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

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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 *Manchenomys* 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.

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.

MOTS CLÉS
Arvicolidae,
Rodentia,
Pléistocène inférieur,
Péninsule ibérique,
Bassin de Guadix-Baza,
Quibas
genre nouveau,
espèce nouvelle,
combinaison nouvelle.

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 confluents. L'émail est négativement differencié (type *Mimomys*) ou parfois indifferencié. 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 *Mimomys Forsyth* Major, 1902, est aussi ajoutée au nouveau genre. Du point de vue chronostratigraphique, *Manchenomys* 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* n. gen. est derivé 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.

INTRODUCTION

A main event in the early Pleistocene evolution of the Palearctic rodent faunas was the emergence and spread of arhizodont voles (arvicolines with rootless molars or superhypsodont; Martin 1993), most of them included in the genus *Allophaiomys* Kormos, 1933 (Van der Meulen 1973; Rabeder 1981; Agustí 1991). In Europe, these early arhizodont voles coexisted with voles with rooted molars of the genus *Mimomys* Forsyth Major, 1902 approximately until the early-middle Pleistocene transition (Rabeder 1981; Laplana & Cuenca-Bescós 2000). While the replacement of *Mimomys* by *Allophaiomys* appears as a clear event in central and eastern Europe, the situation seems to have been more complex in southern Europe, especially in the Iberian Peninsula. In this area, evidence from southern Spain demonstrated a local evolution of endemic *Mimomys* populations towards root loss. This was the case of *Mimomys oswaldoreigi* Agustí, Castillo & Galobart, 1993, present at the sites of Barranco de los Conejos (Guadix-Baza Basin) and Gilena 2 (Agustí *et al.* 1993a), as well as of *Orcemys giberti* Martin, Tesakov, Agustí & Johnston, 2018, present in the Guadix-Baza Basin at the sites of Barranco de los Conejos and Barranco del Paso (Agustí *et al.* 2013; Martin *et al.* 2018). Moreover, in the Guadix-Baza Basin (Barranco de los Conejos), the first evidence of allochthonous arhizodont species cannot be assigned to *Allophaiomys* but rather to *Tibericola* Koenigswald, Fejfar & Tchernov, 1992, a genus of eastern Mediterranean affinities also present in Turkey and Israel (Agustí 1991; Agustí *et al.* 2013).

The first occurrence of true representatives of *Allophaiomys* in the Guadix-Baza Basin is recorded at the sites of Venta Micena, Fuente Nueva 2 and Orce 7 (*Allophaiomys ruffoi* Zone; Agustí *et al.* 2010a, 2015a), where *Orcemys giberti* and *Mimomys oswaldoreigi* are absent. However, it seems that some populations close to *Mimomys oswaldoreigi* persisted during the time-interval represented by the *Allophaiomys ruffoi* Zone, since a fully arhizodont species displaying affinities with *Mimomys oswaldoreigi* is present at the late early Pleistocene sections of Fuente Nueva 3 (FN 3) (Guadix-Baza Basin, *c.* 1.4-1.2 Ma; Duval *et al.* 2012; Lozano-Fernández *et al.* 2015) and the Quibas karstic complex of southeastern Spain (Quibas Cueva [QC]; Quibas Gruta [QG]; Quibas Sima [QS]) (Murcia, late Matuyama to Jaramillo geomagnetic chrons, between 1.1 and 0.99 Ma; Piñero *et al.* 2020, 2022). This new arvicolid has been variously cited as *Mimomys* sp. (Sánchez-Bandera *et al.* 2020) or *Allophaiomys* sp. (Agustí *et al.* 2010b; Piñero *et al.* 2015, 2020), sharing features common to both genera. However, since it cannot be securely allocated to *Allophaiomys* or *Mimomys*, we propose the recognition of the new genus *Manchenomys* and the new species *Ma. orcensis*, for some arvicolid specimens from Fuente Nueva 3 and Quibas. We also include within the new genus *Manchenomys* the species *Mimomys oswaldoreigi*, closely related to the new species and sharing characters that preclude its inclusion in *Mimomys* or *Allophaiomys*.

