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PENSOFT

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A new species of gerbil (Gerbillidae, Rodentia, Mammalia) from the Early Pliocene of the Iberian Peninsula and its bearing on faunal dispersals during the Messinian (Late Miocene)

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Abstract

In this paper, the new gerbil species *Debruijnimys primaevus* **sp. nov.** is described from the Early Pliocene site of La Piquera in central Spain. This species differs from the type species *Debruijnimys julii* in its smaller dimensions and less developed longitudinal ridges in the lower molars. It can be derived from the Moroccan species *Debruijnimys davidi* by an increase in size and modification of the shape of the lower molars. Therefore, it cannot be related to the previously described *Protatera almenarensis* from other Late Miocene sites in Spain. It is proposed that the entry of the two gerbils into the Iberian Peninsula took place in two different phases during the Lago Mare stage of the Messinian. The first, involving the entry of *Protatera almenarensis* as well as other African and Asian elements, coincided with the first substage of the Lago Mare phase, between 5.546 and 5.352 Ma. The second took place during the late stage of the Lago Mare phase, between 5.338 and 5.333 Ma. After the Zanclean flood, members of the genus *Debruijnimys* persisted in several Pliocene sites of the Iberian Peninsula (*D. primaevus* **sp. nov.** and *D. julii*).

Key Words

Early Ruscinian, Gerbillidae, Messinian Salinity Crisis, south-western Europe

Introduction

The Messinian Salinity Crisis (MSC, Late Miocene) had deep effects on the terrestrial faunas around the Mediterranean, opening new corridors that enabled faunal exchanges between Europe, Africa and Asia (Moya-Solà et al. 1984; Agustí 1989a; Benammi et al. 1996; Agustí et al. 2006; Furió et al. 2007; Minwer-Barakat et al. 2009, 2018; García-Alix et al. 2016; Piñero et al. 2017a; Alba et al. 2018; Pérez-García et al. 2020; Ríos et al. 2021; amongst others). In the Western Mediterranean, one of the main consequences

of the MSC was the exchange of mammalian species between Africa and Europe (Agustí et al. 2006; García-Alix et al. 2016). Thus, latest Miocene small mammal faunas from the Iberian Peninsula, such as Almenara-Casablanca M (Castelló/Castellón, eastern Spain; Agustí (1989a); Agustí et al. (2011); Minwer-Barakat et al. (2018)), Salobreña (Granada, southern Spain; Aguilar et al. (1984); Aguilar and Thaler (1987)) and Negratín 1 (Guadix-Baza Basin, southern Spain; Minwer-Barakat et al. (2009)), are characterised by the presence of rodents of African origin belonging to the genera *Myocricetodon* and *Protatera*, both included in the family Gerbillidae.

The living members of this family are widely distributed across a vast corridor covering Africa, the Middle East, northern India and China. They are adapted to survive in arid to sub-desert and even desert environments, such as the African savannahs north and south of the Tropic of Cancer, the desert belt from northern Africa to China and the Asian steppes (Nowak 1999).

After their entry during the Messinian, gerbils persisted into the Early Pliocene of the Iberian Peninsula, being present in several localities such as La Gloria 4 (Teruel Basin, north-eastern Spain; Adrover et al. (1993)), La Bullana 2B (Cabriel Basin, eastern Spain; Mansino et al. (2015)), Alcoy 4B (Alcoi/Alcoy Basin, south-eastern Spain; Agustí (1991); Agustí and Casanovas-Vilar (2003)), Botardo C and D (Guadix-Baza Basin, southern Spain; Martín-Suárez (1988); Piñero and Agustí (2020)), Sifón de Librilla 413 (Fortuna Basin, south-eastern Spain; Piñero and Agustí (2019)), Puerto de la Cadena (Murcia, south-eastern Spain; Piñero et al. (2017a)), Gorafe 4 and Baza 1 (Guadix-Baza Basin, southern Spain; Martín-Suárez (1988); Agustí and Casanovas-Vilar (2003); Piñero et al. (2017b)), and Asta Regia 3 (Jerez Basin, south-western Spain; Castillo and Agustí (1996)). All of them are included in the genus *Debruijnimys*.

The genus *Debruijnimys* was established by Castillo and Agustí (1996) (type species *Debruijnimys julii*) at the Early Pliocene site of Asta Regia 3 to designate a member of the subfamily Taterillinae, characterised by the development of a longitudinal ridge in the lower molars (plate 1, figs 1–8). While the species present at Gorafe 4 and Baza 1 can be assigned to *Debruijnimys julii*, the other early representatives of the genus clearly belong to a more archaic species. However, given the scarcity of material from the sites where it occurs, it has not been possible until now to provide a specific assignment to this older species other than *Debruijnimys* sp.

The discovery of the site of La Piquera (Duero Basin, central Spain; Fig. 1A) now enables the description of a new species, given the large sample of this taxon compared to the previously available material. La Piquera is a karstic locality that has yielded a rich assemblage of fossil vertebrates, including amphibians, squamate reptiles and mammals from the Early Pliocene, dated to about 5.3–4.6 Ma (Piñero et al. 2023).

Material and methods

The fossil material analysed here was collected from La Piquera during the 2021 and 2024 sampling campaigns, comprising remains from levels 1 to 5 as well as from the debris (Fig. 1B, C). All sediment retrieved during these campaigns was water-screened using a set of superimposed 4-, 1- and 0.5-mm mesh sieves. The gerbil assemblage from La Piquera consists of 38 teeth. These fossils are currently housed at the Catalan Institute of Human Palaeoecology and Social Evolution (IPHES), although their final repository will be the Department of Geodynamics, Stratigraphy and Palaeontology at the Complutense University of Madrid (Spain).

All measurements are given in millimetres and were obtained using DinoCapture 2.0 software, based on photographs taken with a digital microscope AM4115TL Dino-Lite Edge. Fossil illustrations were produced from micrographs obtained with the Environmental Scanning Electron Microscope (ESEM) at the 'Servei de Recursos Científics i Tècnics de la Universitat Rovira i Virgili' of the Universitat Rovira i Virgili (Tarragona, Spain). The terminology and measurement procedures applied in the descriptions of the teeth follow Wood and Wilson (1936) and Minwer-Barakat (2005), respectively (see Fig. 2).

Institutional abbreviations. UCM, Universidad Complutense de Madrid, Madrid, Spain.

Anatomical abbreviations. L, length; M1–M3, upper molars; m1–m3, lower molars; W, width.

Systematic Palaeontology

Order Rodentia Bowdich, 1821
Family Gerbillidae Alston, 1876
Subfamily Taterillinae Chaline, Mein & Petter, 1977

Genus *Debruijnimys* Castillo & Agustí, 1996

Type species. *Debruijnimys julii* Castillo & Agustí, 1996; Early Pliocene, Spain.

***Debruijnimys primaevus* sp. nov.**

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Figs 3A–O, 4A–E, I, 5A–I, M–R, T, U

1988 *Protatera* sp. Martín-Suárez, p. 145, pl. 25a.
1991 *Protatera* sp. Agustí.
1993 *Protatera* sp. Adrover et al. p. 60, pl. 5:11.
2003 *Debruijnimys* sp. Agustí and Casanovas-Vilar, p. 17, pl. 15:7–10.
2015 *Debruijnimys* cf. *julii* Mansino et al. p. 283, pl. 5:1.
2017a *Debruijnimys* sp. Piñero et al. p. 108, pl. 5E.
2019 *Debruijnimys* sp. Piñero and Agustí, p. 310, pl. 11N–S.
2020 *Debruijnimys* sp. Piñero and Agustí, p. 911, pl. 5a–d.
2023 *Debruijnimys* sp. Piñero et al. p. 36, pl. 7K.

Derivation of name. From the Latin *primaevus*, meaning "early," in reference to the primitive morphological features of the species.

