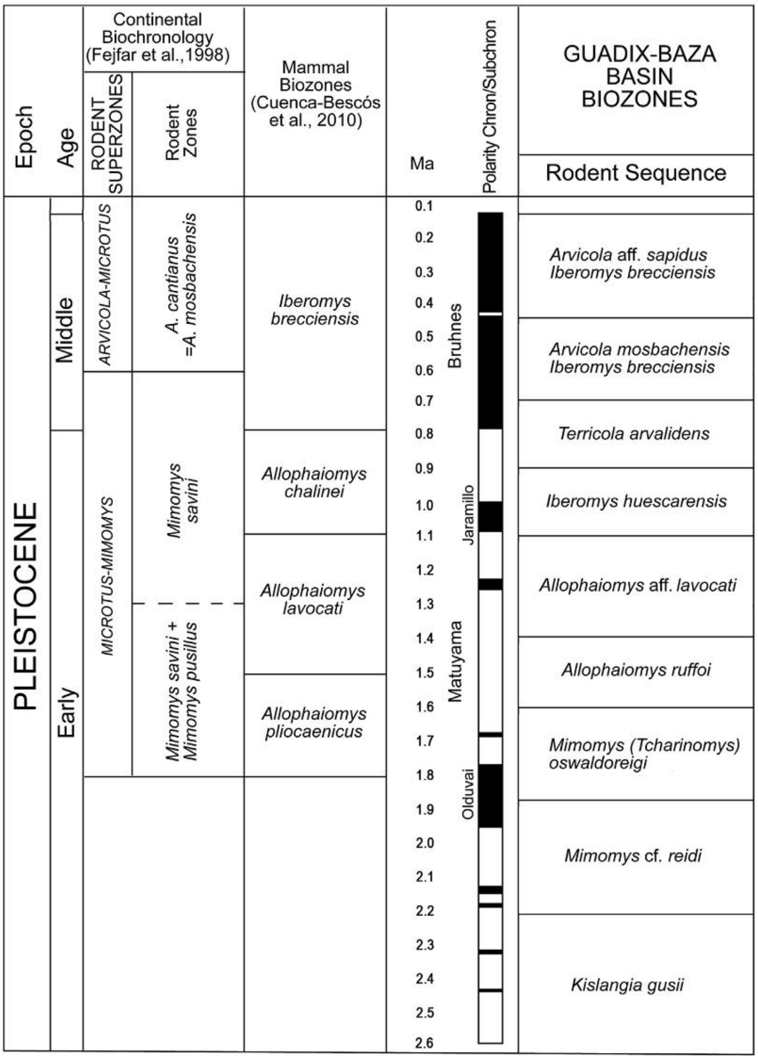


Fig. 2. Succession of rodent biozones in the Early to Middle Pleistocene of the Guadix-Baza Basin, and correlation with the biochronologies proposed by Fejfar et al. (1998) and Cuenca-Bescós et al., 2010, and the geomagnetic polarity time-scale.

rarer. The arvicolid *M. medasensis* is definitively absent from the levels with *M.* cf. *reidi*. At this level, *M. meini* and *D. inflata* are no longer present. At the site of Huélago-carretera, *M.* cf. *reidi* is associated with a typical MN 17, villafranchian fauna, including *M. meridionalis*, *Equus stenonis livenzovensis*, *Stephanorhinus etruscus*, *Gazella borbonica*, *Gazellospira torticornis*, *Leptobos* cf. *elatus* and others (Alberdi and Bonadonna, 1989).

2.2.4. Correlation with other sites

Outside the Guadix-Baza Basin, a form close to *M.* cf. *reidi* was defined as the new species *Mimomys realensis* in the site of Cañada Real (Júcar Basin; Esteban and Martínez-Salanova, 1987). Outside Spain, a species quoted as *M.* cf. *reidi* has been recognized in the earliest Pleistocene of Schambach (Bavaria, Germany; Koegniswald, 1977) and Stranzendorf G (Austria, Rabeder, 1981). However, as in the case of *M. realensis*, the Spanish species looks larger and more hypsodont than the original sample of *M. reidi*.

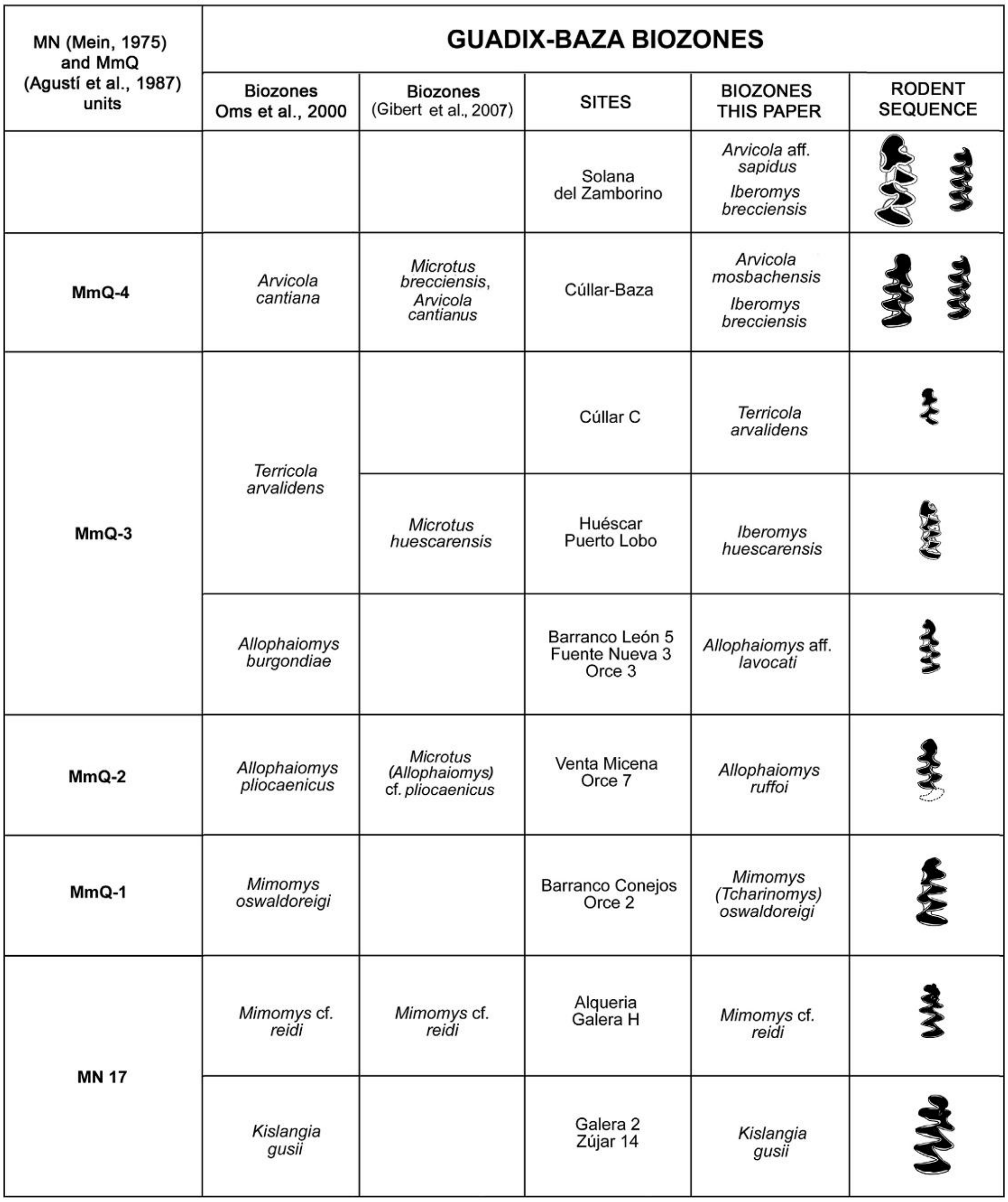
2.3. Mimomys (Tcharinomys) oswaldoreigi zone (Early Pleistocene)

2.3.1. Definition

Interval zone covering the biostratigraphic range of the species *M. (Tcharinomys) oswaldoreigi* (Arvicolidae, Rodentia). The lower boundary of this zone is defined by the FO of this species while the upper boundary is defined by the FO of *Allophaiomys ruffoi*.