TABLE 1. — Measurements (in mm) of the m1 of *Manchenomys orcensis* 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 oswaldoreigi* n. comb. from Gilena 2 (Agustí *et al.* 1993a); *Mimomys tornensis* Janossy & 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.

	L			W			
Locality	min	mean	max	min	mean	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	0.88	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 orcensis* n. gen., n. sp. from Fuente Nueva 3 (levels FN 3-3, FN 3-5 and FN 3-6) and Quibas (levels QC 4-5, QG-1, QS-1 and QS-3). Abbreviations: **FN**, Fuente Nueva; **L**, length; **N**, number of specimens; **QC**, Quibas-Cueva; **QG**, Quibas-Gruta; **QS**, Quibas-Sima; **W**, width.

	L			W			
Locality	min	mean	max	min	mean	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 Institut de Paleoecologia Humana i Evolució Social (IPHES-CERCA) in Tarragona (Spain) and final depòsit is going to be 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-

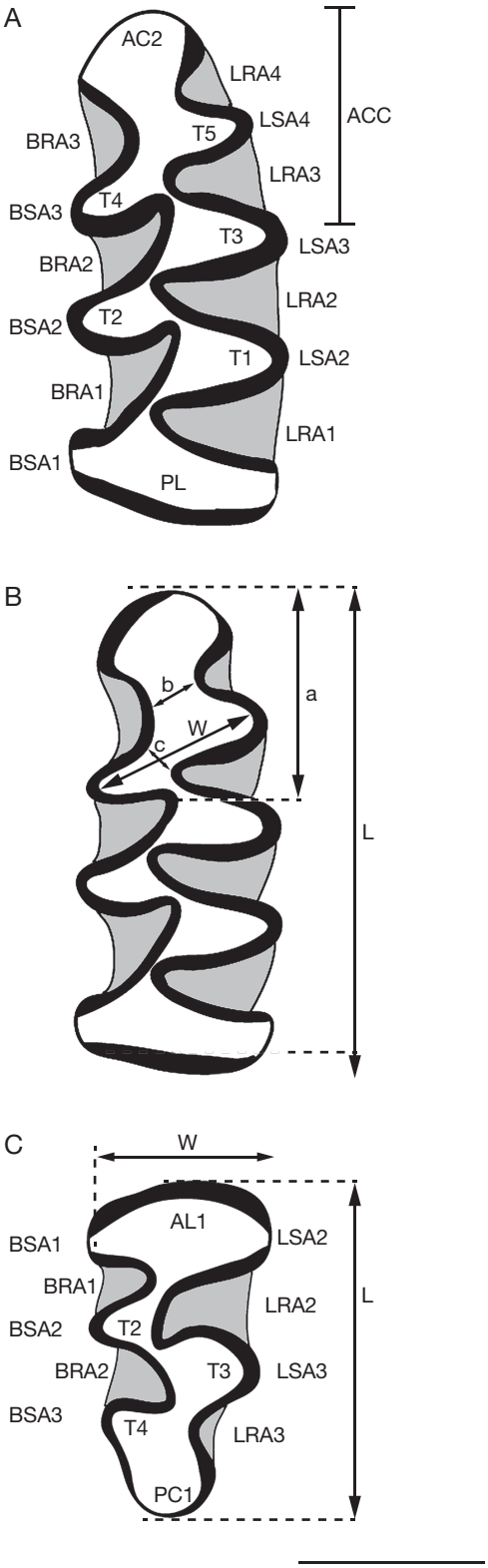

FIG. 1. — Nomenclature and measurements of molars: **A**, left m1 from Quibas-Gruta 1 (QB-10-G1-R/19a); **B**, left m1 from Quibas-Gruta 1 (left, QB-10-G1-R/19b); **C**, right M3 from Quibas-Gruta 1 (QB-10-G1-R/20a). Abbreviations: **a**, ACC length; **AC2**, anteroconid cap; **AL1**, anterior lobe; **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; **LRA**, lingual re-entrant angle; **LSA**, lingual salient angle; **PC1**, posterior cap; **PL**, posterior lobe; **T1**-**T7**, triangles 1-7; **W**, distance between LSA4 and BSA3 for m1, and distance 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 × 100), B/W (= b/W × 100) and C/W (= c/W × 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;
QG	Quibas-Gruta;
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 PALAEONTOLOGY