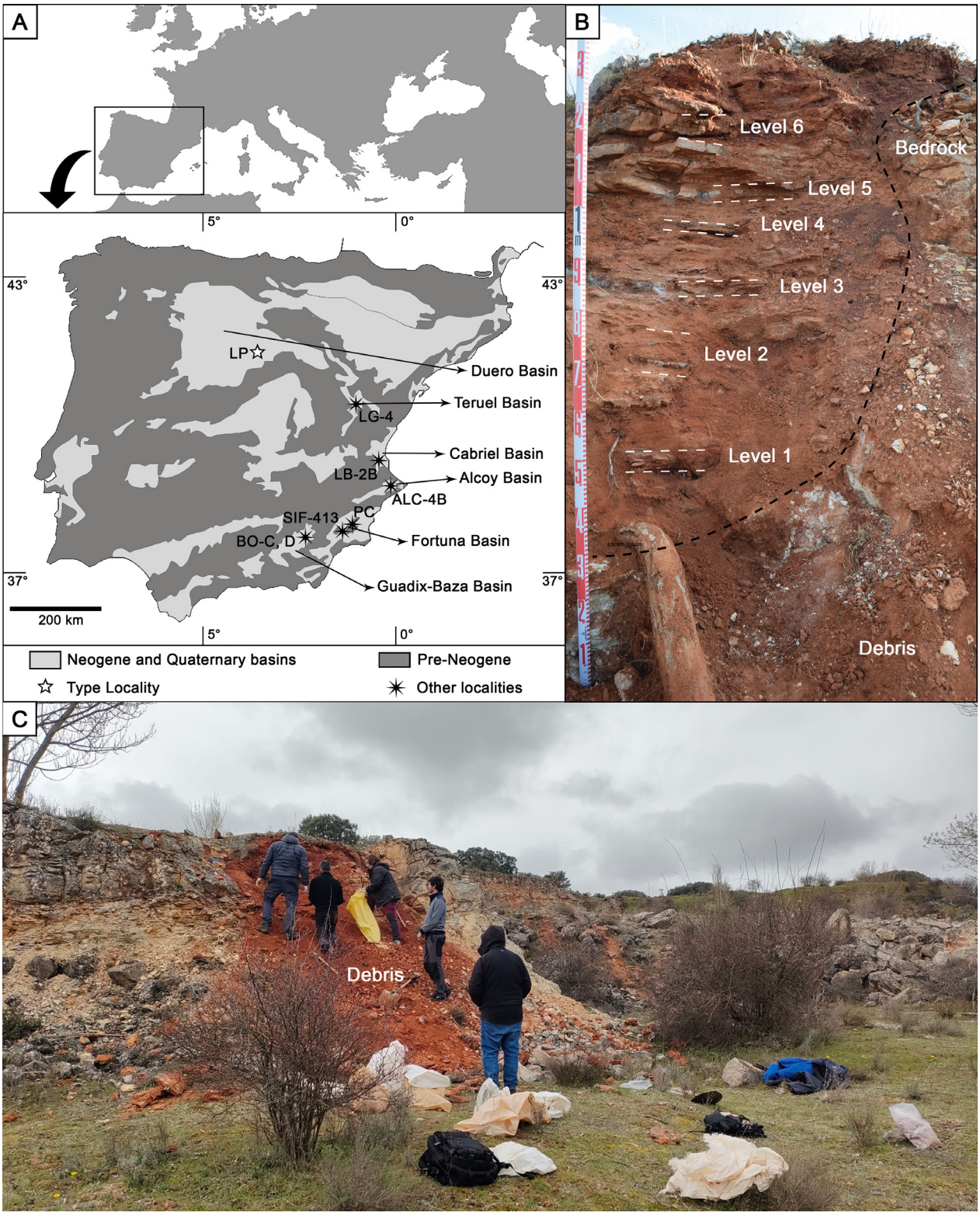

Figure 1. Geographical and stratigraphical context. **A.** Simplified geological map of the Iberian Peninsula showing the localities where *Debruijnimys primaevus* sp. nov. has been recorded. The main Neogene and Quaternary basins mentioned in the text are also indicated; **B.** La Piquera stratigraphic section, type locality of *Debruijnimys primaevus* sp. nov., showing the six lithostratigraphic units containing small vertebrates. The holotype was recovered from level 5, whereas the paratypes come from all the levels (except level 6) and from the debris; **C.** General view of the La Piquera site during the 2024 field campaign. Abbreviations: ALC, Alcoy (Agustí 1991); LB, La Bullana (Mansino et al. 2015); BO, Botardo (Martín-Suárez 1988; Piñero and Agustí 2020); LG, La Gloria (Adrover et al. 1993); LP, La Piquera (Piñero et al. 2023; this work); PC, Puerto de la Cadena (Piñero et al. 2017a); SIF, Sifón de Librilla (Piñero and Agustí 2019).

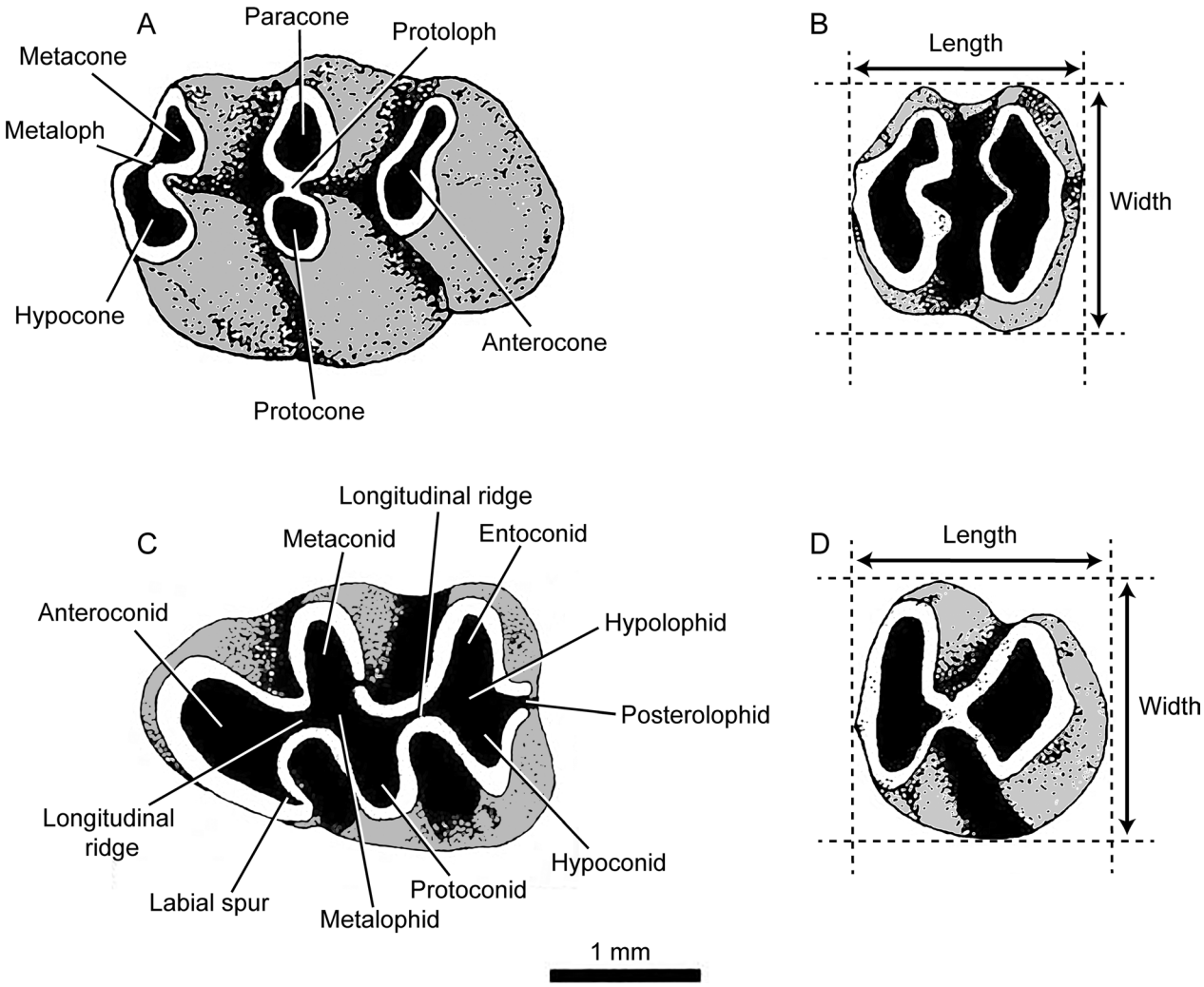

Figure 2. Nomenclature used in the descriptions of dental elements (Wood and Wilson 1936) and measuring methods (Minwer-Barakat 2005). Drawings modified from Agustí and Casanovas-Vilar (2003). **A.** Right M1 of *Debruijnimys julii* from Asta Regia; **B.** Right M2 of *Debruijnimys primaevus* sp. nov. from Alcoy 4B; **C.** Left m1 of *Debruijnimys primaevus* sp. nov. from Alcoy 4B; **D.** Left m2 of *Debruijnimys primaevus* sp. nov. from Alcoy 4B.

Type materials. ***Holotype.*** UCM-LPQ1-N5B-DEB-1, isolated right m1.

Paratypes. 15 M1 (UCM-LPQ1-N1-DEB-1, UCM-LPQ1-N2-DEB-1–3, UCM-LPQ1-N3-DEB-1; UCM-LPQ1-N4-DEB-1–5;UCM-LPQ1-DER-DEB-1–5), 5 M2 (UCM-LPQ1-N1-DEB-3–5, UCM-LPQ1-N2-DEB-6, UCM-LPQ1-DER-DEB-6), 1 M3 (UCM-LPQ1-N2-DEB-7), 8 m1 (UCM-LPQ1-N1-DEB-2, UCM-LPQ1-N2-DEB-4, UCM-LPQ1-N2-DEB-5, UCM-LPQ1-N4-DEB-6, UCM-LPQ1-DER-DEB-8–11), 6 m2 (UCM-LPQ1-N1-DEB-6, UCM-LPQ1-N1-DEB-7, UCM-LPQ1-N4-DEB-7, UCM-LPQ1-DER-DEB-7, UCM-LPQ1-DER-DEB-12, UCM-LPQ1-DER-DEB-13), 2m3(UCM-LPQ1-N1-DEB-8,UCM-LPQ1-N5B-DEB-2).

Type locality. La Piquera (41°25'56"N, 3°40'37"W), Duero Basin, Segovia Province, Castile and Leon, Spain (Piñero et al. 2023).

Type horizon. La Piquera (level 5), 5.3–4.6 Ma, earliest Ruscinian, lower part of the MN14 unit, Early Pliocene.

