A new early Pliocene murine rodent from the Iberian Peninsula and its biostratigraphic implications

PEDRO PIÑERO and DIEGO H. VERZI

In the last years, a murine identified as *Paraethomys* aff. *abaigari* has been repeatedly recognized in several early Pliocene localities of the Iberian Peninsula. We have revised these occurrences, as well as other samples of similar morphology, and propose that all these records correspond to a new species. We diagnose *Paraethomys baeticus* sp. nov. based on a large sample from the early Ruscinian site of Baza-1 (Guadix-Baza Basin, Spain). It is a medium-sized representative of the genus, with relatively well-developed longitudinal connections both in upper and lower molars, but incomplete stephanodonty. M1 displays high tubercles t6–t9 and low t4–t8 connections. M1 and, to a lesser extent, M2 have posterior spurs on t1 and t3. The t9 and t12 are absent in M2. In m1, a round islet of enamel between the anteroconid and the protoconid-metaconid is regularly observed, as well as a general lack of medial anteroconid, moderate labial cingulum with large posterior accessory cuspid, and longitudinal spur. The new species differs from other European representatives of the genus *Paraethomys* mainly in its size, which is intermediate between that of the small-sized *Paraethomys meini* and the large-sized *Paraethomys abaigari*. In addition, both the size and relative width are smaller than those of *Paraethomys jaegeri*. The frequency of posterior spurs on t1 and t3 of M1 and M2 is higher than that of *P. meini* and lower than that of *P. jaegeri*. The new species here described represents a key biochronological and biostratigraphic marker, since it is restricted to levels of late early Ruscinian age. Thus, this species is useful for establishing divisions within the early Ruscinian, and becomes a characteristic taxon for the early Pliocene in the terrestrial record of the Iberian Peninsula. Magnetobiostratigraphic correlations suggest a chronological range for *P. baeticus* sp. nov. between ca. 4.6 and 4.3 Ma.

Key words: Mammalia, Murinae, biochronology, diversification pattern, early Ruscinian, Europe.

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Introduction

Murine rodents, commonly known as Old World rats and mice, are the most diverse and abundant of modern mammal subfamilies, comprising over 650 species (Denys et al. 2017). The first unambiguous member of the subfamily Murinae belongs to the genus *Antemus* (Jacobs et al. 1990; Jacobs and Flynn 2005), whose first record is in the Siwalik (Potwar, Pakistan) about 13.8 Ma (Kimura et al. 2013a, b). This group increased its relative abundance from its first appearance, and then it dominated over the cricetids and successfully replaced them in their ecological niches when the stem murine *Progonomys* emerged about 12 Ma (Jacobs et al. 1989; Lazzari et al. 2010). Because of their diversity, abundance, and rapid evolution, murines represent an essential tool for the description of biochronological units in the late Miocene and Pliocene, and therefore for the dating of continental sediments of this time interval (Van de Weerd 1976; Mein et al. 1990; Fahlbusch 1991; Martín-Suárez and Freudenthal 1998; among others). The high evolutionary rates and rapid diversification of this successful group, its cosmopolitanism and record in a wide variety of environments make it an excellent tool for biochronological correlations. Morphological evolutionary changes among species of murines are frequently reflected in the molars (Lazzari et al. 2008), so they can be traced in the fossil record.

The *Paraethomys* is based on *Paraethomys filfilae* Petter, 1968, from the Pleistocene of Jebel Filfila (Algeria). It was a widely distributed murine rodent both in northern Africa and southwestern Europe since the late Miocene. The populations on both shores of the Mediterranean underwent divergent evolutionary processes after their split as early as the

end of the Messinian Salinity Crisis (De Bruijn 1973; Jaeger et al. 1975; Coiffait and Coiffait 1981; Aguilar et al. 1984; Geraads 1998; Renaud et al. 1999; among others). The North African lineage is the most diversified and longest-lived, reaching the late middle Pleistocene, whereas the European representatives of the genus became extinct during the late Pliocene (late Ruscinian).