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

Manchenomys n. gen.
(Figs 2-4)

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DERIVATIO NOMINIS. — This genus is dedicated to Prof. Miguel Ángel Mancheño (University of Murcia), who excavated the site of Quibas, a key locality for the study of *Manchenomys*.

TYPE SPECIES. — *Manchenomys orcensis* n. sp.

INCLUDED SPECIES. — *Manchenomys orcensis* and *Manchenomys oswaldoreigi* Agustí, Castillo & Galobart, 1993, the latter species was formerly assigned to *Mimomys*.

DIAGNOSIS. — Medium-sized arvicolid with simple dental pattern. Enamel-islet is not present on the m1. Re-entrant angles are filled by abundant cement. In the lower molars the enamel differentiation is negative (*Mimomys*-type), that is, thicker at the posterior edges, although in some specimens it is undifferentiated. Teeth do not develop roots, with the occasional exception of some m3. However, closure of the enamel at the base of the crown can be observed in some molars, presumably from older individuals. The A/L index ranges between 36 and 40. The 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.

Manchenomys orcensis n. sp.
(Figs 2, 3)

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Allophaiomys sp. – Agustí *et al.* 2010a: 164, table 1; 2010b: 125, fig. 2. – Piñero *et al.* 2015: 231, fig. 3A-D; 2020: fig. 5d.
Mimomys sp. – Sánchez-Bandera *et al.* 2020: 12.

TYPE MATERIAL. — **Holotype**. FN-3-N5b-5, isolated right m1 (Fig. 2A).

Paratypes. m1: FN-3-N5-1, FN-3-N5-2, FN-3-N5-4, FN-3-N5a-3, FN-3-N5a-4, FN-3-N5a-5, FN-3-N5a-12, FN-3-N5a-19, FN-3-N5b-2, 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-N5-8, FN-3-N5a-13, 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 33, C/W index ranges between 22 and 26.

DERIVATIO NOMINIS. — After Orce (Guadix-Baza Basin), a town near the section of Fuente Nueva 3.

TYPE LOCALITY. — Level FN 3-5 from the Fuente Nueva 3 site, Guadix-Baza Basin (Granada, Spain).

TYPE HORIZON. — *Allophaiomys* aff. *lavocati* Zone (Agustí *et al.* 2015b), 1.4-1.07 Ma (lower boundary of the geomagnetic subchron Jaramillo), Baza Formation, early Pleistocene.

DIFFERENTIAL DIAGNOSIS. — *Manchenomys orcensis* n. sp. is larger (L, W) than *Manchenomys oswaldoreigi* n. comb. (Table 1; Fig. 5A) The AC2 is also more isolated with respect to T4-T5 (lower B/W values; Table 3; Fig. 5B). Roots have not been observed in FN-3 specimens, although a closing of the sinuous line at the base of the crown is present in some specimens.

All *Allophaiomys* species aside from *Allophaiomys deucalion* differ from *Manchenomys orcensis* n. gen., n. sp. in their relatively longer