2.3.2. Chronostratigraphy

In the Guadix-Baza Basin the arvicoline *M. (Tcharinomys) oswaldoreigi* has been recovered from a number of levels: Barranco de los Conejos, Fuentecica 5, Orce 2 (Agustí et al., 1987a, 2013). The



MN (Mein, 1975) and MmQ (Agustí et al., 1987) units	**GUADIX-BAZA BIOZONES**				
	Biozones Oms et al., 2000	**Biozones (Gibert et al., 2007)**	**SITES**	**BIOZONES THIS PAPER**	**RODENT SEQUENCE**
			Solana del Zamborino	*Arvicola* aff. *sapidus* *Iberomys brecciensis*	
MmQ-4	*Arvicola cantiana*	*Microtus brecciensis*, *Arvicola cantianus*	Cúllar-Baza	*Arvicola mosbachensis* *Iberomys brecciensis*	
MmQ-3	*Terricola arvalidens*		Cúllar C	*Terricola arvalidens*	
		Microtus huescarensis	Huéscar Puerto Lobo	*Iberomys huescarensis*	
	Allophaiomys burgondiae		Barranco León 5 Fuente Nueva 3 Orce 3	*Allophaiomys* aff. *lavocati*	
MmQ-2	*Allophaiomys pliocaenicus*	*Microtus (Allophaiomys)* cf. *pliocaenicus*	Venta Micena Orce 7	*Allophaiomys ruffoi*	
MmQ-1	*Mimomys oswaldoreigi*		Barranco Conejos Orce 2	*Mimomys (Tcharinomys) oswaldoreigi*	
MN 17	*Mimomys* cf. *reidi*	*Mimomys* cf. *reidi*	Alqueria Galera H	*Mimomys* cf. *reidi*	
	Kislangia gusii		Galera 2 Zújar 14	*Kislangia gusii*	

Fig. 3. Correlation between the biozones proposed in this paper and those proposed by Oms et al., 2000a,b, Gibert et al. (2007) and MN and MmQ biozones (Mein, 1975; Agustí et al., 1987b).

section of Barranco de los Conejos is placed in a reverse interval which has been correlated with the upper part of the Matuyama chron, above the Olduvai subchron (Agustí et al., 2013). Moreover, the site of Venta Micena, included in the subsequent biozone with *A. ruffoi* has been dated to ca 1.4 Ma (Duval et al., 2011) but its range could be expanded to 1.6 Ma, given the magnitude of the associated age error. Therefore, the range of the *M. (Tcharinomys) oswaldoreigi* Zone can be established between ca 1.8 Ma (base upper Matuyama chron) and ca 1.6 Ma.

2.3.3. *Associated fauna*

At Barranco de los Conejos and Orce 2, *M. (Tcharinomys) oswaldoreigi* is associated with *Tibericola vandermeuleni*, the first arvicoline with evergrowing molars entering the basin (originally described as *Allophaiomys vandermeuleni*; Agustí, 1992). The oldest record of *Tibericola* comes from the Early Pleistocene site of Degirmendere in Turkey (*T. sakaryaensis*; Unay et al., 2001). It has been also noted at the site of Ubeidiya, in Israel (*T. jordanica*, originally first referred to *Arvicola jordanica*; Haas, 1966). The species from Barranco de los Conejos and Orce 2 presents intermediate characters between the Turkish and Levant species, suggesting an intermediate age. It is clearly an eastern immigrant which predates the first occurrence of *Allophaiomys* in the Guadix-Baza Basin. At Barranco de los Conejos, a third arvicoline species, again with evergrowing molars, is present (*Mimomys* sp., probably related with *Mimomys malezi*). Regarding the associated murids, *C. rivas* is again present, while *S. progressus* is already absent. The insectivores are represented by the desmanine *Galemys kormosi* (or a similar form), and one undetermined species of the red-toothed shrew *Sorex* (Martín-Suárez, 1988; Furió, 2007). In Barranco de los Conejos, a second species of shrew, *S. minutus*, is present as well. Among the large mammals, *M. (Tcharinomys) oswaldoreigi* and *T. vandermeuleni* are associated with *G. torticornis* and *Leptobos etruscus* at the level of Orce 2 (Agustí et al., 1987a). Moreover, Barranco de los Conejos records the FO of the ovibovine *Praeovibos* in the basin (Agustí et al., 2013).

2.3.4. Correlation with other sites

M. (Tcharinomys) oswaldoreigi was originally defined from the Early Pleistocene site of Gilena 2 (*M. oswaldoreigi* n. sp.; Agustí et al., 1993a,b). It has been also quoted at the sites of Huétor Tajar 1 and 8, and Tojaire 1 (Granada Basin, García-Alix et al., 2009). This species has never been identified outside Spain, where apparently coeval sites still retain small rooted arvicolids of the species *Mimomys pusillus* (Fejfar et al., 1998).

2.4. *Allophaiomys ruffoi* zone (Early Pleistocene)

2.4.1. Definition

Interval zone covering the biostratigraphic range of the species *A. ruffoi* (Arvicolidae, Rodentia). The lower boundary of this zone is defined by the FO of this species while the upper boundary is defined by the FO of *Allophaiomys* aff. *lavocati*. This Zone is equivalent to the *Allophaiomys pliocaenicus* Zone of Oms et al., 2000a,b and the *Microtus (Allophaiomys)* cf. *pliocaenicus* Zone of Gibert et al. (2007), as shown in Fig. 3.

2.4.2. Chronostratigraphy

A. ruffoi is the only arvicolid at Venta Micena, a paleontological site which has reversed geomagnetic polarity. Combinaed US-ESR dating of fossil teeth provided a mean age of 1.4 Ma (Duval et al., 2011). As levels with the subsequent *Allophaiomys* species, *A.* aff. *lavocati*, have been dated by OSR at 1.4–1.2 Ma (Duval et al., 2012; Toro et al., 2013), the upper range of this zone can be established around 1.4 Ma, while its lower boundary most probably can be established at an earlier age, ca. 1.6 Ma Fig. 2.

2.4.3. Associated fauna

Allophaiomys ruffoi is associated with *C. rivas* and *Apodemus* aff. *mystacinus* at the site of Venta Micena. Only two species of insectivores, *Galemys* sp. and *Asoriculus gibberodon*, have been reported from the localities included in this zone (Martín-Suárez, 1988). In this site, a very abundant large mammal assemblage includes *Homotherium latidens*, *Megantereon whitei*, *Panthera* cf. *gombaszoegensis*, *Pachycrocuta brevirostris*, *Lycaon lycaonoides*, *Canis mosbachensis*, *Vulpes praeglacialis*, *Ursus etruscus*, *Meles* sp., *M. meridionalis*, *Stephanorhinus* aff. *hundsheimensis*, *Equus altidens*, *Hippopotamus antiquus*, *Bison* sp., *Hemibos* aff. *gracilis*, *Hemitragus albus*, *Praeovibos* sp., *Soergelia minor*, *Praemegaceros* cf. *verticornis* and *Metacervocerus rhenanus* (Palmqvist et al., 2008).

2.4.4. Correlation with other sites

Allophaiomys ruffoi from the Guadix-Baza Basin was originally assigned to the Biharian species *A. pliocaenicus* (Agustí et al., 1987a, 1987b). However, at that time some differences with the original type sample of *A. pliocaenicus* from Betfia were already evident, including a larger size and less derived enamel differentiation (still with negative enamel differentiation). In contrast, direct observation of the sample assigned to *A. ruffoi* from Pirro Nord by De Giuli et al. (1987) showed a remarkable coincidence in size and morphology with the species from Venta Micena, therefore enabling the recognition of this species in the Guadix-Baza Basin (pictures are available on supplementary information).

