A new genus and species of arvicolid rodent (Mammalia) from the early Pleistocene of Spain

Jordi AGUSTÍ, Pedro PIÑERO, Iván LOZANO-FERNÁNDEZ & Juan Manuel JIMÉNEZ-ARENAS
A new genus and species of arvicolid rodent (Mammalia) from the early Pleistocene of Spain

Jordi AGUSTÍ
Institució Catalana de Recerca i Estudis Avançats (ICREA),
Passeig de Lluís Companys 23, 08010 Barcelona (Spain)
and Institut Català de Paleoeocologia Humana i Evolució Social (IPHES-CERCA),
Zona Educacional 4, Campus Sescelades URV (Edifici W3), 43007 Tarragona (Spain)
and Àrea de Prehistòria, Universitat Rovira i Virgili (URV),
Avinguda de Catalunya 35, 43002 Tarragona (Spain)
jordi.agusti@icrea.cat (corresponding autor)

Pedro PIÑERO
Institut Català de Paleoeocologia Humana i Evolució Social (IPHES-CERCA),
Zona Educacional 4, Campus Sescelades URV (Edifici W3), 43007 Tarragona (Spain)
and Àrea de Prehistòria, Universitat Rovira i Virgili (URV),
Avinguda de Catalunya 35, 43002 Tarragona (Spain)
ppinero@iphes.cat

Iván LOZANO-FERNÁNDEZ
Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA),
Zona Educacional 4, Campus Sescelades URV (Edifici W3), 43007 Tarragona (Spain)
and Àrea de Prehistòria, Universitat Rovira i Virgili (URV),
Avinguda de Catalunya 35, 43002 Tarragona (Spain)
ivanlozanof@gmail.com

Juan Manuel JIMÉNEZ-ARENAS
Department of Prehistory and Archeology, University of Granada,
Campus Universitario de Cartuja, 18071 Granada (Spain).
jumajia@ugr.es

Submitted on 30 May 2021 | Accepted on 30 September 2021 | Published on 8 November 2022

ABSTRACT
In this paper, a new genus and species of arvicolid rodent is described from the late early Pleistocene levels of the sections of Fuente Nueva 3 (Guadix-Baza Basin, Granada, southern Iberian Peninsula), and Quibas (Murcia, southeastern Iberian Peninsula). The majority of Manchenomy n. gen. molars lacks roots, and the morphology of the first lower molar (m1) is simple, with a short and rounded anteroconid complex and widely confluent triangles four and five (T4 and T5) fields.

urn:lsid:zoobank.org:pub:36D74A2E-0D49-48AF-9743-8B1ED04BB6D0F

Agustí J., Piñero P., Lozano-Fernández I. & Jiménez-Arenas J. M. 2022. — A new genus and species of arvicolid rodent (Mammalia) from the early Pleistocene of Spain. Comptes Rendus Palevol 21 (39): 847-858. https://doi.org/10.5852/cr-palevol2022v21a39
INTRODUCTION

A main event in the early Pleistocene evolution of the Palearctic rodent faunas was the emergence and spread of arhidont rodents (arvicoline with rootless molars or superrhysodonts; Martin 1993), most of them included in the genus *Allophaiomys* Kormos, 1953 (Van der Meulen 1973; Rabeder 1981; Agustí 1991). In Europe, these early arhidont rodents coexisted with voles with rooted molars of the genus *Mimomys* Forsyth Major, 1902 approximately until 1.8 Ma (after the Olduvai subchron) and 0.99 Ma (Jaramillo subchron). Very probably, the third upper molar (M3) is also simple, with a short posterior cap. *Manchenomys orcensis* n. sp. is described from Fuente Nueva 3, and *Mimomys oswaldoreigi* Agustí, Castillo & Galobart, 1993 from Gilena 2 and Barranco de los Conejos is recombined as *Manchenomys oswaldoreigi* n. comb. The chronostratigraphic range of *Manchenomys* n. gen. covers the upper Matuyama geomagnetic chron, between 1.8 Ma (post-Olduvai subchron) and 0.99 Ma (Jaramillo subchron). *Manchenomys* n. gen. was possibly derived from a local population of *Mimomys tornensis* Janossy & Meulen, 1975, an arvicolid species present in older early Pleistocene levels of Spain.

KEY WORDS

Arvicolidae, Rodentia, early Pleistocene, Iberian Peninsula, Guadix-Baza Basin, Quibas, new genus, new species, new combination.