FIG. 2. — Digital images of isolated teeth (occlusal view) of *Manchenomys orcensis* n. gen., n. sp. (Rodentia, Arvicolidae) from Fuente Nueva 3 (Granada Province, southern Spain): **A**, FN-3-N5b-5, right m1 (holotype), Fuente Nueva 3-5b; **B**, FN-3-N5a-3, right m1, Fuente Nueva 3-5a; **C**, FN-3-N5b-15, right m1, Fuente Nueva 3-5b; **D**, FN-3-N5a-5, right m1, Fuente Nueva 3-5a; **E**, FN-3-N4-13, right m1, Fuente Nueva 3-4; **F**, FN-3-N6-12, left m1, Fuente Nueva 3-6; **G**, FN-3-N5a-13, right M3, Fuente Nueva 3-5a; **H**, FN-3-N5a-14, right M3, Fuente Nueva 3-5a; **I**, FN-3-N3-2, right M3, Fuente Nueva 3-3; **J**, FN-3-N5-8, left M3, Fuente Nueva 3-5; **K**, FN-3-N6-4, left M3, Fuente Nueva 3-6; **L**, FN-3-N6-6, left M3, Fuente Nueva 3-6; **M**, FN-3-N6-5, left M3, Fuente Nueva 3-6. Scale bar: 1 mm.

anteroconid complex (higher A/L values; Table 3). *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, MmQ-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.