2.5. *Allophaiomys aff. lavocati* zone (Late early Pleistocene, pre-Jaramillo)

2.5.1. Definition

Interval zone covering the biostratigraphic range of the species *A.* aff. *lavocati* (Arvicolidae, Rodentia). The lower boundary of this zone is defined by the FO of this species while the upper boundary is defined by the FO of *Iberomys huescarensis*.

2.5.2. Chronostratigraphy

In the Guadix-Baza Basin, *A.* aff. *lavocati* is present at the sites of Orce 3, Barranco León D and Fuente Nueva 3. The last two sites are placed in a reversed geomagnetic interval identified as the upper Matuyama chron (Oms et al., 2000a,b). Duval et al. (2012) and Toro et al. (2013) proposed an age close to 1.4–1.2 Ma for these sites. Levels with *A. lavocati* have been also identified at the Torrent de Vallparadís section, directly below the Jaramillo subchron (Minwer-Barakat et al., 2011). Therefore, an approximate range for the *A.* aff. *lavocati* Zone is between 1.4 Ma and 1.07 Ma (lower boundary of the geomagnetic subchron Jaramillo).

2.5.3. Associated fauna

At the sites of Fuente Nueva 3 and Barranco León D *A.* aff. *lavocati* is associated with the arvicoline *Mimomys savini* and an archaic representative of the genus *Allophaiomys* (*Allophaiomys* sp.). This zone records the FO of *M. savini* in the basin. Moreover, the murid *C. rivas* is still present. Within insectivores, a gracile species of the genus *Galemys*, and the shrews *C. kornfeldi* and *A. gibberodon* are always present. Moreover, the insectivore assemblage in Barranco León D and Fuente Nueva 3 is completed with *Sorex* sp., *S. minutus* and *Erinaceus* cf. *praeglacialis* (Furió, 2007). This is the FO of *Crocidura* in the basin. At Barranco León D and Fuente Nueva 3 they are associated with an abundant large mammal assemblage which includes *Homo* sp., *P. brevirostris*, *L. lycaonoides*, *C. mosbachensis*, *Vulpes* cf. *praeglacialis*, *Ursus etruscus*, *Meles* sp., *M. meridionalis*, *S. hundsheimensis*, *Equus altidens*, *Equus sussenbornensis*, *H. antiquus*, *Bison* sp., *Ammotragus europaeus*, *Hemitragus* aff. *albus*, *P.* cf. *verticornis* and *M. rhenanus* (Toro et al., 2013). Hominin presence is also attested by very abundant lithic tools of Mode 1 (Toro et al., 2013).

2.5.4. Correlation with other sites

A. lavocati was originally described from the site of Sima del Elefante (Atapuerca karst complex; Laplana and Cuenca-Bescós, 2000). Before the description of this new species, the sample from the Guadix-Baza Basin was assigned to *Allophaiomys* aff. *burgondiae* (Martínez-Navarro et al., 1997; Agustí et al., 1999), a species which is present at the French site of Les Valerots (Laplana et al., 2000) and the Italian site of Monte Peglia B (Meulen, 1973).

2.6. *Iberomys huescarensis* zone (Late Early Pleistocene, Jaramillo to uppermost Matuyama)

2.6.1. Definition

Interval zone covering the biostratigraphic range of the species *I. huescarensis* (Arvicolidae, Rodentia) until the entry of *Terricola* *arvalidens*. The lower boundary of this zone is defined by the FO of this species while the upper boundary is defined by the FO of *T. arvalidens*. This Zone is equivalent to the *Microtus huescarensis* Zone of Gibert et al. (2007), as shown in Fig. 3.

2.6.2. Chronostratigraphy

Iberomys huescarensis is present in a number of sections around the town of Huéscar: Huéscar 1 (Mazo et al., 1985), Loma Quemada, Puerto Lobo (Agustí, 1986; Agustí and Moyà-Solà, 1991). We do not have direct estimates for the time range of this biozone in the Guadix-Baza Basin, as the paleomagnetic analysis applied to those sections has proven to be inadequate. However, at the Torrent de Vallparadís section (Terrasa, NE Spain), levels with *I. huescarensis* are found from EVT-12 unit (Normal polarity, Jaramillo age) to EVT-7 (dated by ESR to about 0.8 Ma). Consequently, the time interval covered by this biozone is roughly from 1.07 Ma to 0.8 Ma.

2.6.3. Associated fauna

Iberomys huescarensis is associated with a large *M. savini*, while *C. rivas* is still present. A significant datum is the FO of the hamster *Allocricetus bursae*. The presence of *Galemys* (probably the extant species *G. pyrenaicus* or a closely related form) is the most remarkable fact regarding insectivores. Moreover, an abundant large mammal assemblage is present at the site of Huéscar 1, including *Canis etruscus*, *Panthera gombaszoegensis*, *Homotherium* sp., *Elephas antiquus*, *E. altidens*, *E. sussenbornensis*, *H. antiquus* and others (Alberdi and Bonadonna, 1989). Moreover, human presence is attested by the existence of few lithic tools of Mode 1 (Martínez-Navarro et al., 2006).

2.6.4. Correlation with other sites

As mentioned, the association of *I. huescarensis* and *M. savini* is also present at the Torrent de Vallparadís section (Madurell-Malapeira et al., 2010; Minwer-Barakat et al., 2011). A similar association is found at the karst site of Almenara-Casablanca 3 (Eastern Spain, Agustí et al., 2011). Surprisingly, as a difference with the former sites, there is no record of the iberian vole *Allophaiomys chalinei* in the Guadix-Baza succession.

2.7. *Terricola arvalidens* zone (Latest Early Pleistocene)

2.7.1. Definition

Interval zone covering the biostratigraphic range of the species *T. arvalidens* (Arvicolidae, Rodentia) until the entry of *Iberomys brecciensis*. The lower boundary of this zone is defined by the FO of this species while the upper boundary is defined by the FO of *I. brecciensis*.

2.7.2. Chronostratigraphy

In the Guadix-Baza Basin *T. arvalidens* was only identified in the section of Cúllar-Baza at the level of Cu-C (Agustí et al., 1999). In this section, the level Cu-C is placed in a normal magnetized chron, identified as the base of Brunhes.

2.7.3. Associated fauna

There is no associated fauna with *T. arvalidens* in the Cúllar-Baza section. A few meters below the level of Cu-C, the level of Cu-B, which is placed in a reverse chron identified as upper Matuyama, records the LO of *C. rivas* (Agustí et al., 1999).

2.7.4. Correlation with other sites

T. arvalidens is present at El Chaparral (Cádiz, Southern Spain), a site which shows normal polarity, associated with *I. huescarensis* and *Allophaiomys chalinei* (López-García et al., 2012). In the Gran Dolina section from Atapuerca, *T. arvalidens* is placed at the top of the upper Matuyama chron and the base of Brunhes chron, associated with *M. savini* and *I. huescarensis* (levels TD 3 to TD 8; Cuenca-Bescós et al., 2010). It seems, therefore, that the range of this biozone covers the Matuyama–Brunhes boundary.

2.8. *Iberomys brecciensis–Arvicola mosbachensis* zone (Early middle Pleistocene)

2.8.1. Definition

Concurrent range zone characterized by the association of *I. brecciensis* and *A. mosbachensis* (Arvicolidae, Rodentia). The lower boundary of this zone is defined by the FO of these species while the upper boundary is defined by the FO of *Arvicola* aff. *Sapidus*. This Zone is equivalent to the *Arvicola cantiana* Zone of Oms et al., 2000a,b and the *Microtus brecciensis–Arvicola cantianus* Zone of Gibert et al. (2007), as shown in Fig. 3.

2.8.2. Chronostratigraphy

In the Guadix-Baza Basin, *I. brecciensis* and *A. mosbachensis* appear at the site of Cúllar-Baza 1. The Cúllar Section covers the Matuyama–Brunhes boundary, and in this section the site of Cúllar Baza 1 is placed at the base of the Brunhes chron (Gibert et al., 2007).