In Europe, and particularly in the Iberian Peninsula, there is some diversification of the *Paraethomys*. At present, five valid European species, other than the new one here described, are recognized: *Paraethomys meini* (Michaux, 1969), *Paraethomys jaegeri* Montenat and De Bruijn, 1976, *Paraethomys abaigari* Adrover, Mein, and Moissenet, 1988, *Paraethomys belmezensis* Castillo Ruiz, 1992, and *Paraethomys balearicus* Torres-Roig, Piñero, Agustí, Bover, and Alcover, 2019. *Paraethomys meini* is the oldest representative of the genus in Europe and has a long record, reaching the late Ruscinian (early Pliocene). *Paraethomys anomalus* De Bruijn, Dawson, and Mein, 1970, and *Paraethomys miocaenicus* Jaeger, Michaux, and Thaler, 1975, have been reported from a number of European localities (De Bruijn et al. 1970, 1975; Mein et al. 1978, 1990; Brandy 1979; Agustí et al. 1985; Antunes and Mein 1989; Rook 1992; Opdyke et al. 1997; Agustí and Llenas 1996; among others). However, these two latter species are considered synonyms of *P. meini* by several authors (Montenat and De Bruijn 1976; Van de Weerd 1976; Adrover 1986; Martín-Suárez 1988; Freudenthal and Martín-Suárez 1999; Minwer-Barakat et al. 2005, 2009a, b; García-Alix et al. 2008a; Mansino et al. 2016; Piñero et al. 2017a; Piñero and Agustí 2019; among others). *Paraethomys meini* dispersed into Europe probably from northern Africa during the late Turolian (late Miocene), prior to the Messinian Salinity Crisis, at about 6.2 Ma (Garcés et al. 1998; Agustí et al. 2006; Gibert et al. 2013). *Paraethomys* became more diversified during the Pliocene, when larger species such as *Paraethomys jaegeri*, *Paraethomys abaigari*, *Paraethomys belmezensis*, and *Paraethomys balearicus* occurred.

In the last years, a medium-sized murine identified as *Paraethomys* aff. *abaigari* has been repeatedly recognized in several early Pliocene localities of the Iberian Peninsula (García-Alix et al. 2008a; Mansino et al. 2013, 2015a, b; Piñero et al. 2017a; Piñero and Agustí 2019). Biometric and morphological features of these collections described through open nomenclature justify the definition of a new species. In addition, other samples attributed to *Paraethomys* sp. 1, *P.* cf. *meini*, *P. meini*, and *P. anomalus* (De Bruijn 1974; Ruiz Bustos et al. 1984; Martín-Suárez 1988; Adrover et al. 1993) show characteristics similar to those of *P.* aff. *abaigari,* so they should be transferred to the new taxon. These samples, clearly distinct from other murine species, are distributed over a wide geographical range in the Iberian Peninsula, including the basins of Granada (García-Alix et al. 2008a), Guadix-Baza (De Bruijn 1974; Ruiz Bustos et al. 1984; Martín-Suárez 1988; Piñero et al. 2017a), Fortuna (Piñero and Agustí 2019), Alcoy (Mansino et al. 2013, 2015a), Cabriel (Mansino et al.
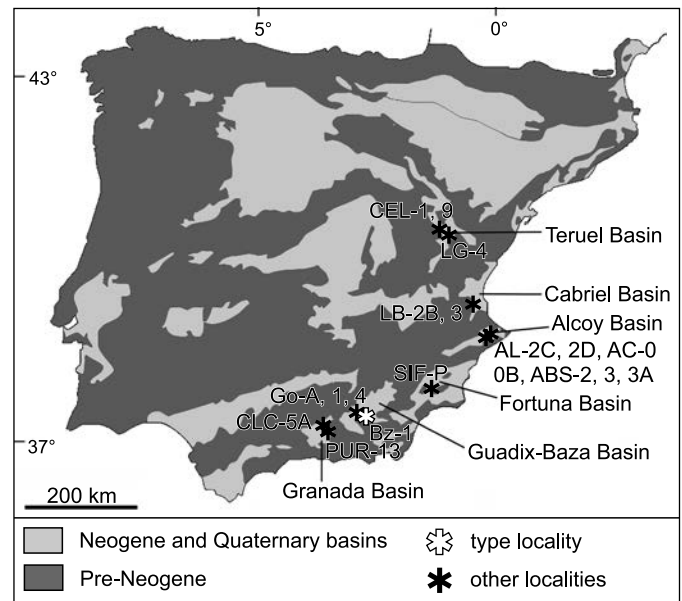