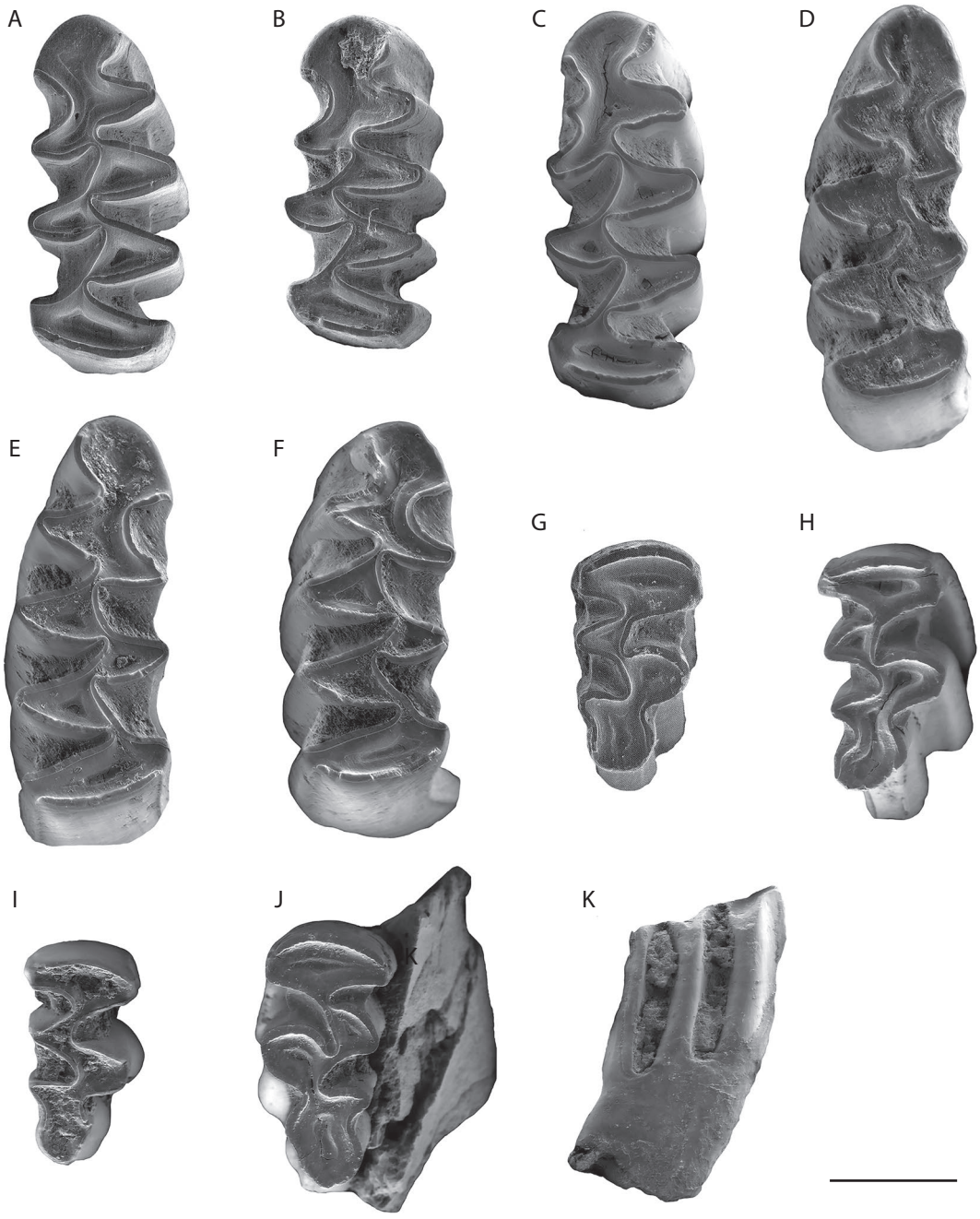


Fig. 3. — ESEM photographs of isolated teeth of *Manchenomys orcensis* n. gen., n. sp. (Rodentia, Arvicolidae) from Quibas (Murcia Region, southeastern Spain): **A**, QB-10-G1-R/19a, left m1 in occlusal view, Quibas-Gruta 1; **B**, QB-10-G1-R/19b, left m1 in occlusal view, Quibas-Gruta 1; **C**, IPHES-QS-3-R/Q1, left m1 in occlusal view, Quibas-Sima 3; **D**, IPHES-QS-3-R/Q2, right m1 in occlusal view, Quibas-Sima 3; **E**, IPHES-QS-3-R/Q6, right m1 in occlusal view, Quibas-Sima 3; **F**, IPHES-QS-3-R/Q7, right m1 in occlusal view, Quibas-Sima 3; **G**, QB-10-G1-R/20a, right M3 in occlusal view, Quibas-Gruta 1; **H**, IPHES-QS-1A-R/F23, right M3 in occlusal view, Quibas-Sima 1.2; **I**, IPHES-QS-1A-R/F26, right M3 in occlusal view, Quibas-Sima 1.2; **J**, IPHES-QS-1Z-R/K32, left M3 in occlusal view, Quibas-Sima 1.3; **K**, IPHES-QS-3-R/Q5, m3 in lateral view (presence of roots), Quibas-Sima 3. Scale bar: 1 mm.