2.8.3. Associated fauna

The site of Cúllar-Baza 1 delivered a rich faunal association of small and large vertebrates. Among the small vertebrates, *I. brecciensis* and *A. mosbachensis* are associated with *Allocricetus bursae*. The large mammal association includes *C. etruscus*, *Crocuta crocuta*, *Mammuthus trogontherii*, *E. altidens*, *E. sussenbornensis*, *Sus* cf. *scropha*, *Dolichodoryceros savini*, among others (Ruiz-Bustos, 1976). Hominin activity at this site is attested by the presence of lithic tools of Mode 1 (Ruiz-Bustos and Michaux, 1976).

2.8.4. Correlation with other sites

In Spain, *A. mosbachensis* has been also found in the EVT-3 unit of the Torrent de Vallparadís section, associated with *T. arvalidens* (Madurell-Malapeira et al., 2010).

2.9. *Iberomys brecciensis–Arvicola aff. sapidus* zone (Middle Pleistocene)

2.9.1. Definition

Concurrent range zone characterized by the association of *I. brecciensis* and *A.* aff. *sapidus* (Arvicolidae, Rodentia). The lower boundary of this zone is defined by the FO of *A.* aff. *sapidus*. The upper boundary is established by the FO of *Iberomys dentatus*.

2.9.2. Chronostratigraphy

In the Guadix-Baza Basin *A.* aff. *sapidus* is present for the first time at the site of Solana de Zamborino. According to the biostratigraphic context, Solana de Zamborino should be placed in the Brunhes geomagnetic chron, above the site of Cúllar-Baza 1, but its position within this chron should be clarified in the future.

2.9.3. Associated fauna

At Solana de Zamborino, *I. brecciensis* and *A.* aff. *sapidus* are associated with a rich large mammal assemblage, which includes *Macaca sylvana*, *Canis* cf. *lupus*, *Panthera spelaea*, *Lynx* cf. *pardina*, *Felis silvestris*, *Palaeoloxodon antiquus*, *Equus caballus torralbae*, *Stephanorhinus hemitoechus*, *Bos primigenius*, *Bison priscus*, *Cervus elaphus*, *Capreolus capreolus*, *Sus scropha*, *Hippopotamus* sp., among others (Martín Penela, 1988). Moreover, human presence is attested by abundant lithic tools of Mode 2 (Acheulian).

2.9.4. Correlation with other sites

Association of *I. brecciensis* with *A.* aff. *sapidus* is also present in the levels TD 10-11 from Gran Dolina section and in the levels TGIII-TZ from Galeria section, both in the Atapuerca karst complex, dated to ca 0.3–0.4 Ma (Cuenca-Bescós et al., 2010).

3. Conclusions

The small mammal Pleistocene sequence of the Guadix-Baza Basin enabled the recognition of up to 9 biozones, basically based on the arvicolid succession. Seven of these biozones are placed in the Early Pleistocene (from 2.6 Ma to 0.8 Ma) while two belong to the middle Pleistocene. Mean duration of each biozone is about 0.25 My. More precise results can be obtained by the joint use of cyclostratigraphy, magnetostratigraphy and radiometric dating methods (ESR). The earliest Pleistocene biozones (*K. gusii*, *M. cf. reidi*, *M. (Tcharinomys) oswaldoreigi* biozones) are among the ones with longer durations (about 0.4 My). However, this datum can be biased by the lower level of resolution attained in this part of the sequence. The duration of the Early and late Early Pleistocene biozones *A. ruffoi* and *A.* aff. *lavocati* is considerably shorter, about 0.2 My in each case. The latest early Pleistocene biozones (*I. huescarensis*, *T. arvalidens*) record even shorter durations, about 0.1 My or less. Duration of the middle Pleistocene biozones cannot be established on the basis of the Guadix-Baza Basin record, due to the lack of numerical ages for this time range. However, mean duration could be roughly estimated between 0.3 and 0.4 My.

The biostratigraphic small mammal succession from Guadix-Baza displays a high number of endemic or local species (*K. gusii*, *M. (Tcharinomys) oswaldoreigi*, *I. huescarensis* and others), which makes it difficult its correlation with the Central and Eastern European record. In contrast, in the Guadix-Baza Basin it is noticeable a much more Mediterranean influence (*A. ruffoi*, *T. vandermeuleni*). The biozonation demonstrates a pattern of replacement more than one of continuity. With exceptions, each new taxon cannot be rooted in the previous biozone. This is the case, for instance, of *M.* cf. *reidi*, *Tcharinomys oswaldoreigi*, *A. ruffoi*, *M. savini*, *I. huescarensis* or *T. arvalidens*. However, some cases of “Lazarous taxa” can be identified. Therefore, *M.* cf. *reidi* appears as a feasible ancestor for the small sized *M. savini* from Fuente Nueva 3 and Barranco León D (but no *Mimomys* species is present in the *A. ruffoi* Zone). Similarly, *M. (Tcharinomys) oswaldoreigi* could be the ancestor population of the archaic *Allophaiomys* sp. present in the same levels (but there is no trace of such a species at the *A. ruffoi* Zone). The only possible cases of continuity can be in the case of *A.* aff. *lavocati* (which could root in *A. ruffoi*) and *I. brecciensis* (which most probably roots on *I. huescarensis*). Central or Eastern European influences are restricted to *M. cf. reidi* and *T. arvalidens*. However, some of the ancestors of the endemic taxa can be identified in the European record: *Allophaiomys nutiensis* in the case of *I. huescarensis*, *M. tornensis* or a related form in the case of *M. (Tcharinomys) oswaldoreigi*, *Allophaiomys deucalion* in the case of *A. ruffoi*.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quaint.2014.11.005.

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Chronological and environmental context of the first hominin dispersal into Western Europe: The case of Barranco León (Guadix-Baza Basin, SE Spain)

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Paleoclimate

ABSTRACT

The early Pleistocene site of Barranco León (Guadix-Baza Basin, SE Spain), dated to 1.4 Ma (millions of years ago), records the oldest hominin occurrence in Western Europe, as evidenced by the discovery of one tooth and thousands of Mode 1 stone tools. In this paper a detailed analysis of the microvertebrate content of the D1 and D2 units from this site is presented. The early Pleistocene in the Guadix-Baza Basin is characterized by a sharp climatic deterioration, which possibly impeded the settlement of this region by the early hominin population from the southern Caucasus. Shortly afterwards, when the climatic conditions were again favorable, a hominin presence is suddenly evidenced at the units D1 and D2 of Barranco León. According to the microvertebrate analysis of these units, the mean annual temperature at the time of deposition was significantly higher than 13 °C, with prevalent humid conditions. However, although most of the species were inhabitants of water edges, an open landscape was present in the vicinity of the lake. The data reported here clearly support the idea that the early hominin occupation of Europe was strongly constrained by climatic and environmental conditions, rather than by physiography or cultural factors.

Introduction

The early Pleistocene site of Barranco León (Guadix-Baza Basin, SE Spain) records the oldest hominin occurrence in Europe (Toro Moyano et al., 2013). This site has delivered a great number of stone tools of Mode 1 and one hominin tooth, associated with an abundant fauna of large and small vertebrates. Barranco León was first discovered in the summer of 1983, and originally reported as a purely paleontological site (Agustí et al., 1987a). Subsequent excavations in the nineties led to the discovery of a number of stone tools (Turq et al., 1996; Gibert et al., 1998). Re-excavation at the beginning of the twenty-first century considerably enlarged the stone tool assemblage (Toro Moyano et al., 2010) and led to the recovery of the hominin tooth (Toro Moyano et al., 2013).

The Guadix-Baza intramontane basin is located in the Betic Ranges (south of Iberian Peninsula; see Fig. 1a), in the contact area between the Mesozoic basement rocks (Internal Zones, to the South of the basin) and the cover Mesozoic rocks (External Zones, to the North). This basin was filled by marine deposits during part of the Miocene. The basin uplift that took place by 8 Ma (millions of years ago) (see Hüsing et al., 2010 and references therein) created a disconnection from the sea, and the basin became continental.