Molar enamel is predominantly negatively differentiated (*Mimomys*-type). The third upper molar (M3) is also simple, with a short posterior cap. *Manchenomys orcensis* n. sp. is described from Fuente Nueva 3, and *Mimomys oswaldoreigi* Agustí, Castillo & Galobart, 1993 from Gilena 2 and Barranco de los Conejos is recombined as *Manchenomys oswaldoreigi* n. comb. The chronostratigraphic range of *Manchenomys* n. gen. covers the upper Matuyama geomagnetic chron, between 1.8 Ma (post-Olduvai subchron) and 0.99 Ma (Jaramillo subchron). *Manchenomys* n. gen. was possibly derived from a local population of *Mimomys tornensis* Janossy & Meulen, 1975, an arvicolid species present in older early Pleistocene levels of Spain.

RÉSUMÉ

Un nouveau genre et une nouvelle espèce de rongeur arvicolidé (*Mammalia*) du Pléistocène inférieur de l’Espagne. Dans ce travail, nous décrivons un nouveau genre et une nouvelle espèce d’arvicolidé *Manchenomys orcensis* n. gen., n. sp., provenant des niveaux de la partie supérieure du Pléistocène inférieur des sections de Fuente Nueva 3 (bassin de Guadix-Baza, Grenade, sud de l’Espagne) et de Quibas (Murcia, sud-est de l’Espagne). Les molaires de *Manchenomys orcensis* n. gen., n. sp. ne présentent pas de racines, mais leur ligne sinueuse peut commencer à se fermer. La morphologie de la première molaire inférieure (m1) est typiquement mimomyienne, avec un dessin dentaire simple, un complexe de l’antéroconide court et arrondi et des triangles T4 et T5 largement confluentes. L’émail est négativement différencié (*type Mimomys*) ou parfois indifférencié. La troisième molaire supérieure (M3) présente aussi un dessin typiquement mimomyien, avec une partie postérieure courte et simple. Une deuxième espèce décrite antérieurement *Manchenomys oswaldoreigi* n. comb., qui avait été incluse dans le genre *Manchenomys Forsyth* Major, 1902, est aussi ajoutée au nouveau genre. Du point de vue chronostratigraphique, *Manchenomys orcensis* n. gen. se situe dans le chron géomagnétique Matuyama, entre 1.8 Ma (après le subchron Olduvai) et 0.99 Ma (subchron Jaramillo). Très probablement, *Manchenomys orcensis* n. gen. est dérivé d’une population locale de *Mimomys tornensis* Janossy & Meulen, 1975, une espèce d’arvicolidé déjà présente dans des niveaux plus anciens du Pléistocène inférieur de l’Espagne.
TABLE 1. — Measurements (in mm) of the m1 of Manchenomys arcen-
sis n. gen., n. sp. from Fuente Nueva 3 (levels FN 3-3, FN 3-4, FN 3-5 and FN 3-6) and Quibas (levels QC 4-5, QG-1, QS-1, QS-3 and QS-4); Manchenomys oswaldoregi n. comb. from Gilena 2 (Agustí et al. 1993a); Mimomys tornensis Janosay & Meulen, 1975 from Almenara-Casablanca 1 (this work). Abbreviations: ACS, Almenara-Casablanca; FN, Fuente Nueva; L, length; N, number of specimens; QC, Quibas-Cueva; QG, Quibas-Gruta; QS, Quibas-Sima; W, width.

| Locality  | L min | L mean | L max | W min | W mean | W max | N  |
|-----------|-------|--------|-------|-------|--------|-------|----|
| ACS-1     | 2.76  | 2.85   | 2.96  | 1.05  | 1.07   | 1.08  | 3  |
| Gilena 2  | 2.61  | 2.71   | 2.82  | 0.89  | 0.95   | 1.10  | 11 |
| FN 3-3    | 2.80  | 2.94   | 3.04  | 1.05  | 1.14   | 1.19  | 3  |
| FN 3-4    | –     | 2.86   | –     | –     | 1.03   | –     | 1  |
| FN 3-5    | 2.81  | 3.00   | 3.23  | 0.99  | 1.11   | 1.23  | 16 |
| FN 3-6    | –     | 3.06   | –     | 1.16  | 1.17   | 1.18  | 2  |
| QC 4-5    | 2.58  | 2.87   | 3.57  | 1.03  | 1.12   | 1.24  | 12 |
| QG-1      | 2.65  | 2.74   | 2.82  | 0.97  | 1.04   | 1.11  | 2  |
| QS-1      | 2.70  | 2.90   | 3.11  | 1.00  | 1.13   | 1.21  | 6  |
| QS-3      | 2.86  | 3.05   | 3.21  | 1.11  | 1.15   | 1.23  | 5  |
| QS-4      | 2.66  | 2.77   | 2.89  | 1.07  | 1.12   | 1.16  | 2  |

TABLE 2. — Measurements (in mm) of the M3 of Manchenomys arcen-
sis n. gen., n. sp. from Fuente Nueva 3 (levels FN 3-3, FN 3-4, FN 3-6) and Quibas (levels QC 4-5, QG-1, QS-1 and QS-3); Manchenomys oswaldoregi n. comb. from Gilena 2 (Agustí et al. 1993a); Mimomys tornensis Janosay & Meulen, 1975 from Almenara-Casablanca 1 (this work). Abbreviations: FN, Fuente Nueva; L, length; N, number of specimens; QC, Quibas-Cueva; QG, Quibas-Gruta; QS, Quibas-Sima; W, width.