Diagnosis. Small species of *Debruijnimys*, characterised by its small, oval anteroconid and weak connections between this cusp and the loph formed by the protoconid and the metaconid. In the m2, a small posterolophid can be distinguished. In the M1, a longitudinal connection between the anterocone and the protocone is present only at advanced stages of wear. In the M2, a small anteroloph can be present, while the hypocone and metacone are differentiated cusps.

Differential diagnosis. *Debruijnimys primaevus* sp. nov. differs from the type species *D. julii* by its smaller size (Fig. 6) and less developed longitudinal ridges in the m1. Moreover, the oval anteroconid is smaller and does not present a labial cingulum. The connection between the anteroconid and the loph formed by the protoconid and the metaconid is weaker. The m2 still presents a small posterolophid. In the M1, a longitudinal connection between the anterocone and the protocone is absent, except in highly worn teeth. In the M2, a small anteroloph

is still present, while the hypocone and metacone are differentiated cusps.

Debruijnimys primaevus sp. nov. differs from *Debruijnimys davidi* (Geraads, 1998) by its larger size (Fig. 6). The anterocone is larger and less rounded than in *D. davidi*. Moreover, the anteroconid is also larger and lacks the longitudinal connection between the protoconid and the loph formed by the hypoconid and the entoconid that is present in the m1 of *D. davidi*. In the M2, the paracone and metacone are not connected, as occasionally occurs in *D. davidi*. The M3 of *D. primaevus* sp. nov. is larger than that of *D. davidi*.

Debruijnimys primaevus sp. nov. differs from *Protatera almenarensis* Agustí, 1989 by the presence of a longitudinal ridge in the m1 and its small, simple anteroconid. Although the size ranges overlap, *P. almenarensis* is, on average, slightly larger than this species (Fig. 6).

Stratigraphic and geographic range. Early Pliocene (MN14) of the Iberian Peninsula: La Piquera (Duero Basin); Botardo C, Botardo D (Guadix-Baza Basin); Alcoy-4B (Alcoi/Alcoy Basin); Puerto de la Cadena, Sifón de Librilla 413 (Fortuna Basin); La Bullana-2B (Cabriel Basin); La Gloria-4 (Teruel Basin).

Measurements. See Tables 1–3.

Description. The M1 (n = 15) presents an occlusal pattern formed by three transverse rows. The anterior one is formed by the anterocone. This cusp presents a triangular shape, the anterior wall being its widest side. In less worn teeth (Fig. 3C, D), the anterocone appears to be formed by two independent cusps, the lingual one being larger than the labial one. The posterior walls of the anterocone are projected backwards without reaching the protocone in most cases. A second transverse row is formed by the protocone and the paracone, which are medially fused in worn specimens. In less worn teeth (Fig. 3C, D), the two cusps are already connected, but not fused into a single row, both displaying a similar size. The third transverse row is formed by the hypocone and the metacone, the hypocone being larger than the metacone. In less worn specimens, both cusps are connected, but not fused (Fig. 3C, D, K). Finally, in three cases, the three parallel rows are found medially connected by a longitudinal ridge (Fig. 3F, H, I).

The M2 (n = 5) presents an occlusal pattern formed by two transverse rows. The anterior one is formed by the protocone and the paracone. A small anteroloph attached to this anterior lobe may be present (Fig. 4B, C). The protocone and paracone are always medially connected (Fig. 4D, E), the two cusps becoming fused as wear advances (Fig. 4A, B, C). The posterior lobe is formed by the hypocone and the metacone. The hypocone is larger than the metacone, the latter cusp being reduced to a smaller, rounded cusp. Both cusps are medially connected and become fused in advanced worn molars (Fig. 4B).

The M3 (n = 1) presents an occlusal pattern formed by a main lobe that includes the protocone and the paracone. A small, oblique cuspule can be recognised, connected to the posterior wall of the main lobe.

The m1 (n = 9) presents an oval and asymmetric anteroconid, with no evidence of a labial spur. In unworn teeth (Fig. 5H, I), it is still isolated, but as wear advances, its posterior wall reaches the medial part of the row formed by the protoconid and the metaconid, developing an anterior longitudinal ridge (Fig. 5A, D, G). The protoconid and metaconid are always connected, even in unworn teeth (Fig. 5H, I). As wear advances, they become widely confluent, forming a simple transverse ridge (Fig. 5A, D, G). The hypoconid and entoconid are always fused, forming a simple,

Table 1. Measurements (in mm) of the teeth of *Debruijnimys primaevus* sp. nov. from La Piquera, Early Pliocene, Duero Basin, Spain. σ, standard deviation.

		Length					Width				
Element	**Level**	**N**	**Min**	**Mean**	**Max**	**σ**	**N**	**Min**	**Mean**	**Max**	**σ**
M1	Level 1						1		1.90		
	Level 2	2	2.82	2.84	2.85	0.02	3	1.91	1.98	2.09	0.09
	Level 3	1		2.90			1		2.04		
	Level 4	4	2.78	2.88	3.05	0.12	5	1.96	1.99	2.00	0.02
	Debris	5	2.68	2.80	2.93	0.12	5	1.78	1.96	2.08	0.11
M2	Level 1	3	1.60	1.68	1.74	0.07	3	1.88	1.90	1.92	0.02
	Level 2	1		1.78			1		1.76		
	Debris	1		1.89			1		1.94		
M3	Level 2	1		0.99			1		1.19		
m1	Level 1	1		2.63			1		1.68		
	Level 2	2	2.80	2.91	3.01	0.15	2	1.75	1.76	1.76	0.01
	Level 4	1		2.88			1		1.87		
	Level 5	1		2.94			1		1.74		
	Debris	3	2.71	2.83	2.92	0.11	3	1.68	1.78	1.86	0.09
m2	Level 1	2	1.71	1.73	1.75	0.03	2	1.72	1.76	1.79	0.05
	Level 4	1		1.80			1		1.91		
	Debris	3	1.71	1.81	1.88	0.09	3	1.81	1.85	1.88	0.04
m3	Level 1	1		0.92			1		1.28		
	Level 5	1		0.97			1		1.20		