DESCRIPTION

The m1 of *Ma. 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

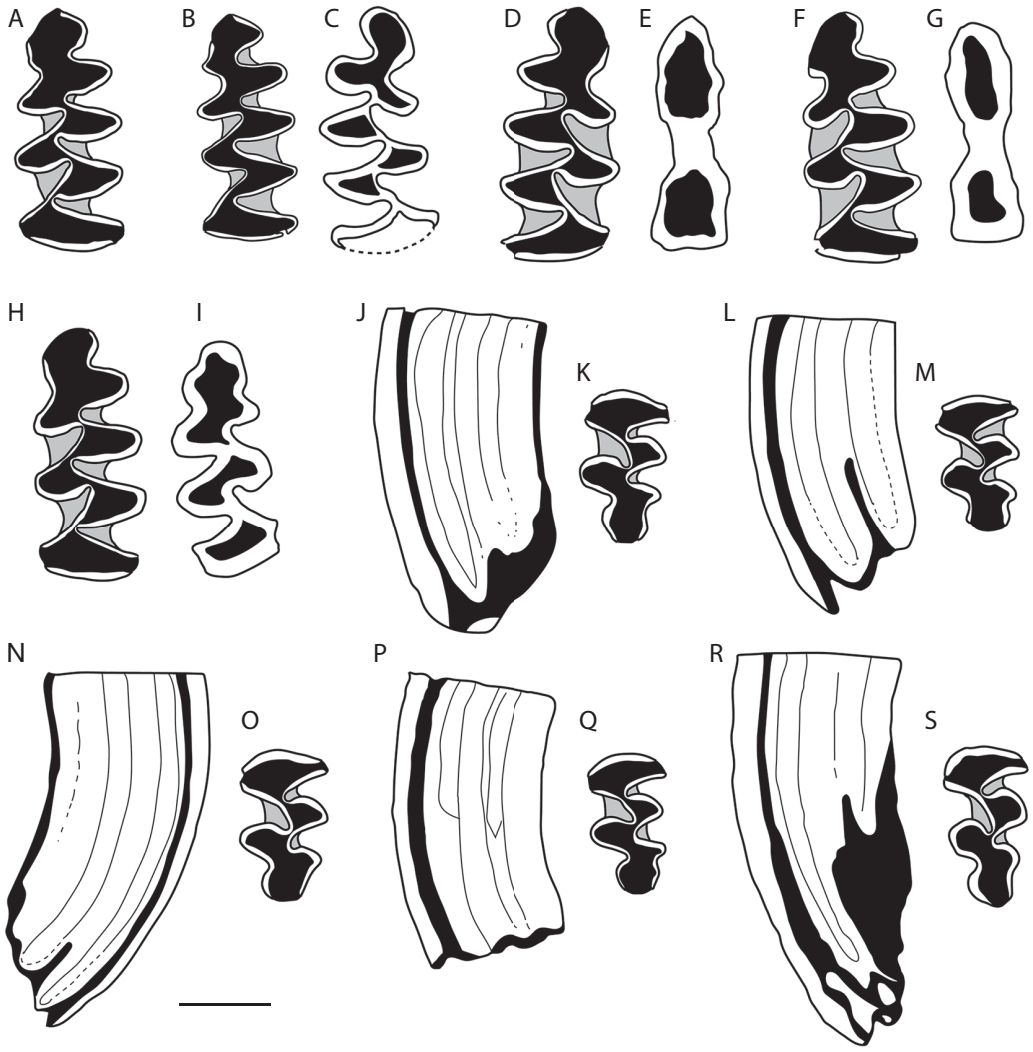


Fig. 4. — *Manchenomys oswaldoreigi* n. comb. (Rodentia, Arvicolidae) from the Guadix-Baza Basin (Granada Province, southern Spain): **A**, CB 1-01, left m1, Cortes de Baza 1, in occlusal view; **B**, **C**, CB 1-03, left m1, Cortes de Baza 1, in occlusal (B) and inferior (C) views; **D**, **E**, CB 1-05, right m1, Cortes de Baza 1, in occlusal (D) and inferior (E) views; **F**, **G**, CB 1-06, left m1, Cortes de Baza 1, in occlusal (F) and inferior (G) views; **H**, **I**, Fc-5-01, left m1, Fuentecica 5, in occlusal (H) and inferior (I) views; **J**, **K**, CB 1-08, left M3, Cortes de Baza 1, in lateral (J) and occlusal (K) views; **L**, **M**, CB 1-09, left M3, Cortes de Baza 1, in lateral (L) and occlusal (M) views; **N**, **O**, CB 1-07, left M3, in lateral (N) and occlusal views (O); **P**, **Q**, Fc-5-19, left M3, Fuentecica 5, in lateral (P) and occlusal (Q) views; **R**, **S**, Fc-5-18, left M3, Fuentecica 5, in (R) lateral and (S), occlusal view. Scale bar: 1 mm.