| Locality  | L min | L mean | L max | W min | W mean | W max | N  |
|-----------|-------|--------|-------|-------|--------|-------|----|
| FN 3-3    | 1.74  | –      | –     | 1.00  | –      | –     | 1  |
| FN 3-5    | 1.75  | 1.90   | 1.99  | 0.90  | 0.98   | 1.06  | 4  |
| FN 3-6    | 1.79  | 1.89   | 1.99  | 0.82  | 0.93   | 1.03  | 5  |
| QC 4-5    | 1.76  | 1.93   | 2.12  | 0.85  | 0.99   | 1.07  | 10 |
| QG-1      | –     | 1.81   | –     | 0.96  | –      | –     | 1  |
| QS-1      | 1.60  | 1.88   | 2.15  | 0.78  | 0.95   | 1.03  | 6  |
| QS-3      | –     | 1.87   | –     | 0.99  | –      | –     | 1  |

MATERIAL AND METHODS

SITE AND INSTITUTIONAL

The material included in this study comes from the sections of Fuente Nueva 3 (levels FN 3-3, FN 3-4, FN 3-5 and FN 3-6; Guadix-Baza Basin, Granada, Spain) and Quibas (levels QS-1, QS-3, QS-4, QC 4-5 and QG-1; Quibas karstic complex, Murcia, Spain). The material from the Fuente Nueva 3 section includes the 22 first lower molars (m1) documented here and ten third upper molars (M3). The material from the Quibas section is documented by 28 first lower molars (m1) and 18 third upper molars (M3). The distribution of molars in each level of the two sections is documented in Tables 1 and 2. This material is currently housed at the Museo Arqueológico de Granada (Fuente Nueva 3) and the Museo Arqueológico de Murcia (Quibas).

The nomenclature used for the description of the diagnostic molars, i.e., m1 and M3, follows Van der Meulen (1973) (Fig. 1). The linea sinuosa is defined according to Rabeder (1981). Enamel differentiation is defined as nega-

Fig. 1. — Nomenclature and measurements of molars: A, left m1 from Quibas-Gruta 1 (QB-10-G1-R/19a); B, left m1 from Quibas-Gruta 1 (left, QB-10-G1-R/19b); C, right M3 from Quibas-Gruta 1 (QB-10-G1-R/20a). Abbreviations: a, ACC length; AC2, anteroconid cap; AL1, anterior lobe; b, shortest distance between BRA3 and LRA4; BRA, buccal re-entrant angle; BSA, buccal salient angle; c, shortest distance between LRA3 and BRA3; L, occlusal surface length; LRA3, lingual re-entrant angle; LSA3, lingual salient angle; PC1, posterior cap; PL, posterior lobe; T1-T7, triangles 1-7; W, distance between LSA4 and BSA3 for m1, and between BSA1 and LSA2 for M3. Scale bar: 1 mm.
tive (Mimomys-type), undifferentiated, or positive (Microtus-type), according to Martin & Tesakov (1998). Length (L) and width (W) for the m1 have been measured according to Van der Meulen (1973), as well as the standard arvicolid quantities a, b and c (Fig. 1B). Parameters A/L (= a/L x 100), B/W (= b/W x 100) and C/W (= c/W x 100) were calculated according to Van der Meulen (1973). All measurements are expressed in millimetres and were taken with the software DinoCapture 2.0, using photographs from the Digital Microscope AM4115TL Dino-Lite Edge. Some molars represent micrographs taken with Environmental Scanning Electron Microscopy (ESEM) at the Servei de Recursos Científics i Tècnics de la Universitat Rovira i Virgili (Tarragona); other images are taken with the Digital Microscope AM4115TL Dino-Lite Edge.

ABBREVIATIONS AND ACRONYMS

Institutions
ACS Almenara-Casablanca;
FN Fuente Nueva;
IPHES Institut de Paleoecologia Humana i Evolució Social;
QC Quibas-Cueva;
QS Quibas-Sima;
VM Venta Micena.

Other abbreviations
AC2 anteroconid cap;
BRA buccal re-entrant angle;
BSA buccal salient angle;
L length;
LRA lingual re-entrant angle;
LSA lingual salient angle;
M upper molar;
m lower molar;
N number of specimens;
PC1 posterior cap;
T1-T7 triangles 1-7;
W width.