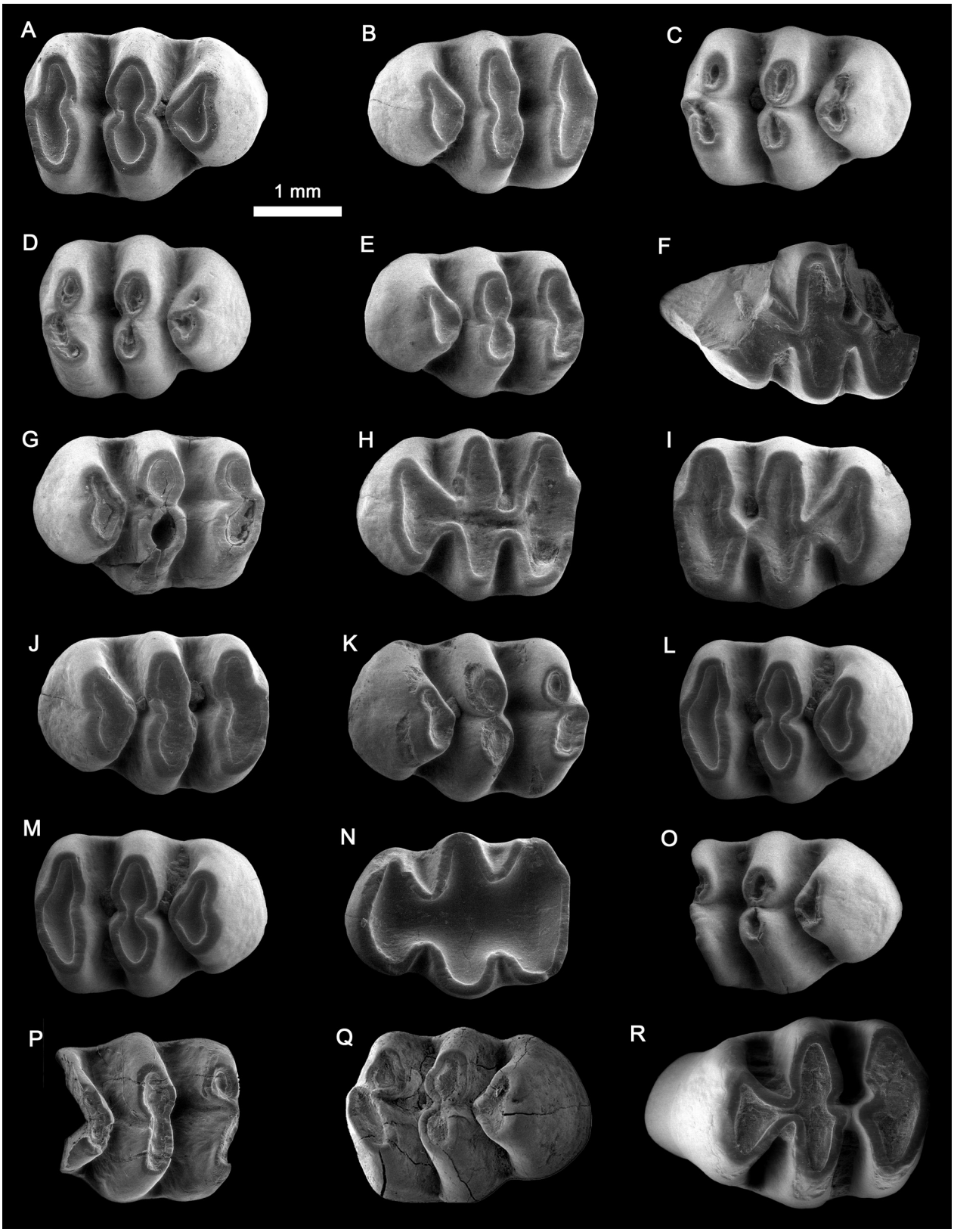

Figure 3. Upper dentition of the gerbils *Debruijnimys primaevus* sp. nov. from La Piquera (A–O; Early Pliocene, Duero Basin, Spain), Sifón de Librilla 413 (P; Early Pliocene, Fortuna Basin, Spain) and Puerto de la Cadena (Q; Early Pliocene, Fortuna Basin, Spain) and *Debruijnimys julii* from Baza-1 (R; Early Pliocene, Guadix-Baza Basin, Spain), in occlusal view. **A.** UCM-LPQ1-DER-DEB-1, right M1 of *D. primaevus* sp. nov. from La Piquera (debris); **B.** UCM-LPQ1-DER-DEB-2, left M1 of *D. primaevus* sp. nov. from La Piquera (debris); **C.** UCM-LPQ1-DER-DEB-3, right M1 of *D. primaevus* sp. nov. from La Piquera (debris); **D.** UCM-LPQ1-DER-DEB-4, right M1 of *D. primaevus* sp. nov. from La Piquera (debris); **E.** UCM-LPQ1-DER-DEB-5, left M1 of *D. primaevus* sp. nov. from La Piquera (debris); **F.** UCM-LPQ1-N1-DEB-1, left M1

Table 2. Individual tooth measurements (in mm) of *Debruijnimys primaevus* sp. nov. from La Piquera, Early Pliocene, Duero Basin, Spain.

Level	Acronym	Element	Length	Width
Level 1	UCM-LPQ1-N1-DEB-1	Left M1 (fragment)	-	1.90
Level 1	UCM-LPQ1-N1-DEB-3	Right M2	1.60	1.89
Level 1	UCM-LPQ1-N1-DEB-4	Right M2	1.70	1.88
Level 1	UCM-LPQ1-N1-DEB-5	Right M2	1.74	1.92
Level 1	UCM-LPQ1-N1-DEB-2	Left m1	2.63	1.68
Level 1	UCM-LPQ1-N1-DEB-6	Left m2	1.75	1.79
Level 1	UCM-LPQ1-N1-DEB-7	Left m2	1.71	1.72
Level 1	UCM-LPQ1-N1-DEB-8	Right m3	0.92	1.28
Level 2	UCM-LPQ1-N2-DEB-1	Left M1 (fragment)	-	1.91
Level 2	UCM-LPQ1-N2-DEB-2	Left M1	2.85	1.95
Level 2	UCM-LPQ1-N2-DEB-3	Left M1	2.82	2.09
Level 2	UCM-LPQ1-N2-DEB-6	Right M2	1.78	1.76
Level 2	UCM-LPQ1-N2-DEB-7	Right M3	0.99	1.19
Level 2	UCM-LPQ1-N2-DEB-4	Left m1	3.01	1.76
Level 2	UCM-LPQ1-N2-DEB-5	Left m1 (Holotype)	2.80	1.75
Level 3	UCM-LPQ1-N3-DEB-1	Right M1	2.90	2.04
Level 4	UCM-LPQ1-N4-DEB-1	Left M1	2.89	1.96
Level 4	UCM-LPQ1-N4-DEB-2	Left M1	3.05	2.00
Level 4	UCM-LPQ1-N4-DEB-3	Right M1	2.78	2.00
Level 4	UCM-LPQ1-N4-DEB-4	Right M1 (fragment)	-	2.00
Level 4	UCM-LPQ1-N4-DEB-5	Left M1	2.81	1.99
Level 4	UCM-LPQ1-N4-DEB-6	Left m1	2.88	1.87
Level 4	UCM-LPQ1-N4-DEB-7	Left m2	1.80	1.91
Level 5	UCM-LPQ1-N5B-DEB-2	Left m3	0.97	1.20
Level 5	UCM-LPQ1-N5B-DEB-1	Right m1	2.94	1.74
Debris	UCM-LPQ1-DER-DEB-1	Right M1	2.93	2.08
Debris	UCM-LPQ1-DER-DEB-2	Left M1	2.79	1.93
Debris	UCM-LPQ1-DER-DEB-3	Right M1	2.90	2.00
Debris	UCM-LPQ1-DER-DEB-4	Right M1	2.69	1.99
Debris	UCM-LPQ1-DER-DEB-5	Left M1	2.68	1.78
Debris	UCM-LPQ1-DER-DEB-6	Left M2	1.89	1.94
Debris	UCM-LPQ1-DER-DEB-8	Left m1	2.85	1.86
Debris	UCM-LPQ1-DER-DEB-9	Right m1	2.92	1.80
Debris	UCM-LPQ1-DER-DEB-10	Left m1	2.71	1.68
Debris	UCM-LPQ1-DER-DEB-11	Left m1 (fragment)	-	-
Debris	UCM-LPQ1-DER-DEB-12	Right m2	1.84	1.86
Debris	UCM-LPQ1-DER-DEB-13	Left m2	1.71	1.81
Debris	UCM-LPQ1-DER-DEB-7	Right m2	1.88	1.88

transverse isolated ridge. In advanced stages of wear, the posterior wall of the protoconid reaches the anterior wall of this ridge, developing a posterior longitudinal ridge. A small, rounded posterolophid is always present, which, in worn teeth, is fused to the posterior lobe (Fig. 5E, F, G).

The m2 (n = 6) presents a simple dental pattern formed by two lobes. The protoconid and metaconid are always fused, forming a transverse lobe. The hypoconid and entoconid are equally fused, forming a simple transverse lobe. In one tooth, a longitudinal ridge connects both transverse lobes (Fig. 5R). In some cases, a small posterolophid can be recognised, attached to the posterior wall of this posterior lobe (Fig. 5M, N).

The m3 (n = 2) presents a very simple occlusal pattern formed by a single transverse lobe.

Remarks. The oldest representatives of *Debruijnimys* are found at the Lissasfa site (Morocco), where Geraads (1998) described the species *Protatera davidi*, later transferred to the genus *Debruijnimys* by Agustí and Casanovas-Vilar (2003). This species differs from *D. primaevus* sp. nov. by its smaller size and more reduced M3. The origin of *Debruijnimys* most probably lies in an archaic species of the genus *Abudhabia* Bruijn and Whybrow 1994, the type species *A. baynunensis* from the Shuwayhat Site S4 (Baynunah Formation, Abu Dhabi; Bruijn and Whybrow (1994)) or the more derived species *A. yardangensis* (Munthe 1987) from the site of Sahabi (Libya; Agustí (2008)). Thus, a slight connection between the anteroconid and the protoconid is already present in the m1 of the latter species (Agustí and Casanovas-Vilar 2003; Agustí 2008), a character that is fully developed in *Debruijnimys* and absent in *Protatera*.

At the site of Lissasfa, *Debruijnimys davidi* appears associated with a small mammal fauna that includes at least two European genera, *Ruscinomys* (*R. africanus*) and *Prolagus* (*P. michauxi*) (Geraads 1998; Sen et al. 2024). The presence of species of European origin in Morocco has already been described at the sites of Aïn Guettara (*Apodemus* aff. *jeanteti*, *Apocricetus* cf. *barrierei*, *Eliomys truci*; Brandy and Jaeger (1980)) and Argoub Kemellal (*Ruscinomys* cf. *lasallei*, *Stephanomys numidicus*, *Castillomys africanus*, *Apodemus gudrunae*; Coiffait et al. (1985); Coiffait-Martin (1991)). Although there is no precise dating for these African sites, it has been assumed that the entry of these European elements into Morocco was a consequence of the terrestrial pathways opened between northern Africa and the Iberian Peninsula during the MSC. Conversely, African rodents of the genus *Debruijnimys* also entered western Europe from northern Africa (Agustí 1989b; Agustí and Casanovas-Vilar 2003; García-Alix et al. 2016).