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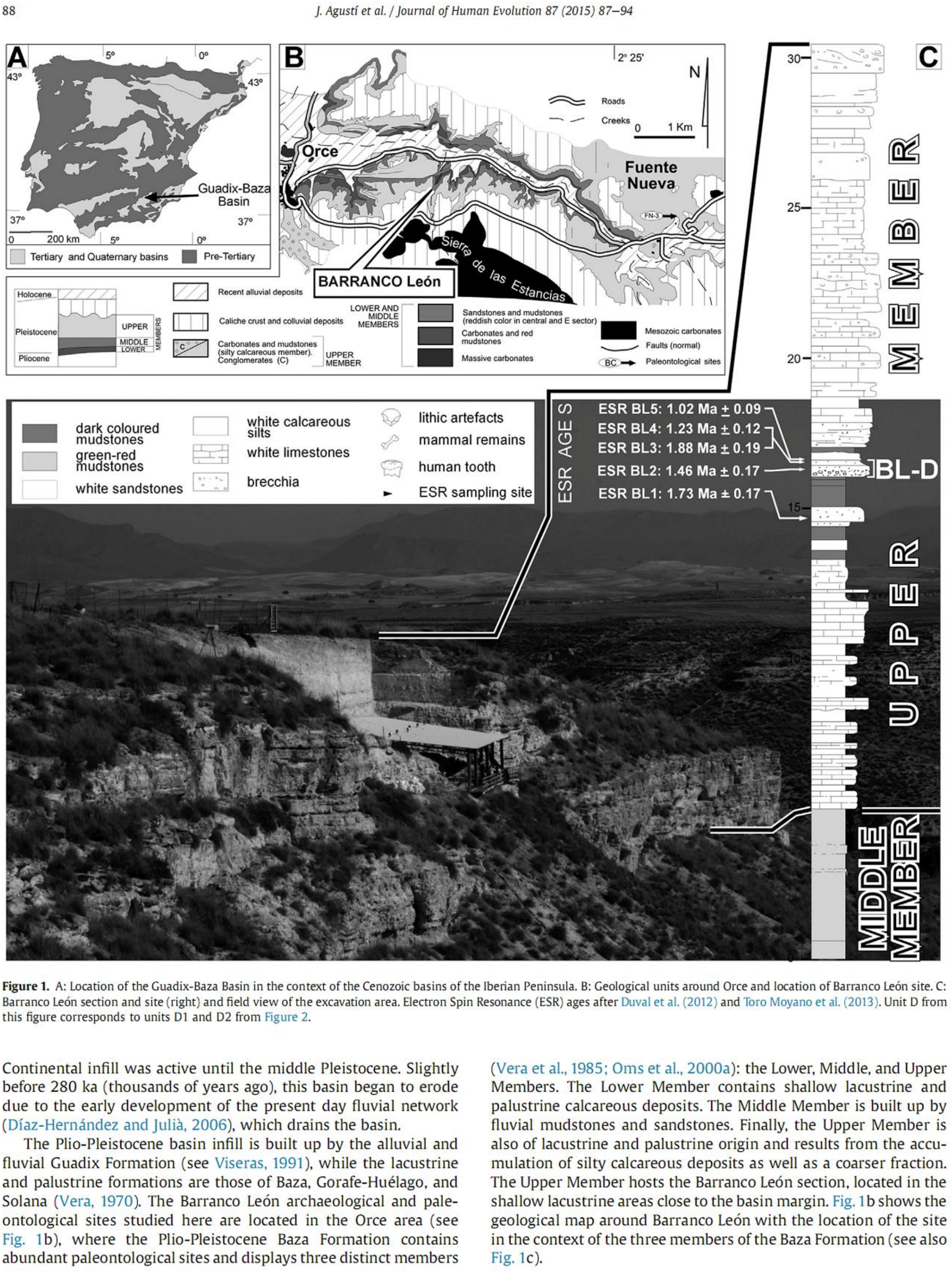

Figure 1. A: Location of the Guadix-Baza Basin in the context of the Cenozoic basins of the Iberian Peninsula. B: Geological units around Orce and location of Barranco León site. C: Barranco León section and site (right) and field view of the excavation area. Electron Spin Resonance (ESR) ages after Duval et al. (2012) and Toro Moyano et al. (2013). Unit D from this figure corresponds to units D1 and D2 from Figure 2.

Continental infill was active until the middle Pleistocene. Slightly before 280 ka (thousands of years ago), this basin began to erode due to the early development of the present day fluvial network (Díaz-Hernández and Julià, 2006), which drains the basin.

The Plio-Pleistocene basin infill is built up by the alluvial and fluvial Guadix Formation (see Viseras, 1991), while the lacustrine and palustrine formations are those of Baza, Gorafe-Huélago, and Solana (Vera, 1970). The Barranco León archaeological and paleontological sites studied here are located in the Orce area (see Fig. 1b), where the Plio-Pleistocene Baza Formation contains abundant paleontological sites and displays three distinct members (Vera et al., 1985; Oms et al., 2000a): the Lower, Middle, and Upper Members. The Lower Member contains shallow lacustrine and palustrine calcareous deposits. The Middle Member is built up by fluvial mudstones and sandstones. Finally, the Upper Member is also of lacustrine and palustrine origin and results from the accumulation of silty calcareous deposits as well as a coarser fraction. The Upper Member hosts the Barranco León section, located in the shallow lacustrine areas close to the basin margin. Fig. 1b shows the geological map around Barranco León with the location of the site in the context of the three members of the Baza Formation (see also Fig. 1c).

Geological setting

The Barranco León section is roughly 25 m thick and hosts the archaeo-paleontological site of Barranco León 5 (Turq et al., 1996; Oms et al., 2000a). This section includes limestones, lutites, sandstones, conglomerates, and brecchias. This succession of lithologies records the paleoenvironmental changes of the lake margin conditions from saline to freshwater (Anadón and Gabàs, 2009). Geochemical studies of this succession (Anadón and Gabàs, 2009) detected hydrochemical variations due to changes in water source, solute composition, and water level. Thus, three water types interacted in the area: (1) those of the main Baza lake, which underwent large precipitation and evaporation, (2) dilute, meteoric surface waters and shallow groundwaters, and (3) saline groundwaters of meteoric origin that became saline after the dissolution of previously formed evaporates. Four main hydrochemical stages have been recorded in the Barranco León section (Anadón and Gabàs, 2009). Stage 4 (around meter 15 to 30 in Fig. 1c) contains the two levels studied here (D1 and D2). This stage is characterized by type 2 waters, belonging to a through-flowing open lacustrine system, which in the studied area was fed by both groundwater and streams.

Detailed sedimentological data for the two units analyzed here, D1 and D2, can be found in Anadón and Julià (2010), and microstratigraphic data can be found in Rodriguez Rivas (2009). Nomenclature for these units is shown in Fig. 2b, including nomenclature proposed by Turq et al. (1996). Unit D1 is composed of gravels with a sandy matrix and has a thickness from 65 to 0 cm. The base of this unit (see Fig. 2a, b) partially or completely erodes the previous unit, unit C (composed of beige calcisiltite to calcarenite). When the latter unit is completely eroded, D1 is directly in contact with unit B (black and dark green quartz-feldspatic sands). Figure 2.3 shows unpublished profiles from excavations held in 2010 that clearly illustrate these features. The sedimentology and lateral variations of this level have been studied in detail by Anadón et al. (2003; see also Oms et al., 2011). The cobbles and the pebbles of the gravels were studied by Anadón and Julià (2010), who show that they are dominated by palustrine intrabasinal limestones with scarce Mesozoic limestones from the adjacent External Zones. Unit D1 formed due to a sudden high energy current that transported gravels, matrix, bones, and archaeological remains. This high energy event is unique in the whole sequence at Barranco León. Gravels are broadly fining upwards and may display small-scale cross bedding. The single event nature of the deposition is also supported by the lack of lateral accretion surfaces or erosive features indicating recurrence of the process. Slightly reworked or in situ invertebrate fauna indicates fresh to oligosaline shallow lacustrine conditions.