SYSTEMATIC PALAEOONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order RODENTIA Bowdich, 1821
Family ARVICOLIDAE Gray, 1821

Manchenomys n. gen.
(Figs 2-4)

urn:lsid:zoobank.org:act:E8F3F1F5-D492-481F-82A8-315C10B249E3

Allophaiomys sp. – Agustí et al. 2010a: 164, table 1; 2010b: 125, fig. 2. – Piñero et al. 2015: 231, fig. 3A-D; 2020: fig. 3d.
Mimomys sp. – Sánchez-Bandera et al. 2020: 12.

Type material. – Holotype. FN-3-N5b-5, isolated right m1 (Fig. 2A).

Paratypes. m1: FN-3-N5b-1, FN-3-N5b-2, FN-3-N5b-3, FN-3-N5b-4, FN-3-N5b-5, FN-3-N5a-4, FN-3-N5a-7, FN-3-N5a-12, FN-3-N5a-19, FN-3-N5b-1, FN-3-N5b-3, FN-3-N5b-4, FN-3-N5b-14, FN-3-N5b-15, FN-3-N5c-3, FN-3-N5c-4; m3: FN-3-N5a-1, FN-3-N5a-14, FN-3-N5a-15, FN-3-N5c-2.

Diagnosis. – Manchenomys species with virtually arhizodont molars. Root folds can be seen in some specimens of presumably older individuals. B/W index ranges between 25 and 35. The C/W index ranges between 20 and 26. The M3 is simple, with a shallow LRA3 and absence of LRA4.

Differential diagnosis. – Manchenomys n. gen. presents a typical Mimomys m1 occlusal pattern, with a short, rounded anteroconid, without BSA4 or LSA5. The enamel is also either negatively differentiated or undifferentiated. However, Manchenomys differs from other contemporaneous Mimomys species by absence of roots on all the molars, with the occasional exception of the m3, in which they can appear at a late stage of development. It also differs from most Allophaiomys species in the relatively short anteroconid complex (lower values of A/L index), with the exception of Allophaiomys deucalion (Kretzoi, 1969). The M3 of Manchenomys n. gen. shows a morphology simpler than any Allophaiomys species except A. deucalion, with a shallow LRA3 and absence of LRA4.

Occurrence. – Early Pleistocene of southern Iberian Peninsula, c. 1.8-0.99 Ma.
A new genus and species of arvicolid rodent (Mammalia) from the early Pleistocene of Spain

COMPTES RENDUS PALEVOL • 2022 • 21 (39)

Manchenomys orcensis n. gen., n. sp. also differs from A. deucalion in its larger size (L, W) and its more isolated AC2 with respect to T4-T5 (lower B/W values, Table 3). All examples of M3 of Manchenomys orcensis n. gen., n. sp. present a simpler morphology than most Allophaiomys species, with a very shallow LRA3 and absence of LRA4. Only Allophaiomys deucalion presents an M3 with a comparable morphology (Van der Meulen 1974: fig. 3g). However, the M3 of Manchenomys orcensis n. gen., n. sp. never develops a deep LRA3 or LSA4, as is the case for Allophaiomys deucalion M3s (Van der Meulen 1974: fig. 3h).

Measurements. — See Tables 1, 2.

Stratigraphic range. — Early Pleistocene, Biharian Mammal Age, MnQ-3 Mammal unit (Agustí et al. 1987).

Occurrence. — Manchenomys orcensis n. gen., n. sp. is present at the sites of Fuente Nueva 3 (levels FN 3-3, FN 3-4, FN 3-5 and FN 3-6; Sánchez-Bandera et al. 2020) and Barranco León D (Agustí et al. 2010a) in the Guadix-Baza Basin (Granada), and Quibas (levels QS-1, QS-3, QS-4, QC4-5 and QG-1; Piñero et al. 2015, 2020) in the Quibas karstic complex (Murcia), southern Spain.
DESCRIPTION

The m1 of *Manchenomys orcensis* n. gen., n. sp. from Fuente Nueva 3 displays an anteroconid cap (AC2), five alternating triangles and a posterior lobe. All the re-entrant angles are filled with abundant cement. The anteroconid is short and wide in 14 m1s. Enamel is always lacking in the anterior half of the wall of the anteroconid complex. Specimens show negative enamel differentiation, with the exception of one specimen with undifferentiated enamel. The T4 is wider and in some cases shorter than the T5. LRA4 and BRA3 are well developed, therefore constraining the connection between AC2 and the T4-T5 dentine fields. The T4 and T5 alternate, although they are usually widely confluent. Dentine channels between the posterior lobe, T1, T2, T3 and T4 are very narrow. Lower first molars from different
levels of the Quibas section present the same morphology as those from Fuente Nueva 3. However, in two m1s from Quibas a Mimomyan-ridge is present (levels QS-1 and QS-3; Fig. 3C). In addition, the number of teeth showing undifferentiated enamel is higher (8 out of 28 m1).