After its entry into the Iberian Peninsula in the Late Miocene, *Debruijnimys primaevus* sp. nov. persisted into the Early Pliocene (Agustí 1991; Adrover et al. 1993; Agustí and Casanovas-Vilar 2003; Mansino et al. 2015; Piñero et al. 2017a, 2017b, 2023; Piñero and Agustí 2019, 2020), the last representatives of the genus (*D. julii*)

of *D. primaevus* sp. nov. from La Piquera (level 1); **G.** UCM-LPQ1-N2-DEB-2, left M1 of *D. primaevus* sp. nov. from La Piquera (level 2); **H.** UCM-LPQ1-N2-DEB-3, left M1 of *D. primaevus* sp. nov. from La Piquera (level 2); **I.** UCM-LPQ1-N3-DEB-1, right M1 of *D. primaevus* sp. nov. from La Piquera (level 3); **J.** UCM-LPQ1-N4-DEB-1, left M1 of *D. primaevus* sp. nov. from La Piquera (level 4); **K.** UCM-LPQ1-N4-DEB-2, left M1 of *D. primaevus* sp. nov. from La Piquera (level 4); **L.** UCM-LPQ1-N4-DEB-3, right M1 of *D. primaevus* sp. nov. from La Piquera (level 4); **M.** UCM-LPQ1-N4-DEB-3, right M1 of *D. primaevus* sp. nov. from La Piquera (level 4); **N.** UCM-LPQ1-N4-DEB-5, left M1 of *D. primaevus* sp. nov. from La Piquera (level 4); **O.** UCM-LPQ1-N4-DEB-4, right M1 of *D. primaevus* sp. nov. from La Piquera (level 4); **P.** IPS-101286, left M1 of *D. primaevus* sp. nov. from Sifón de Librilla 413; **Q.** MAM/DA/2012-0019/A5′06-1, right M1 of *D. primaevus* sp. nov from Puerto de la Cadena; **R.** BA1-2001-R11/1, right M1 of *D. julii* from Baza-1.

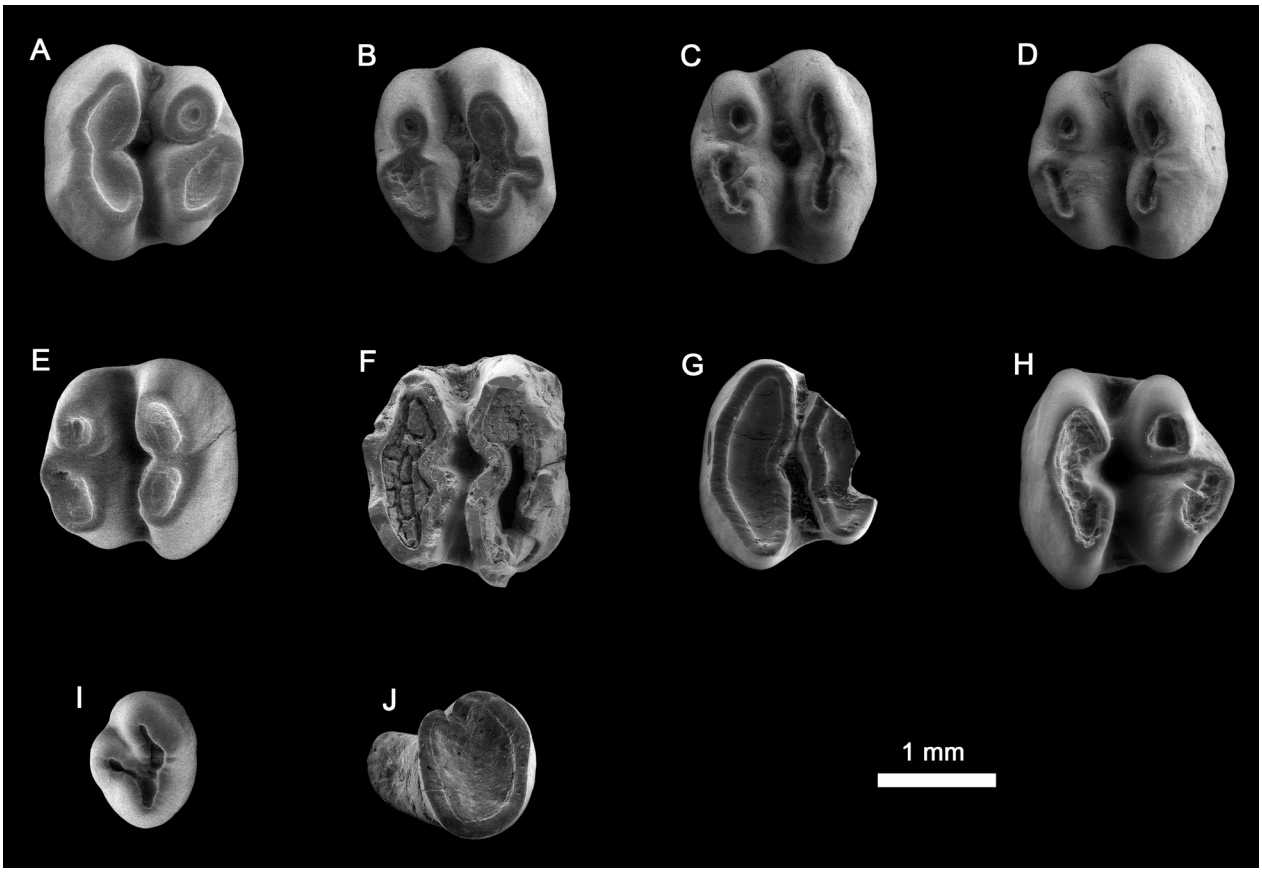

Figure 4. Upper dentition of the gerbils *Debruijnimys primaevus* sp. nov. from La Piquera (A–E, I; Early Pliocene, Duero Basin, Spain), Botardo D (F; Early Pliocene, Guadix-Baza Basin, Spain) and Sifón de Librilla 413 (G, J; Early Pliocene, Fortuna Basin, Spain) and *Debruijnimys julii* from Baza-1 (H; Early Pliocene, Guadix-Baza Basin, Spain), in occlusal view. **A.** UCM-LPQ1-DER-DEB-6, left M2 of *D. primaevus* sp. nov. from La Piquera (debris); **B.** UCM-LPQ1-N1-DEB-3, right M2 of *D. primaevus* sp. nov. from La Piquera (level 1); **C.** UCM-LPQ1-N1-DEB-4, right M2 of *D. primaevus* sp. nov. from La Piquera (level 1); **D.** UCM-LPQ1-N1-DEB-5, right M2 of *D. primaevus* sp. nov. from La Piquera (level 1); **E.** UCM-LPQ1-N2-DEB-6, right M2 of *D. primaevus* sp. nov. from La Piquera (level 2); **F.** IPS-116139, right M2 of *D. primaevus* sp. nov. from Botardo D; **G.** IPS-101291, left M2 of *D. primaevus* sp. nov. from Sifón de Librilla 413; **H.** BA1-2001-R11/3, right M2 of *D. julii* from Baza-1; **I.** UCM-LPQ1-N2-DEB-7, right M3 of *D. primaevus* sp. nov. from La Piquera (level 2); **J.** IPS-101289, right M3 of *D. primaevus* sp. nov. from Sifón de Librilla 413.

Table 3. Measurements (in mm) of the teeth of the Spanish gerbils *Debruijnimys primaevus* sp. nov. (Early Pliocene), *Debruijnimys julii* (Early Pliocene), *Protatera salvadori* (Early Pliocene), and *Protatera almenarensis* (Late Miocene), as well as the Moroccan *Debruijnimys davidi* (Mio-Pliocene boundary) and the Algerian *Protatera algeriensis* (Late Miocene). Abbreviations: ACB-M, Almenara Casablanca M (Agustí 1989a); AMA-2, Amama 2 (Jaeger 1977); AR-3, Asta Regia 3 (Castillo and Agustí 1996); BO-C, Botardo C (Martín-Suárez 1988); BO-D, Botardo D (Piñero and Agustí 2020); BZ-1, Baza 1 (Piñero et al. 2017b); LB-2B, La Bullana 2B (Mansino et al. 2015); GOR-4, Gorafe 4 (Martín-Suárez 1988); LG-4, La Gloria 4 (Adrover et al. 1993); LP, La Piquera (this paper); LSF, Lissasfa (Geraads 1998); NEG-1, Negratín 1 (Minwer-Barakat et al. 2009); PC, Puerto de la Cadena (Piñero et al. 2017a); SAL, Salobreña (Aguilar et al. 1984); SF, Ses Fontanelles (Agustí et al. 2026); SIF-413, Sifón de Librilla 413 (Piñero and Agustí 2019); ZOR, Zorreras (Martín-Suárez et al. 2000).