Unit D2 is composed of greyish quartz-bioclastic sands capped by whitish limestones. Thickness is around 20 cm. Anadón and Julià (2010) report the occurrence of remains of fish teeth, *Valvata*, *Bithynia* opercules, and *Melanoides tuberculata*, the latter being particularly abundant. These sands and their faunal content are very similar to the matrix of unit D1 and here appear to have been formed in situ. The upper part of D2 is a level of whitish chalky limestone with abundant ostracods, mollusks, and charophyte remains.

Material and methods

The small vertebrate fossil remains used for this study consist of disarticulated bone fragments collected by water-screening during the 2010–2013 excavation campaigns at the Barranco León site. All of the sediment was water-screened using superimposed 5.0 and 0.5 mm mesh screens and bagged by square, layer, and excavation level. In subsequent years, the microfossils were processed, sorted, and classed in broad categories at the Institut Catalá de Paleoecologia Humana i Evolucio Social in Tarragona (IPHES, Spain). The sample includes more than 300 recognizable remains, representing 20 different species, including four fishes, four amphibians, five squamate reptiles, three insectivores, and four rodents (Table 1). The number of individuals for a particular species was determined by counting diagnostic elements.

In order to reconstruct the environment of the site, we used the method of habitat weightings (see Blain et al., 2008, 2011), distributing each taxon in the habitat(s) where it is possible to find them or their morphologically similar modern relatives at present in the Iberian Peninsula. The habitats were divided into five types: dry open land, wet meadows, woodland and woodland-margin areas, areas surrounding water, and rocky areas.

Each species was given a maximum possible score of 1.00, which was broken down according to the habitat preference of that species, so that if an animal occurred in more than one habitat type, its score was proportional to its habitat preference. Scores for higher-level taxonomic categories (providing no representatives have opposite ecological requirements) were calculated by counting the individual species scores of all the species contained within categories. Family-level groups or groups containing species with opposite ecological distributions (such as lacertids) were disregarded.

Because Spanish Pleistocene amphibians and reptiles are considered specifically identical to modern populations, the current species habitat distribution may be used for the habitat weightings. The distribution data are from Pleguezuelos and Martínez-Rica (1997), Salvador (1997), Carrascal and Salvador (2002–2006), García-París et al. (2004), and Pleguezuelos et al. (2004). In contrast with fishes, amphibians, and squamate reptiles, insectivores and rodents are represented by species that went extinct during the Pleistocene. However, some climatic inferences can be drawn on the basis of their generic assignment. The habitat distribution of the species represented in Barranco León is shown in Table 1.

Results

Unit D1

The unit D1 has yielded about 300 recognizable remains, including fish, amphibians, reptiles, insectivores, and rodents. The rodent association is dominated by the arvicolid species *Mimomys savini*. A second microtine species, *Allophaiomys* aff. *lavocati*, is much rarer. Finally, murids are represented by the species *Castillomys rivas* and *Apodemus mystacinus*. As direct ancestor of the middle Pleistocene *Arvicola mosbachensis*, the first recognized species of the water-rat lineage, it is assumed that *M. savini* had aquatic affinites. In contrast, both *Allophaiomys* aff. *lavocati* and *C. rivas* possibly indicate an open landscape. *Castillomys rivas* is an extinct rodent that is interpreted as a eurytopic species, i.e., it does not provide information about specific ecological conditions (Minwer-Barakat, 2005). Nevertheless, the development of wall-shaped ridges connecting the cusps of the crowns of the upper molars and a longitudinal ridge in the lower molars suggests a diet based on grains, so open meadows should be expected as a preferred habitat (Montoya et al., 1999). In addition to *C. rivas*, a second murid species, *A. mystacinus*, is present. Today, *A. mystacinus* and *Apodemus epimelas* (recorded as *A. mystacinus*) are found in areas with a relatively warm climate in the Balkan Peninsula and the Middle East. They are associated with dry forest and shrubland in rocky areas. Their presence can be related to the presence of rocky environments in the vicinity of the site (Agustí,

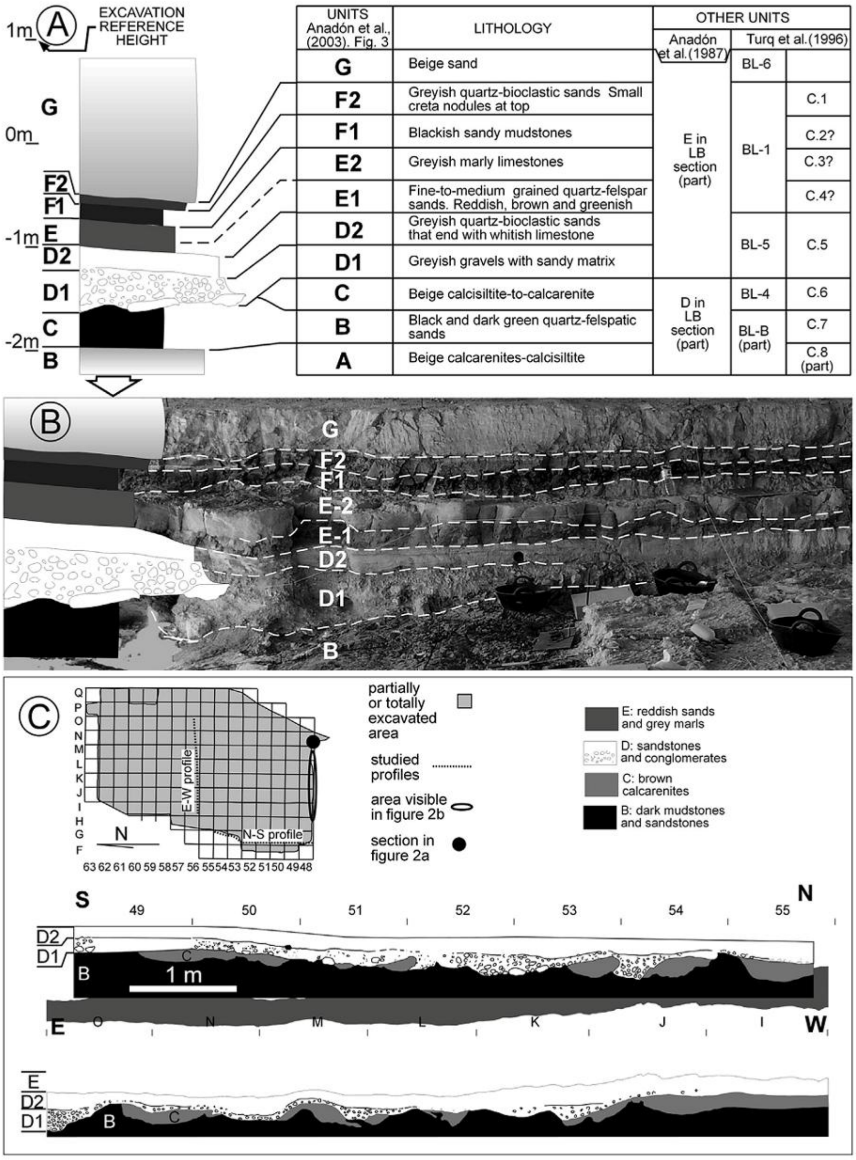

Figure 2. A: Barranco León section with the units by Anadón et al. (2003). Nomenclature by Turq et al. (1996) are also included. B: Section and view of the excavation profile (see below). C: Location of the section in Figure 2B and of the two sections at the bottom. Picture and sections from 2010 excavation.

1982; Mitchell-Jones et al., 1999; Storch, 2004; Minwer-Barakat, 2005). An equal proportion of the two murid species may indicate an ecological equilibrium between shrubland in rocky areas and open meadows.