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

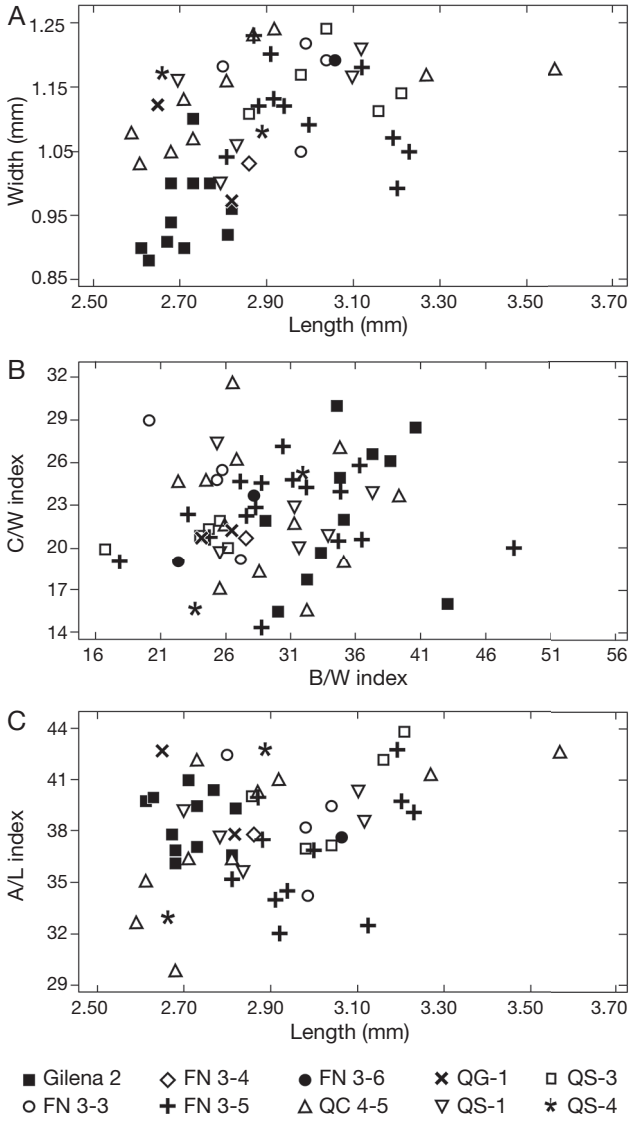


FIG. 5. — Scatter diagrams for the m1 of *Manchenomys orcensis* n. gen., n. sp. from Fuente Nueva 3 and Quibas, and *Manchenomys oswaldoreigi* n. comb. from Gilena 2. **A**, Length–width scatter plot; **B**, B/W–C/W index scatter plot; **C**, Length–A/L index scatter plot. Abbreviations: **FN**, Fuente Nueva; **QC**, Quibas-Cueva; **QG**, Quibas-Gruta; **QS**, Quibas-Sima.

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 early Pleistocene of southern Spain parallels a similar persistence of small-sized *Mimomys* [*Mimomys pusillus* (Mehely, 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 m 3, 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 appearence 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