Fig. 1. Simplified geological map of the Iberian Peninsula, indicating the location of the sites where *Paraethomys baeticus* sp. nov. has been reported. The main Neogene and Quaternary basins referred to in the text are also shown. Abbreviations: ABS, Alcoi Barranc Sud (Mansino et al. 2015a); AC, Alcoi Cristian (Mansino et al. 2015a); AL, Alcoy (Mansino et al. 2013); Bz, Baza (Piñero et al. 2017a); CEL, Celadas (Adrover et al. 1993); CLC, Calicasas (García-Alix et al. 2008a); Go, Gorafe (De Bruijn 1974; Agustí and Martín-Suárez 1984; Ruiz Bustos et al. 1984; Martín-Suárez 1988); LB, La Bullana (Mansino et al. 2015b); LG, La Gloria (Adrover et al. 1993); PUR, Purcal (García-Alix et al. 2008a); SIF-P, Sifón Pista (Piñero and Agustí 2019).

2015b) and Teruel (Adrover et al. 1993) (Fig. 1). As the novel species is restricted to levels of similar age, it has significant biochronological value. This fact was recognized in previous works when *P.* aff. *abaigari* was used to name and define biozones from different Iberian basins (Granada Basin, García-Alix et al. 2008b; Alcoy Basin, Mansino et al. 2017; Guadix-Baza Basin, Piñero et al. 2018).

The aim of this paper is to give a clear description of the new species based on the largest and most complete sample from Baza-1 (Piñero et al. 2017a). In addition, we discuss the significance of this new taxon for understanding the biochronology and biostratigraphy of the Pliocene continental deposits from the Iberian Peninsula.

Institutional abbreviations.—IPHES, Institut de Paleoecologia Humana i Evolució Social, Tarragona, Spain; IPS, Institut de Paleontologia de Sabadell (currently named Institut Català de Paleontologia Miquel Crusafont), Barcelona, Spain.

Other abbreviations.—L, length; M1–M3, upper molars; m1–m3, lower molars; t1–t12, numbered tubercles from 1 to 12; tma, medial anteroconid; W, width.

Nomenclatural acts.—This published work and the nomenclatural acts it contains, have been registered in ZooBank: urn:lsid:zoobank.org:act:469E1CBA-4E2F-45BD-8900-0A1F804C0F5A

Material and methods

The sample from Baza-1 assigned to *Paraethomys* aff. *abaigari* by Piñero et al. (2017a) comprised 155 isolated molars. New provisions of sediment from Baza-1 have yielded 19 unpublished specimens attributable to that same taxon. Both samples are used here to characterize *Paraethomys baeticus* sp. nov., comprising a total of 174 isolated teeth (minimum number of individuals = 24). Fossils are owned by the Junta de Andalucía and will be housed in the Museo Arqueológico de Granada, but currently part of the collection (122 specimens) is stored at the Institut de Paleoecologia Humana i Evolució Social (IPHES; Tarragona, Spain), whereas the other part (52 specimens) is kept at the Institut Català de Paleontologia Miquel Crusafont (ICP; Sabadell, Barcelona, Spain). The dental nomenclature and measuring methods for the studied material follow Van de Weerd (1976) and Martín-Suárez and Freudenthal (1993), respectively (see Fig. 2). Homologies of "medial anteroconid", "posterior cingulum", and "labial anteroconid" (in m2 and m3) follow López-Antoñanzas et al. (2019). Measurements of previously published material have been taken again using the same devise as for the novel material. All the measurements are expressed in millimetres and were taken with the software DinoCapture 2.0, using photographs from the Digital Microscope AM4115TL Dino-Lite Edge. Measurements of each specimen are listed in SOM 1: table S1 (Supplementary

Online Material available at http://app.pan.pl/SOM/app65-Pinero_Verzi_SOM.pdf). The illustrations of fossils were made by means of micrographs taken with the environmental scanning electron microscopy (ESEM) of the Servei de Recursos Científics i Tècnics de la Universitat Rovira i Virgili (Tarragona, Spain). Additional archives of digital photographs are included in SOM 2: figs. S1, S2.

Systematic palaeontology

Order Rodentia Bowdich, 1821

Family Muridae Illiger, 1811

Subfamily Murinae Illiger, 1811

Genus *Paraethomys* Petter, 1968

Type species: *Paraethomys filfilae* Petter, 1968; Late Pleistocene, Algeria.