Insectivores are represented by *Galemys* sp. and *Sorex minutus*. *Galemys* sp., the water mole, is an aquatic species, while the species of *Sorex* are usually associated with rather moist environments with abundant vegetation cover.

In addition to this small mammal association, unit D1 yielded the following amphibians and squamate reptiles species: *Discoglossus* sp., *Pelobates cultripes*, *Pelophylax* cf. *perezi*, cf. *Dopasia* sp., *Natrix maura*, *Coronella* cf. *girondica*, and *Rhinechis scalaris*. Taxa requiring presence of permanent aquatic environments (*Discoglossus*, *Pelophylax*, and *N. maura*) are well represented. Open environments are also represented with taxa of arid and stony areas like *P. cultripes* and *Rhinechis*. The genus *Dopasia* and *P. cultripes* may indicate the existence of warm wet Mediterranean woodland areas with soft soil. The presence of *Rh. scalaris* together with *C.* cf. *girondica* suggests warm climatic conditions.

Unit D1 has also yielded remains of three Cyprinid species, *Luciobarbus* aff. *sclateri*, *Squalius* aff. *cephalus*, and *Squalius* aff. *pyrenaicus*. *Luciobarbus sclateri* is a benthic species that has limnophilous habits. It usually occupies different sections of the river in the same range but usually disappears in cold and fast waters. In general, it is a typical inhabitant of the middle course of rivers, preferring rapid current and clear waters with rocky or gravelly

Table 1
Terrestrial small-vertebrates from the early Pleistocene of Barranco León in minimum number of individuals (MNI), with the distribution of each taxon in their potential habitats.

	Level D2		Level D1		TOTAL		Ecological requirements				
	MNI	%	MNI	%	MNI	%	Open dry	Open humid	Woodland	Rocky	Water edge
Amphibians											
Discoglossus sp.	4	20.0%	13	20.6%	17	20.5%					1
Pelobates cultripes			1	1.6%	1	1.2%	0.50			0.50	
cf. *Bufo* sp.	1	5.0%			1	1.2%					
Pelophylax cf. *perezi*	1	5.0%	14	22.2%	15	18.1%					1
Squamates											
cf. *Dopasia* sp.			1	1.6%	1	1.2%		0.25	0.75		
Natrix maura	1	5.0%	2	3.2%	3	3.6%					1
Coronella cf. *girondica*			1	1.6%	1	1.2%	0.25	0.25	0.25	0.25	
Rhinechis scalaris	1	5.0%	1	1.6%	2	2.4%		0.40	0.45	0.15	
Colubrinae indet.	1	5.0%			1	1.2%					
Insectivores											
Galemys sp.	1	5.0%	1	1.6%	2	2.4%					1
Sorex minutus	1	5.0%	1	1.6%	2	2.4%		0.50	0.50		
Erinaceus sp.	1	5.0%			1	1.2%	0.50	0.25	0.25		
Rodents											
Apodemus gr. *mystacinus-epimelas*			1	1.6%	1	1.2%			0.50	0.50	
Castillomys rivas	1	5.0%	1	1.6%	2	2.4%	0.50	0.50			
Mimomys savini	6	30.0%	19	30.2%	25	30.1%					1
Allophaiomys aff. *lavocati*	1	5.0%	7	11.1%	8	9.6%					
Total	20	100.0%	63	100.0%	83	100.0%					

beds, especially during the breeding season. *Luciobarbus sclateri* can also be found in lakes and lagoons, including coastlines and standing water such as springs and ponds. It tolerates water with some organic contamination, with a wide range of thermal tolerance and oxygenation (Granado Lorencio, 2001). This species is endemic of the Iberian Peninsula, being present in most Spanish central and southern river basins as well as in Portugal. *Squalius cephalus* is an inhabitant of the water column and prefers clear waters and areas of pools and tables. Nowadays, this species lives in northern Spain, in Catalonia, Aragon, and Basque Country (Doadrio, 2002). *Squalius pyrenaicus* is a ubiquitous species that is able to survive in several environments. Although a generalist species, it usually prefers quiet and clean waters. It tolerates large temperature and dissolved oxygen differences (Doadrio and Casado, 1989). Currently, this species is found in the central and southern Iberian Peninsula, especially in the basins of the Tajo, Guadiana, Guadalquivir, Segura, Júcar rivers, and the Albufera of Valencia (Doadrio, 2002).

Unit D2

Unit D2 has delivered more than 50 recognizable remains of small vertebrates, including fishes, amphibians, reptiles, insectivores, and rodents. Rodents form the most abundant group of small mammals, and again the water-rat *M. savini* is the most abundant species. The microtine *Allophaiomys* aff. *lavocati* is scarcely represented, while murids are less diversified than in unit D1, represented only by *C. rivas*.

The insectivore association includes *Galemys* sp., *S. minutus*, and *Erinaceus* sp. The hedgehog *Erinaceus* is generally indicative of rather dry conditions, or at least some species of this genus nowadays are adapted to environments in which water, rainfall, and/or vegetation cover are not abundant.

Among the herpetofauna, this unit has yielded fossil remains of *Discoglossus* sp., cf. *Bufo* sp., *Pelophylax* cf. *perezi*, *N. maura*, *Rh. scalaris*, and one indeterminate colubrine snake. With the exception of *Bufo* and *Rhinechis*, all of the taxa document the presence of sunny aquatic environments and their neighborhoods. The presence of the thermophilous snake *Rh. scalaris* suggests relatively warm climatic conditions with a mean annual temperature higher than 13 °C (Llorente et al., 1995).

This unit has also yielded the remains of Cyprinid fishes *Luciobarbus* aff. *bocagei* and *Squalius* aff. *pyrenaicus*. *Luciobarbus bocagei* tends to occupy regional sections of the river with less steep, farthest from the source and with large-sized basins. Adults occupy areas with lower rainfall and lower runoff and are also locally found in wider and deeper rivers (Salvador, 2012). *Luciobarbus bocagei* is endemic to the Iberian Peninsula and is currently present in central and western basins such as the Tajo, Duero, and Limia.

Chronological context

The first indications of the age of the Barranco León section were provided by Oms et al. (2000b), who showed that the whole section had a reverse geomagnetic polarity. A combination of magnetostratigraphy and biostratigraphy indicates that Barranco León fits within the upper Matuyama chron, between the Olduvai and Jaramillo subchrons. Further refinements in the dating of the archaeological and paleontological levels of Barranco León were proposed by Duval et al. (2012) and Toro Moyano et al. (2013). Application of ESR dating to *Equus* teeth and quartz grains provided an overall age around 1.4 Ma (Duval et al., 2012).

Regarding the biochronology of the sites, the most valuable elements are the arvicolids *M. savini* and *Allophaiomys* aff. *lavocati*. *Mimomys savini*, the most abundant small mammal in all the levels of Barranco León, is characterized by its large size and rooted molars in adults. The molars are longer than those of several primitive populations of *M. savini* such as at Betfia 2 and Nogaisk (Maul, 2001), whose average length values are less than 3 mm. The mean length of the measured molars from units D1 and D2 of Barranco León are quite similar to the mean value from Monte Peglia (3.30 mm; Meulen, 1973). In turn, the samples from D1 and D2 show lower values than those of *M. savini* from the Gran Dolina section in Atapuerca (Spain). This is the case for Trinchera Dolina level (TD) 4 (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; Lozano-Fernández et al., 2013a, b).

The teeth of *Allophaiomys* aff. *lavocati* from Barranco León are clearly more derived than those of archaic populations of this genus, such as *Allophaiomys pliocaenicus* from Betfia 2 and Brielle (Meulen and Zagwijn, 1974) and *Allophaiomys ruffoi* from the Guadix-Baza Basin (Agustí et al., 1987b; Agustí, 1992), with less confluent triangles T4 and T5 and clearly distinct triangle T7 and lingual re-entrant angle LRA5 (sensu Meulen, 1973). The studied specimens are smaller than those of *A. burgondiae* from Monte Peglia (Meulen, 1973) and Valerots (Laplana et al., 2000).