Species	Site	Element	Length				Width			
			N	Min	Mean	Max	N	Min	Mean	Max
D. primaevus	LP	M1	12	2.68	2.84	3.05	15	1.78	1.97	2.09
		M2	5	1.60	1.74	1.89	5	1.76	1.88	1.94
		M3	1		0.99		1		1.19	
		m1	8	2.63	2.84	3.01	8	1.68	1.77	1.87
		m2	6	1.71	1.78	1.88	6	1.72	1.83	1.91
		m3	2	0.92	0.95	0.97	2	1.20	1.24	1.28
D. primaevus	PC	M1	2	2.76	2.82	2.88	1		2.07	
D. primaevus	BO-D	M1	1		>2.60		1		2.00	
		M2	1		1.82		1		2.00	
		m1	1		2.73		1		1.83	
		m2	1		1.85		1		1.91	

Species	Site	Element	Length				Width			
			N	Min	Mean	Max	N	Min	Mean	Max
D. primaevus	BO-C	m2					1		>1.60	
D. primaevus	SIF-413	M1					2	2.01	2.02	2.03
		M2					1		1.86	
		M3	1		1.21		1		1.01	
		m1	1		2.94		3		1.85	
D. primaevus	LB-2B	M1	1		2.78		1		2.03	
D. primaevus	LG-4	M2	1		1.64		1		1.84	
D. julii	AR-3	M1	4	2.76	3.02	3.19	3	2.14	2.18	2.26
		M2	2	1.75	1.89	2.03	2	2.00	2.01	2.02
		M3	1		0.92		1		1.30	
		m1	4	2.84	2.98	3.11	4	1.87	1.94	2.05
		m2	2	1.80	1.89	1.98	2	1.99	2.00	2.01
D. julii	GOR-4	m2	1		1.87		1		2.21	
D. julii	BZ-1	M1	1		3.16		1		2.23	
		M2	1		1.96		1		1.97	
		m1	1		3.05		2	1.97	2.06	2.14
D. davidi	LSF	M1	302	2.04	2.30	2.56	288	1.40	1.59	1.69
		M2	151	1.22	1.36	1.49	153	1.27	1.45	1.71
		M3	20	0.76	0.82	0.91	20	0.85	0.92	1.04
		m1	269	2.10	2.31	2.53	263	1.31	1.42	1.56
		m2	152	1.28	1.36	1.56	142	1.27	1.41	1.54
		m3	28	0.73	0.82	0.93	29	0.91	1.02	1.13
P. salvadori	SF	M1	1		3.77		1		>2.15	
		M3	1		1.28		1		1.56	
		m2					1		2.54	
P. almenarensis	ACB-M	M1	3	2.85	2.93	3.09	6	2.00	2.10	2.22
		M2	4	1.71	1.75	1.83	4	1.86	1.97	2.06
		M3	4	1.01	1.11	1.19	4	1.39	1.42	1.44
		m1	3	2.91	2.97	3.03	4	1.77	1.89	1.99
		m2	3	1.76	1.81	1.88	3	1.81	1.86	1.92
		m3	5	1.23	1.34	1.43	5	1.35	1.45	1.52
P. almenarensis	ZOR-2B	M1	1		2.98		1		2.08	
P. almenarensis	ZOR-3A	M2	1		1.83		1		2.06	
P. almenarensis	NEG-1	M1	2	2.91	2.92	2.93	2	2.06	2.08	2.10
		M2	2	1.76	1.77	1.77	2	1.84	1.85	1.86
		M3	1		1.08		1		1.40	
		m2	1		1.68		1		1.78	
		m3	1		1.11		1		1.22	
P. almenarensis	SAL	m1	1		>2.43		1		1.83	
P. algeriensis	AMA-2	M1	11	2.88	2.92	3.04	14	1.79	1.95	2.15
		M2	8	1.60	1.70	1.74	8	1.57	1.76	1.89
		M3	6	1.11	1.25	1.36	6	1.25	1.33	1.45
		m1	7	2.45	2.67	2.88	7	1.76	1.87	1.95
		m2	15	1.61	1.70	1.78	15	1.57	1.79	1.92
		m3	6	0.99	1.13	1.23	6	1.35	1.42	1.57

being present in the late Early Pliocene of Asta Regia 3 (Castillo and Agustí 1996), Baza 1 (Piñero et al. 2017b) and Gorafe 4 (Martín-Suárez 1988) (Fig. 7).

Discussion

Besides *Debruijnimys primaevus* sp. nov., a second Taterillinae gerbil, *Protatera almenarensis*, was also present in the Iberian Peninsula during the Miocene–Pliocene transition (Fig. 7). It was first recognised at the site of Almenara-Casablanca M (Castelló/Castellón, Spain; Agustí 1989a), in association with a mammalian assemblage including *Parasorex ibericus*, *Blarinella* cf. *europaea*, *Protatera almenarensis*, *Myocricetodon jaegeri*, *Apodemus gudrunae*, *Paraethomys meini*, *Occitanomys* sp., *Stephanomys ramblensis*, *Ruscinomys lasallei*, *Apocricetus alberti*, *Blancomys* sp., *Calomyscus delicatus*, *Pseudomeriones abbreviatus*, *Macaca* sp. and *Pliohyrax graecus* (Agustí 1989a; Pickford et al. 1997; Köhler et al. 2000; Minwer-Barakat et al. 2009; Agustí et al. 2011; Furió and Agustí 2017). The presence of *P. almenarensis* in the latest Messinian reddish continental beds of the Zorreras Fm. in the Sorbas Basin (southern Spain; Martín-Suárez et al. (2000)) suggests that the entry of these allochthonous elements into the Iberian

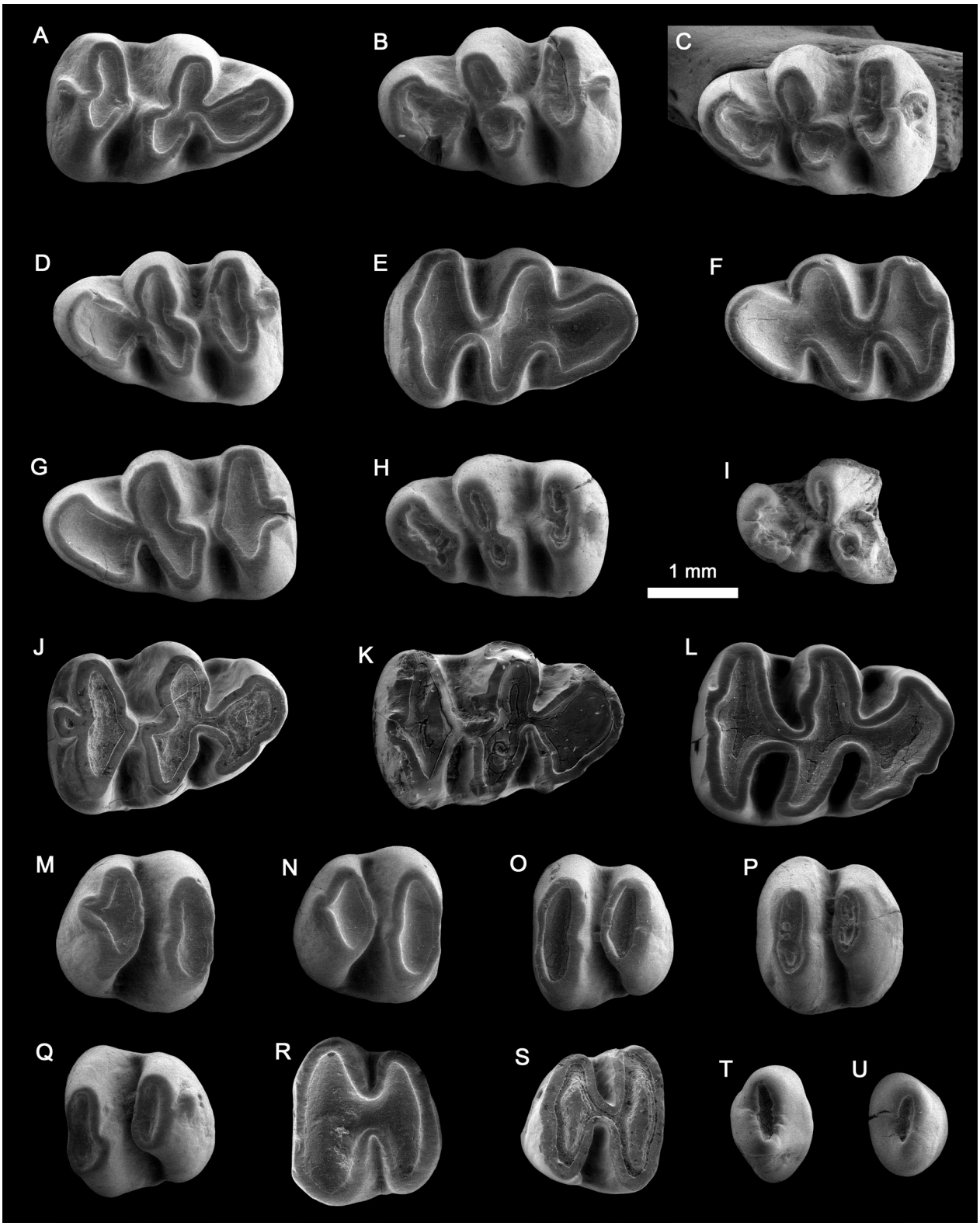

Figure 5. Lower dentition of the gerbils *Debruijnimys primaevus* sp. nov. from La Piquera (A–I, M–R, T, U; Early Pliocene, Duero Basin, Spain), Botardo D (J, S; Early Pliocene, Guadix-Baza Basin, Spain) and Sifón de Librilla 413 (K; Early Pliocene, Fortuna Basin, Spain), and *Debruijnimys julii* from Baza-1 (L; Early Pliocene, Guadix-Baza Basin, Spain), in occlusal view. **A.** UCM-LPQ1-N5B-DEB-1, right m1, holotype of *D. primaevus* sp. nov. from La Piquera (level 5); **B.** UCM-LPQ1-N4-DEB-6, left m1 of *D. primaevus* sp. nov. from La Piquera (level 4); **C.** UCM-LPQ1-N2-DEB-5, left m1 of *D. primaevus* sp. nov. from La Piquera (level 2); **D.** UCM-LPQ1-DER-DEB-8, left m1 of *D. primaevus* sp. nov. from La Piquera (debris); **E.** UCM-LPQ1-DER-DEB-9, right m1 of *D. primaevus* sp. nov. from La Piquera (debris); **F.** UCM-LPQ1-DER-DEB-10, left m1 of *D. primaevus* sp. nov. from La Piquera (debris); **G.** UCM-LPQ1-N2-DEB-4, left m1 of *D. primaevus* sp. nov. from La Piquera (level 2); **H.** UCM-LPQ1-N1-DEB-2, left

Peninsula took place during the Lago Mare episode of the late Messinian, which correlates with the upper evaporites dated between 5.55 and 5.33 Ma (Krijgsman et al. 2024; Roveri et al. 2025).