Examples of M3 from Fuente Nueva 3 show an occlusal pattern composed of a transverse anterior lobe, two alternating triangles (T2-T3) and a posterior cap (PC1). There is always a relatively wide connection between T3 and PC1. The PC1 is simple, in some cases rounded. Some M3s present a very shallow LRA3, while it is lacking in others. No M3 expresses LSA4. Other than FN 3-5, the remaining M3s from the levels FN 3-3 and FN 3-6 of the Fuente Nueva 3 section present a similar dental pattern. This is also the case for the three specimens coming from the levels QS-1, QS-3 and QC 4-5 from the section of Quibas.

**REMARKS**

The first occurrence of *Manchenomys* n. gen. (*Ma. oswaldoreigi* n. comb.) is recorded at the post-Olduvai site of Barranco de los Conejos (Guadix-Baza Basin; Agustí et al. 2013). This species is also present at other coeval levels of the *Mimomys* (now *Manchenomys*) *oswaldoreigi* Zone in the Guadix-Baza Basin, such as Cortes de Baza 1 and Fuentecica 5 (Agustí et al. 1999, 2015b; Oms et al. 2000a; Fig. 4). In the Guadix-Baza Basin, *Manchenomys* n. gen. seems to be absent at the levels of the *Allophaiomys ruffoi* Zone, such as Venta Micena 1 and 2, Orce 7 and Cañada de Murcia 1 (Agustí et al. 2015b). However, a form close to *Manchenomys oswaldoreigi* n. comb. appears to be associated with *Allophaiomys ruffoi* (Pasa, 1947) in the early Pleistocene sites of Huétor-Tajar and Tojaire in the nearby Granada Basin (García-Alix et al. 2009). Venta Micena has been dated to c. 1.4 Ma (Duval et al. 2011), the lower boundary of the *Allophaiomys ruffoi* Zone can be
extended to 1.6 Ma (Agustí et al. 2015b). Manchenomys orcensis n. gen., n. sp. reappears at the late early Pleistocene levels of Fuente Nueva 3 and Barranco Leon D, associated with the arvicolid rodents Mimomys savini Hinton, 1910 and Allophaiomys aff. lavocati (Allophaiomys aff. lavocati Zone; Agustí et al. 2015a, b; Sánchez Bandera et al. 2020). These sites, which record the earliest hominin presence in Europe, have been dated between 1.4–1.2 Ma (Oms et al. 2011; Duval et al. 2012; Toro-Moyano et al. 2013; Lozano-Fernández et al. 2015). Manchenomys orcensis n. gen., n. sp. is still present in the lower levels of the section of Quibas, covering the Matuyama-Jaramillo transition at 1.07 Ma. However, it is already absent from the post-Jaramillo upper level of this section (QS-7, between 0.99 and 0.78 Ma), the last occurrence of this species being recorded within the Jaramillo geomagnetic subchron (Piñero et al. 2020, 2022). Therefore, the stratigraphic range of Manchenomys n. gen. covers the whole upper Matuyama geomagnetic chron between the Olduvai and Jaramillo subchrons (Fig. 6). The persistence of Manchenomys n. gen. in the late Pleistocene of southern Spain parallels a similar persistence of small-sized Mimomys [Mimomys pusillus (Mechely, 1914), Mimomys blanci Van der Meulen, 1973] in the late early Pleistocene of western (including Italy) and central Europe, in all the cases associated with late representatives of Mimomys savini (Van der Meulen 1973).

Previous to the findings of Fuente Nueva 3 and Quibas, Agustí et al. (1993a) already defined a new species of Mimomys characterized by its arhizodont molars, with the rare exception of the lower m3, at the site of Gilena 2, again in southern Spain. The inclusion of M. oswaldoreigi within the genus Mimomys was always problematic, provided the practical absence of roots in its molars. The appearance of a more derived arhizodont vole, Manchenomys orcensis, in younger levels enables us to clarify the position of M. oswaldoreigi, as a first member of an independent, endemic lineage of arhizodont voles. Therefore, the new combination Manchenomys oswaldoreigi is presented in this paper.

**DISCUSSION**

The m1 of Manchenomys n. gen. presents a simple occlusal pattern also being present in some advanced early Pleistocene Mimomys species, such as Mi. pusillus and Mi. tornensis (Janossy & Van der Meulen 1975; Rabeder 1981). There is no record of Mi. tornensis in the Guadix-Baza Basin in southern Spain, although it is present in eastern Spain in the early Pleistocene pre-Olduvai section of Almenara-Casablanca 1 (Castellón, Spain), where it is associated with the arvicolid Kistangia gusii (Gusti, Galobart & Martín-Suárez, 1993 (Esteban Aenlle & López Martínez 1987; Agustí et al. 1993b, 2011). Nevertheless, provided its proximity to the Guadix-Baza Basin, Mi. tornensis appears as a feasible ancestor for Manchenomys n. gen. Mi. tornensis is similar in size to Manchenomys orcensis n. gen., n. sp., although it is larger than Ma. oswaldoreigi n. comb. from the type-locality of Gilena 2 (Table 1). The A/L index of Mi. tornensis is similar to the two species of Manchenomys n. gen. (Table 3). The B/W index is similar to Ma. orcensis n. gen., n. sp., although smaller than Ma. oswaldoreigi n. comb. The main difference lies in the C/W index, which is considerably lower in Mi. tornensis. Mi. tornensis has been proposed as the ancestor of the arhizodont arvicolid of the genus Allophaiomys (Rabeder 1986; however, see Garapich & Naddachowski 1996 for a different view), and this may have been also the case for Manchenomys n. gen. However, currently this question remains unanswered.