The measurements of the small number of specimens of *Allophaiomys* from Barranco León fit the size ranges of the population of *Allophaiomys lavocati* from the Lower Red Unit of the Sima del Elefante (Laplana and Cuenca-Bescós, 2000). The average tooth length, width, and anteroconid complex length of *Allophaiomys* aff. *lavocati* from Barranco León are also very close to those of *A. lavocati* from Sima del Elefante. The sample from Barranco León, however, differs in its anterior lobe, which is not as narrow as in *A. lavocati* from this site. Therefore, the evidence provided by the shape and size of the molars from *M. savini* and *Allophaiomys* aff. *lavocati* points to the fact that the units of Barranco León are older than those of the base of Sima del Elefante in Atapuerca. Since these last levels have been dated to 1.22 ± 0.16 Ma (Carbonell et al., 2008), this result is consistent with the numerical age of 1.4 Ma provided by ESR (Duval et al., 2012).

Environmental context

Today, the Guadix-Baza Basin is a quasi desert plateau located at an altitude of 1000 m above sea level with an extremely arid continental climate, though with Mediterranean characteristics. The mean annual temperature ranges between 11 °C and 15 °C, but with extreme seasonality (harsh winters and very warm summers) and mean annual precipitation ranges from between 300 and 400 mm, mainly occurring in March, April, and September with very irregular, torrential pattern rainfall (Espigares and Ros, 2003).

Previous paleoecological and paleoclimatical studies of Barranco León (unit D) suggested a warmer and more humid climate than actual conditions in the Guadix-Baza Basin (Blain et al., 2011). Mean annual temperatures were 4.9 °C higher and mean annual precipitation was 371 mm higher than today's values. In addition, there was a less pronounced difference between winter and summer temperatures: winters were warmer and summers were about the same as they are now or possibly slightly cooler. There were high levels of precipitation throughout the year, but the summer was slightly drier than today, in keeping with the characteristically Mediterranean climate (i.e., periods of drought during summer). The landscape was composed of a body of water exposed to the sun with rich lakeside vegetation and surrounded by loose, stony soil. The terrestrial landscape consisted of rich and diverse environments that alternated between dry meadows or shrublands alongside more humid areas favorable to the development of wetter woodlands and meadows.

The presence of wet woodlands around Barranco León is well supported in unit D1 by the occurrence of large cervids such as *Praemegaceros* cf. *verticornis* and *Metacervocerus rhenanus* (Abbazzi, 2010) and by palynological data, which indicate the existence of well-developed woodlands (50% of arboreal pollen) with predominantly Mediterranean taxa (Cupressaceae, *Quercus* sp. -evergreen oak-, *Olea*, *Phillyrea*), although some taxa (like *Betula*, *Corylus*, *Quercus* -deciduous oak-, *Cedrus*, and *Picea*) indicate more humid conditions (Jiménez Moreno, 2003). Large herbivores like *Mammuthus meridionalis* and *Stephanorhinus* cf. *hundsheimensis* as well as the prevalence of *Equus altidens* suggest wet, open meadows. The occurrence of *Hippopotamus antiquus*, which accounts for 27.1% of the large mammals at Barranco León, provides evidence supporting the presence of large bodies of water (Martínez-Navarro et al., 2003, 2010).

The results of the present study of the two fossiliferous levels of Barranco León enable a closer analysis of the paleoenvironmental and paleoclimatic conditions occurring when each of the units were deposited. The paleoherpetological and paleoichtyological data indicate that the temperature was higher than today, with the mean annual temperature higher than 13 °C. Moreover, the two units are dominated by vertebrates associated with areas bordering water (close to 90%; Fig. 3; Table 1). Unit D1 is characterized by the prevalence of woodland elements (35%), followed by open humid (27.1%), rocky (20%), and open dry elements (17.9%). However, the situation changes in unit D2, which is clearly dominated by open humid elements (more than 40%) and very few rocky small mammals (less than 4%; see Fig. 3). Therefore, although the microvertebrate evidence indicates the existence of a significant water column during the deposition of the two units, an open landscape was always present in the vicinity of the lake. The evolution of the microvertebrate associations suggests a trend towards more humid, less open conditions from D1 to D2 (see Fig. 4).

Discussion

Thus far, Barranco León records the oldest evidence of hominin presence in Western Europe, both in terms of lithic industry and physical remains (Toro Moyano et al., 2013). However, there is a difference of about 0.5 Ma between the first hominin evidence out of Africa and the Iberian record: hominin presence in Georgia has been reported at the site of Dmanisi as early as 1.8 Ma (Vekua et al., 2002; Lordkipanidze et al., 2007; Ferring et al., 2011). How to explain this difference in age? In contrast with other Pleistocene successions in Western Europe, the Guadix-Baza Basin records an almost continuous stratigraphic and paleontological sequence. In this way, it has been possible to elaborate a very accurate biostratigraphic scale based on small mammals (Agustí et al., 2010). The levels biostratigraphically below Barranco León, such as Venta Micena, do not show any evidence of hominin presence, both in terms of lithic industries or hominin remains, in contrast with Barranco Léon, where the number of lithic tools so far reaches 1240 artefacts, including cores, flakes or fragments of flakes, and cobbles (Toro Moyano et al., 2013). However, Venta Micena has yielded more than 15,000 fossil remains, much more than Barranco León.

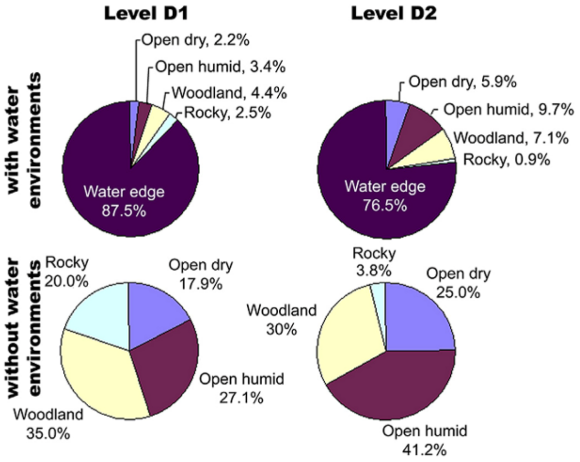

Figure 3. Distribution of relative abundances of small vertebrate habitat preferences and their MNI values. Top row: relative abundances of habitat preferences. Bottom row: relative abundances of habitat preferences without aquatic and water-edge habitats.

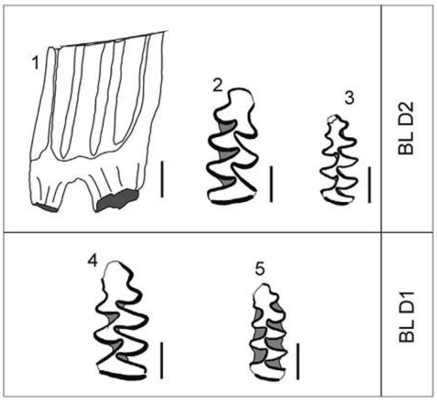

Figure 4. Occlusal view of lower first molars of the arvicolid species represented at D1 and D2. *Mimomys savini*: 1 (lateral view), 2, and 4. *Allophaiomys* aff. *lavocati*: 3 and 5.

Difference in age between the fossiliferous levels of Venta Micena and Barranco Léon can be estimated at about 200 ka (Agustí et al., 2010). Venta Micena and age-equivalent levels in Spain display evidence of drier and cooler conditions compared with the geologically younger desposits of Barranco León, (Agustí et al., 2009). Therefore, according to the Guadix-Baza record, it seems that hominin presence in the area was strongly influenced by climatic conditions, with the first hominin occurrence taking place only when mild, favorable conditions, both in terms of temperature and humidity, were present. The data reported here clearly support the idea that early human occupation of Europe was strongly constrained by climatic and environmental conditions, rather than by physiography or cultural factors.

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