According to this scenario, the presence of *Debruijnimys primaevus* sp. nov. in the Early Pliocene of the Iberian Peninsula could be easily explained as a case of local evolution from *Protatera almenarensis*. However, as discussed above, *Debruijnimys primaevus* sp. nov. derives from the African species *Debruijnimys davidi*. This is also supported by the more derived features of *Protatera almenarensis* with respect to *Debruijnimys primaevus* sp. nov., such as its slightly larger size and larger, bilobate anteroconid. In turn, the origin of *Protatera almenarensis*, as well as its local descendant *Protatera salvadori* from Eivissa (Agustí et al. 2026), most probably lies in *Protatera algeriensis* from the locality of Amama 2 (Algeria; Jaeger (1977)), although an Asian origin cannot be excluded. This makes it difficult to consider *Protatera almenarensis* as a feasible ancestor of *Debruijnimys primaevus* sp. nov. Therefore, the entry of *Debruijnimys primaevus* sp. nov. into the Iberian Peninsula should be interpreted as the result of a second, more recent mammalian dispersal from Africa.

Thus, during the Lago Mare stage of the Messinian, at least two different episodes of mammalian exchange occurred between the two shores of the Mediterranean. The first is represented by the fauna of Almenara-Casablanca M, which includes species of African affinities, such as *Macaca* sp., *Myocricetodon jaegeri* and possibly *Protatera almenarensis*, as well as others of clear Asian affinities, such as *Blancomys* sp., *Calomyscus delicatus*, *Pseudomeriones abbreviatus* and *Pliohyrax graecus*. Therefore, the mammalian faunas from Almenara-Casablanca M, as well as those from Salobreña (Aguilar et al. 1984) and Negratín 1 (Minwer-Barakat et al. 2009), show a mixed character, including both African and Asian elements. This indicates that, at this stage, the MSC opened new corridors not only with northern Africa, but also with Asia, including taxa originating as far as China, such as *Pseudomeriones abbreviatus*. This episode is consistent with the scenario proposed by Moyà-Solà et al. (1984), according to which eastern mammals entered western Europe and northern Africa through both northern and southern Mediterranean terrestrial corridors opened during the late Messinian. This would explain the mixture of Asian and African elements found in the Almenara-Casablanca M, Salobreña and Negratín 1 faunas, as well as in that of Maritsa (Rhodes, Greece), in the Paratethyan domain, which again includes species of the genera *Paraethomys*, *Calomyscus* and *Pseudomeriones* (Bruijn et al. 1970).

In turn, Agustí (1989b) proposed an alternative scenario involving direct Iberia–North Africa exchange, which would explain the persistence of *Debruijnimys* in several Early Pliocene sites of the Iberian Peninsula. Both scenarios are now compatible within the framework of a complex third stage of the Messinian that included at least three different substages (Andreetto et al. 2021; García-Castellanos et al. 2025). A first substage at 5.546 Ma involved the reduction of the average surface area of the Pannonian and Paratethys lakes to around 635,000 km^2 (García-Castellanos et al. 2025). This reduction led to the opening of broad terrestrial corridors between the emerged Paratethyan areas and the western Mediterranean margins (both north and south), favouring the dispersal of western Eurasian and North African taxa, as evidenced by the Almenara-Casablanca M and Salobreña faunas.

During the second Lago Mare episode, the western Mediterranean Basin level rose by about 100 m due to the inflow of fresh water from the eastern Mediterranean, reaching levels close to present sea level. This explains the presence of Lago Mare facies in places such as Mallorca (Balearic archipielago, Spain), at 70 m above present sea level (Mas and Fornós 2020). This sea-level rise also explains the insular phase recorded at the site of Ses Fontanelles in Eivissa (Balearic archipielago, Spain), characterised by the presence of African elements such as *Protatera salvadori* and *Myosorex* sp. (Agustí et al. 2026), which most probably entered the Eivissa area during the first mammalian dispersal in substage 1 of the Lago Mare stage. Tentatively, this could also be the case for the insular faunas including the leporid *Nuralagus rex*, the dormouse *Muscardinus cyclopaeus* and giant tortoises from Punta Nati–Cala es Pous in Menorca (Balearic archipelago, Spain; Agustí et al. (1982); Quintana et al. (2011)), which predate the Plio-Pleistocene faunas, characterised by *Myotragus*, *Hypnomys* and *Nesiotites*. The existence of a Messinian, pre-Pliocene phase of insularity in the Balearic archipelago was already proposed by Moyà-Solà et al. (1984).

At 5.338 Ma, a new sea-level drop is recorded, which explains the end of the insular phase documented at Ses

m1 of *D. primaevus* sp. nov. from La Piquera (level 1); **I.** UCM-LPQ1-DER-DEB-11, anterior portion of left m1 of *D. primaevus* sp. nov. from La Piquera (debris); **J.** IPS-116124, right m1 of *D. primaevus* sp. nov. from Botardo D; **K.** IPS-101292, right m1 of *D. primaevus* sp. nov. from Sifón de Librilla 413; **L.** BA1-2001-R11-1, right m1 of *D. julii* from Baza-1; **M.** UCM-LPQ1-DER-DEB-7, right m2 of *D. primaevus* sp. nov. from La Piquera (debris); **N.** UCM-LPQ1-DER-DEB-12, right m2 of *D. primaevus* sp. nov. from La Piquera (debris); **O.** UCM-LPQ1-DER-DEB-13, left m2 of *D. primaevus* sp. nov. from La Piquera (debris); **P.** UCM-LPQ1-N1-DEB-6, left m2 of *D. primaevus* sp. nov. from La Piquera (level 1); **Q.** UCM-LPQ1-N1-DEB-7, left m2 of *D. primaevus* sp. nov. from La Piquera (level 1); **R.** UCM-LPQ1-N4-DEB-7, left m2 of *D. primaevus* sp. nov. from La Piquera (level 4); **S.** IPS-116138, right m2 of *D. primaevus* sp. nov. from Botardo D; **T.** UCM-LPQ1-N1-DEB-8, right m3 of *D. primaevus* sp. nov. from La Piquera (level 1); **U.** UCM-LPQ1-N5B-DEB-2, left m3 of *D. primaevus* sp. nov. from La Piquera (level 5).