At Barranco de los Conejos, Ma. oswaldoreigi n. comb. is associated with two other arvicoids, Orcemys giberti and Tibericola Vandermeulen (Agustí, 1991) (Agustí et al. 2013; Martin 2014; Martin et al. 2018), which both have achieved an arhizodont, superhypodont stage independently: Tibericola originates most probably from an eastern population of Allo-
A new genus and species of arvicolid rodent (Mammalia) from the early Pleistocene of Spain

**Table 3.** A/L, B/W and C/W indices for the m1 of *Manchenomys orcesensis* n. gen., n. sp. (Fuente Nueva 3 and Quibas; this work); *Manchenomys oswaldoreigi* n. comb. (Gilena 2; Agustí et al. 1993a); *Mimomys tornerissii* Janossy & Van der Meulen, 1975 (Almenara-Casablanca 1; this work); *Allophaiomys deucalion* (Kretzoi, 1969) (Villany 5; Van der Meulen 1974); *Allophaiomys pliocaenicus* (Kormos, 1933) (Betfia 2; Van der Meulen 1974); *Allophaiomys ruffoi* (Pasa, 1947) (Venta Micena 1; Agustí 1991). Abbreviations: ACS, Almenara-Casablanca; FN, Fuente Nueva; N, number of specimens; QC, Quibas-Cueva; QS, Quibas-Gruta; QS, Quibas-Sima; VM, Venta Micena.

| Locality          | A/L Min. | A/L Mean | A/L Max. | B/W Min. | B/W Mean | B/W Max. | C/W Min. | C/W Mean | C/W Max. | N |
|-------------------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----|
| ACS-1             | 36.0     | 38.0     | 41.0     | 25.0     | 28.0     | 33.0     | 10.0     | 15.0     | 19.0     | 3  |
| Gilena 2          | 36.1     | 38.5     | 40.9     | 29.0     | 35.2     | 43.0     | 15.5     | 22.6     | 30.0     | 11 |
| FN 3-3            | 34.2     | 38.5     | 42.4     | 20.0     | 24.5     | 27.1     | 19.2     | 24.5     | 28.9     | 3  |
| FN 3-4            | –        | 37.7     | –        | 27.6     | –        | –        | –        | 20.7     | –        | 1  |
| FN 3-5            | 31.9     | 36.6     | 42.7     | 17.7     | 29.1     | 48.1     | 14.3     | 22.3     | 27.0     | 16 |
| FN 3-6            | –        | 23.5     | –        | 27.6     | –        | –        | –        | 20.7     | –        | 1  |
| QC 4-5            | 29.9     | 34.4     | 42.6     | 22.3     | 29.3     | 39.3     | 15.6     | 22.6     | 31.5     | 12 |
| QQ-1              | 37.8     | 40.1     | 42.5     | 24.2     | 25.3     | 26.4     | 20.6     | 20.9     | 21.1     | 2  |
| QQ-1              | 35.7     | 38.3     | 40.3     | 25.3     | 30.7     | 37.4     | 19.8     | 22.5     | 27.4     | 6  |
| QS-3              | 36.9     | 39.9     | 43.7     | 16.7     | 23.4     | 26.1     | 19.8     | 20.7     | 21.9     | 5  |
| QS-4              | 32.9     | 37.8     | 42.7     | 23.6     | 27.7     | 31.9     | 15.7     | 20.4     | 25.1     | 2  |
| Villany 5         | 35.0     | 39.0     | 43.0     | 30.0     | 36.0     | 50.0     | 15.0     | 24.0     | 34.0     | 16 |
| Betfia 2          | 40.0     | 43.0     | 48.0     | 8.0      | 25.0     | 35.0     | 15.0     | 24.0     | 30.0     | 96 |
| VM 1              | 38.0     | 42.0     | 46.0     | 14.0     | 25.0     | 36.0     | 11.0     | 18.0     | 28.0     | 21 |