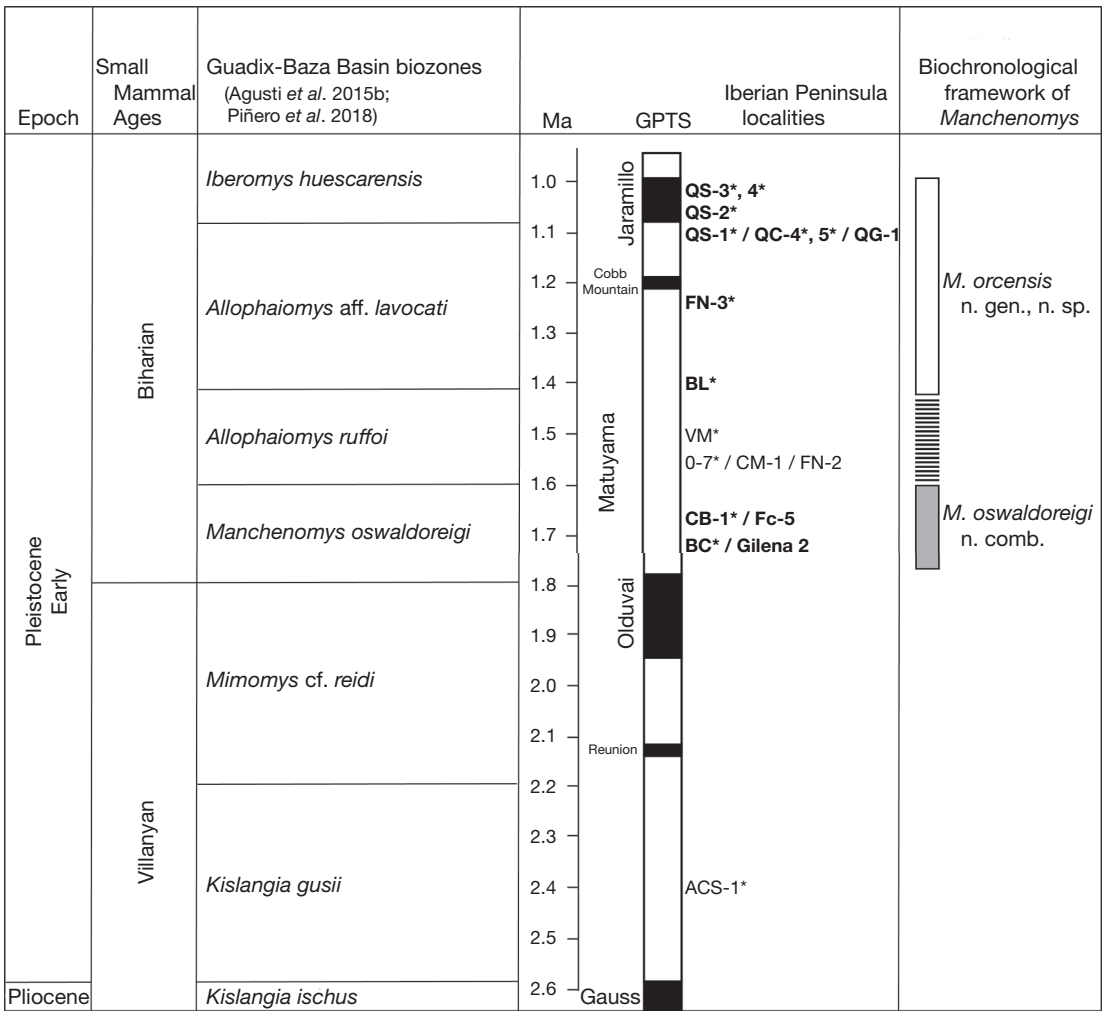
The m1 of *Manchenomys* n. gen. presents a simple occlusal pattern also being present in some advanced early Pleistocene *Mimomys* species, such as *Mi. pusillus* and *Mi. tornensis* (Janossy & Van der Meulen 1975; Rabeder 1981). There is no record of *Mi. tornensis* in the Guadix-Baza Basin in southern 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 *Kislangia gusii* Agustí, 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 arvicolids of the genus *Allophaiomys* (Rabeder 1986; however, see Garapich & Nadachowski 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 arvicolids, *Orcemys giberti* and *Tibericola vandermeuleni* (Agustí, 1991) (Agustí *et al.* 2013; Martin 2014; Martin *et al.* 2018), which both have achieved an arhizodont, superhypsodont stage independently: *Tibericola* originates most probably from an eastern population of *Allo-*

TABLE 3. — A/L, B/W and C/W indices for the m1 of *Manchenomys orcensis* n. gen., n. sp. (Fuente Nueva 3 and Quibas; this work); *Manchenomys oswaldoreigi* n. comb. (Gilena 2; Agustí *et al.* 1993a); *Mimomys tornensis* 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; **QG**, Quibas-Gruta; **QS**, Quibas-Sima; **VM**, Venta Micena.

	A/L			B/W			C/W			
Locality	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	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	–	22.4	25.2	28.1	19.0	21.2	23.5	2
QC 4-5	29.9	34.4	42.6	22.3	29.3	39.3	15.6	22.6	31.5	12
QG-1	37.8	40.1	42.5	24.2	25.3	26.4	20.6	20.9	21.1	2
QS-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); Olduvai (1.94-1.78 Ma); Cobb Mountain (1.22-1.19 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; **QG**, Quibas-Gruta; **QS**, Quibas-Sima; **VM**, Venta Micena.



phaiomys, *Orcemys* from the endemic Iberian species *Mimomys medasensis* Michaux, 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 *Allophaiomys* (*A. deucalion*), 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 sinuous 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 superhypsodont 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 *Allophaiomys 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 Léon 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.

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