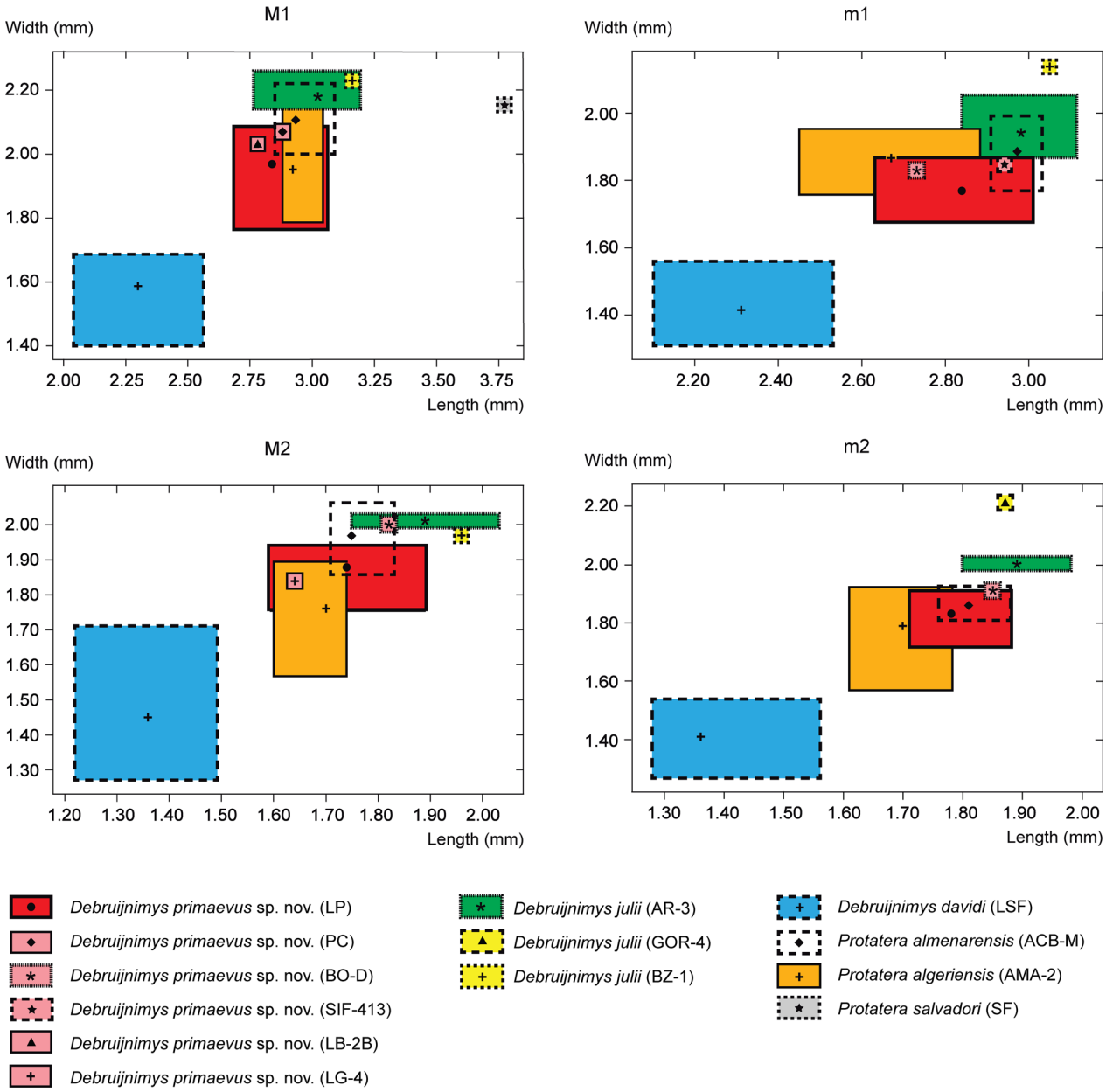

Figure 6. Ranges of size variation (in mm) in the upper (M1 and M2) and lower (m1 and m2) teeth of *Debruijnimys primaevus* sp. nov. from La Piquera (LP, type locality; this paper), Puerto de la Cadena (PC; Piñero et al. (2017a)), Botardo D (BO-D; Piñero and Agustí (2020)), Sifón de Librilla 413 (SIF-413; Piñero and Agustí (2019)), La Bullana 2B (LB-2B; Mansino et al. (2015)) and La Gloria 4 (LG-4; Adrover et al. (1993)); *Debruijnimys julii* from Asta Regia 3 (AR-3, type locality; Castillo and Agustí 1996), Gorafe 4 (GOR-4; Martín-Suárez (1988)) and Baza 1 (BZ-1; Piñero et al. (2017b)); *Debruijnimys davidi* from Lissasfa (LSF, type locality; Geraads (1998)); *Protatera almenarensis* from Almenara Casablanca M (ACB-M, type locality; Agustí (1989a)); *Protatera algeriensis* from Amama 2 (AMA-2; Jaeger (1977)); and *Protatera salvadori* from Ses Fontanelles (SF, type locality; Agustí et al. (2026)). Mean sizes are marked by symbols inside the boxes.

Fontanelles in Eivissa and possibly that of Punta Nati-Cala es Pous in Menorca. Most probably this is the time at which *Debruijnimys* dispersed into Iberia directly from northern Africa, as proposed by Agustí (1989b) (Fig. 7). This is probably also the time when the ancestors of the endemic taxa *Myotragus*, *Hypnomys* and *Nesiotites* dispersed into the emerged areas of Mallorca and Menorca. The Zanclean flood at 5.333 Ma led to the present configuration of the Balearic archipelago and the isolation of these faunas.

Conclusions

The new gerbil species *Debruijnimys primaevus* sp. nov. is described for the first time from the Early Pliocene site

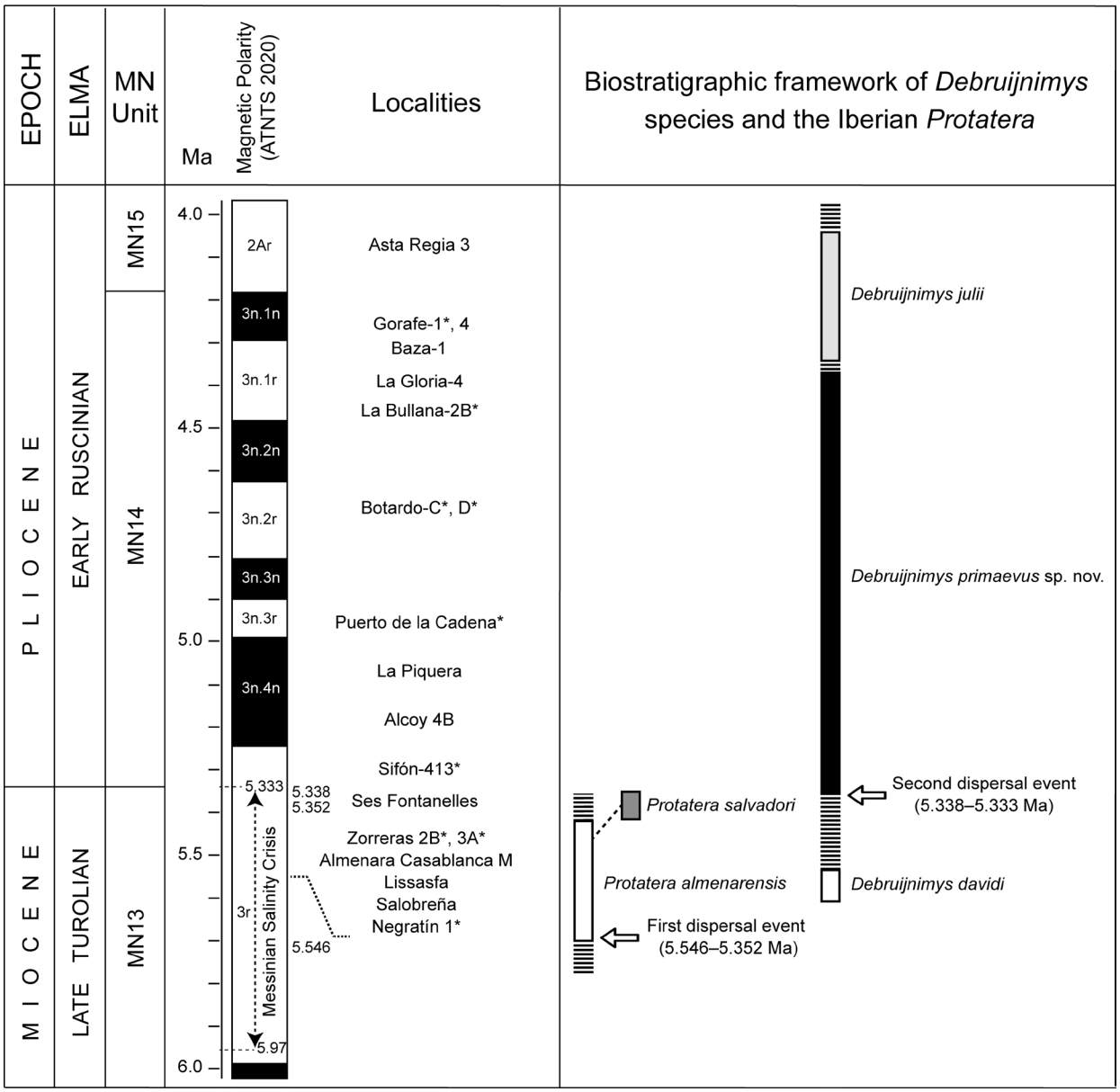

Figure 7. Biostratigraphic distribution and evolution of *Debruijnimys* species and the Iberian *Protatera*, showing their chronological ranges. The localities marked with an asterisk are calibrated with palaeomagnetic data (Garcés et al. 1998, 2001;Martín-Suárez et al. 2000; Mansino et al. 2015; Piñero et al. 2017a, 2018). Arrows indicate the two dispersal events of gerbils into the Iberian Peninsula. Abbreviations: ATNTS, Astronomically Tuned Neogene Time Scale; ELMA, European Land Mammal Ages; MN, Mammal Neogene.

of La Piquera (Duero Basin, central Spain). Its distribution range also includes the Teruel, Alcoi/Alcoy, Cabriel, Fortuna and Guadix-Baza basins, all in Spain. This species occupies an intermediate position between *D. davidi* from the Moroccan site of Lissasfa and the type species of the genus, *D. julii*, from the site of Asta Regia (Jerez Basin, southern Spain). *Debruijnimys primaevus* sp. nov. is not related to the previously described *Protatera almenarensis* from the site of Almenara-Casablanca M.

Therefore, the presence of the two gerbils in the Iberian Peninsula corresponds to two separate dispersal events during the Messinian (Fig. 7). According to the proposed scenario, the first took place during the first substage of the Lago Mare phase of the Messinian, between 5.546 and 5.352 Ma, involving the entry of African as well as Asian immigrants, such as those present at the sites of Almenara-Casablanca M and Salobreña. The second, corresponding to the third substage of the Lago Mare phase (5.338–5.333 Ma), involved the entry of members of the genus *Debruijnimys* into the Iberian Peninsula directly from northern Africa, where they survived until the Early Pliocene (species *D. primaevus* sp. nov. and *D. julii*).

In between, the intra-Messinian highstand of the Lago Mare facies in the western Mediterranean, between 5.352 and 5.338 Ma, led to the development of endemic insular faunas in the Balearics, such as that of Ses Fontanelles (Eivissa), prior to the Zanclean flood.

Competing interests

The authors declare that they have no conflict of interest.

Author contributions

The study is based on fieldwork conducted by all authors. The systematic study was carried out by JA and PP. All authors contributed to the discussion. HAB was responsible for funding acquisition. The manuscript was prepared by JA with contributions from all co-authors.

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