**Fig. 6.** Biochronological distribution of *Manchenomys* n. gen. The localities marked with an asterisk are calibrated with paleomagnetic data (Oms et al. 1994, 2000b; Gibert et al. 2006; Scott et al. 2007; Agustí et al. 2011, 2013; Piñero et al. 2020, 2022). The sites with presence of the new genus are in bold. GPTS (Geomagnetic Polarity Time Scale) shows Gauss, and four normal polarity intervals within Matuyama: subchrons Reunion (2.12-2.13 Ma); Cobb Mountain (1.19-2.05 Ma); Jaramillo (1.07-0.99 Ma). Abbreviations: ACS, Almenara-Casablanca; BC, Barranco de los Conejos; BL, Barranco León; CB, Cortes de Baza; CM, Cañada de Murcia; FC, Fuentecica; FN, Fuente Nueva; O, Orce; QC, Quibas-Cueva; QQ, Quibas-Gruta; QS, Quibas-Sima; VM, Venta Micena.
phaiomys, Orcemys from the endemic Iberian species Mimomys medasensis Michelau, 1971 and Manchenomys n. gen. possibly from local populations of Mimomys tornensis. Outside Spain, in a similar and almost coeval process the loss of roots led to the first representatives of Allophaionmys (A. devolcean), most probably from Mimomys tornensis (Rabeder 1981, 1986). Root loss has been explained on the basis of a paedomorphic heterochronic process consisting of the retention of a juvenile stage (when roots are still not formed) in adult stages (that is, the sinusine line never closes and therefore the roots never start to develop; Agustí et al. 1993a). After the early-middle Pleistocene transition, arhizodonty was the common condition in most arvicolid lineages.

Development of ever-growing, superhypsodont molars has usually been explained in terms of adaptation to a diet based on grasses (Martin 1984; Janis 1988; Piperno 1988). However, in small voles an alternative explanation is also possible, development of ever-growing molars being a consequence of adaptation to a fossorial behaviour (Maul et al. 2014). In these voles, use of incisors for burrowing leads to strong abrasion of teeth because of the high amount of grit present during chewing (Janis 1988; Martin 1993). Development of ever-growing molars would have been an adaptive response to the high abrasion rates associated with a fossorial way of life. Therefore, root loss in Manchenomys n. gen. teeth is possibly linked to a subterranean life, in relation with the strong glacial pulses that are recorded at about 1.8 Ma. This interpretation is consistent with the joint presence of Manchenomys n. gen. and two other superhypysodont arvicolid species at Barranco de los Conejos.

CONCLUSIONS

Manchenomys n. gen. is defined as an arhizodont vole lineage (although occasionally roots can develop in the lower m3) which ranges from c. 1.8 Ma (post-Olduvai geomagnetic subchron) to 0.99 Ma (Jaramillo geomagnetic subchron). Its first representatives, belonging to the species Ma. oswaldoreigi n. comb., are recorded at a number of sites in the Guadix-Baza Basin (Barranco de los Conejos, Cortes de Baza 1, Fuentecica 5). Ma. oswaldoreigi n. comb. possibly derives from a local Iberian population of the species Mi. tornensis. Manchenomys n. gen. is absent in the levels with Allophaionmys ruffoi from the Guadix-Baza Basin, between 1.6-1.4 Ma, but reappears in the late early Pleistocene levels of Fuente Nueva 3 and Barranco León D, represented by Ma. orcensis n. gen., n. sp., associated with the first evidence of hominin peopling of western Europe. This species persists in the pre-Jaramillo and Jaramillo levels of the section of Quibas, at about 1 Ma; its last occurrence being recorded within this geomagnetic subchron.

Acknowledgements

This research was supported by the Consejería de Cultura, Junta de Andalucía (BC.03.052/17, Proyecto General de Investigación “Primera ocupaciones humanas y contexto paleoecológico a partir de los depósitos pлиoleistocenos de la cuenca Guadix-Baza. Zona Arqueológica de la cuenca de Orce”), the Comunidad Autónoma de la Región de Murcia (ARQ115/2018, Subvención para la Investigación e Intervención en el Patrimonio Arqueológico y Paleontológico de la Región de Murcia) and the Palarq Foundation. The Institut Català de Paleocèologia Humana i Evolució Social (IPHES-CERCA) has received financial support from the Spanish Ministry of Science and Innovation through the “María de Maeztu” program for Units of Excellence (CEX2019-000945-M). PP is beneficiary of a postdoctoral contract from the “María de Maeztu” program. The authors thank the two reviewers of Comptes Rendus Palévol for their insightful comments.

REFERENCES

Agustí J. 1991. — The Allophaionmys complex in Southern Europe. Geobios 25 (1): 133-144. https://doi.org/10.1016/S0016-6995(09)90043-2
Agustí J., Moya Solà S. & Pons Moya J. 1987. — La sucesión de mamíferos en el Pleistoceno inferior de Europa: proposición de una nueva escala bioestratigráfica. Paleontologia i Evolució (Memòria Especial 1): 287-295.
Agustí J., Castello C. & Galobart A. 1993a. — Heterochronic evolution in the late Pliocene – early Pleistocene arvicoldic of the Mediterranean area. Quaternary International 19: 51-56. https://doi.org/10.1016/1040-6182(93)90022-8
Agustí J., Galobart A. & Martín Suárez E. 1993b. — Kisangia gusii sp. nov., a new arvicolid (Rodentia) from the late Pliocene of Spain. Scripta Geologica 103: 119-134.
Agustí J., Oms O. & Pàrés J. M. 1999. — Calibration of the early-middle Pleistocene transition in the continental beds of the Guadix-Baza Basin (SE Spain). Quaternary Science Review 18 (12): 1409-1417. https://doi.org/10.1016/S0277-3791(98)00116-4
Agustí J., Blain H.-A., Furió M., de Marfà R. & Santos-Cubedo A. 2010a. — The early Pleistocene small vertebrate succession from the Orce region (Guadix-Baza Basin, SE Spain) and its bearing on the first human occupation of Europe. Quaternary International 223-224: 162-169. https://doi.org/10.1016/j.quaint.2009.12.011
Agustí J., de Marfà R. & Santos-Cubedo A. 2010b. — Roe- dores y lagomorfos (Mammalia) del Pleistoceno inferior de Barranco León 5 y Fuente Nueva 3 (Orce, Granada), in Toro-Moyano I., Martinez-Navarro B. & Agustí J. (eds), Ocupaciones humanas en el Pleistoceno inferior y medio de la Cuenca de Guadix-Baza. Junta de Andalucía, Dirección General de Bienes Culturales, Consejería de Cultura (coll. Arqueología Monográfica), Sevilla: 121-140.
Agustí J., Santos-Cubedo A., Furió M., de Marfà R., Blain H.-A., Oms O. & Sevilla P. 2011. — The late Neogene-early Quaternary small vertebrate succession from the Almenara-Casablanca karstic complex (Castellón, eastern Spain): chronologic and paleoclimatic context. Quaternary International 243 (1): 183-191. https://doi.org/10.1016/j.quaint.2010.11.016
Agustí J., Blain H.-A., Furió M., de Marfà R., Martinez-Navarro B. & Oms O. 2013. — Early Pleistocene environments and vertebrate dispersals in Western Europe: the case of Barranco de los Conejos (Guadix-Baza Basin, SE Spain). Quaternary International 295: 59-68. https://doi.org/10.1016/j.quaint.2012.02.004
Agustí J., Blain H.-A., Loxano-Fernández I., Piñero P., Oms O., Furió M., Blanco A., López-García J. & Sala R. 2015a. — 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. https://doi.org/10.1016/j.jhevol.2015.02.014
Piperno R. D. 1988. — Phytolith Analysis: An Archaeological and Geological Perspective. Academic Press, San Diego, 280 p.

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

Rabeder G. 1986. — Herkunft und frühe Evolution der Gattung Microtus (Arvicolidae, Rodentia). *Zeitschrift für Säugetierkunde* 51 (6): 350-367.

Sánchez-Bandera C., Oms O., Blain H.-A., Lozano-Fernandez I., Bisbal-Chinesta J., Agustí J., Saarinen J., Fortelius M., Titton S., Serrano-Ramos A., Luzon C., Solano-Garcia J., Barsky D. & Jimenez-Arenas J. M. 2020. — New stratigraphically constrained palaeoenvironmental reconstructions for the first human settlement in Western Europe: The early Pleistocene herpetofaunal assemblages from Barranco Leon and Fuente Nueva 3 (Granada, SE Spain). *Quaternary Science Reviews* 243: 106466. [https://doi.org/10.1016/j.quascirev.2020.106466](https://doi.org/10.1016/j.quascirev.2020.106466)

Scott G., Gibert L. & Gibert J. 2007. — Magnetostratigraphy of the Orce region (Baza Basin), SE Spain: new chronologies for early Pleistocene faunas and hominid occupation sites. *Quaternary Science Reviews* 26 (3-4): 415-435. [https://doi.org/10.1016/j.quascirev.2006.09.007](https://doi.org/10.1016/j.quascirev.2006.09.007)

Van der Meulen A. 1973. — Middle Pleistocene smaller mammals from the Monte Peglia, (Orvieto, Italy) with special reference to the phylogeny of Microtus (Arvicolidae, Rodentia). *Quaternaria* 17: 1-114.

Van der Meulen A. 1974. — On Microtus (Allophaiomys) deucalion (Kretzoi, 1969), (Arvicolidae, Rodentia), from the Upper Villanyian (Lower Pleistocene) of Villany-5, S. Hungary. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B* 77: 259-266.

Submitted on 30 May 2021; accepted on 30 September 2021; published on 8 November 2022.