Paraethomys baeticus sp. nov.

Fig. 3; SOM 2: figs. S1, S2.

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1974 *Paraethomys* sp. 1; De Bruijn 1974: 438: pl. 2: 7; text-figs. 1, 3.
1984 *Paraethomys meini* (Michaux, 1969); Agustí and Martín-Suárez 1984: 277.
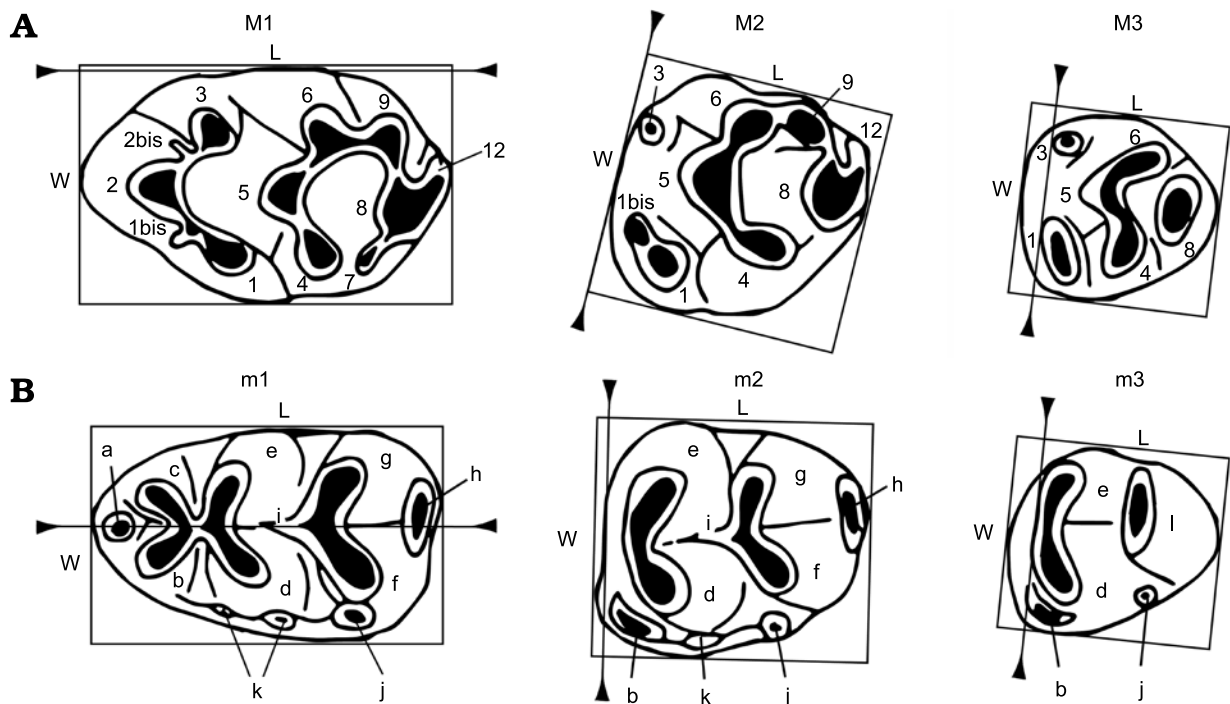

Fig. 2. Nomenclature used in the descriptions of dental elements (modified from Van de Weerd 1976; López-Antoñanzas et al. 2019) and measuring methods (Martín-Suárez and Freudenthal 1993). Length (L) and width (W) are measured as the smallest circumscribed rectangle with sides parallel and perpendicular to the reference line (indicated by triangles). **A**. Upper dentition (M1–M3): 1–12, tubercle (1–12); 1, anterostyle; 2, lingual anterocone; 1bis, 2bis, accessory cusps; 3, labial anterocone; 4, enterostyle; 5, protocone; 6, paracone; 7, posterostyle; 8, hypocone; 9, metacone; 12, posterior cingulum. **B**. Lower dentition (m1–m3): a, medial anteroconid (= tma); b, labial anteroconid; c, lingual anteroconid; d, protoconid; e, metaconid; f, hypoconid; g, entoconid; h, posterior cingulum; i, longitudinal spur; j, posterior accessory cuspid; k, accessory cuspids on the labial cingulum; l, posterior complex.
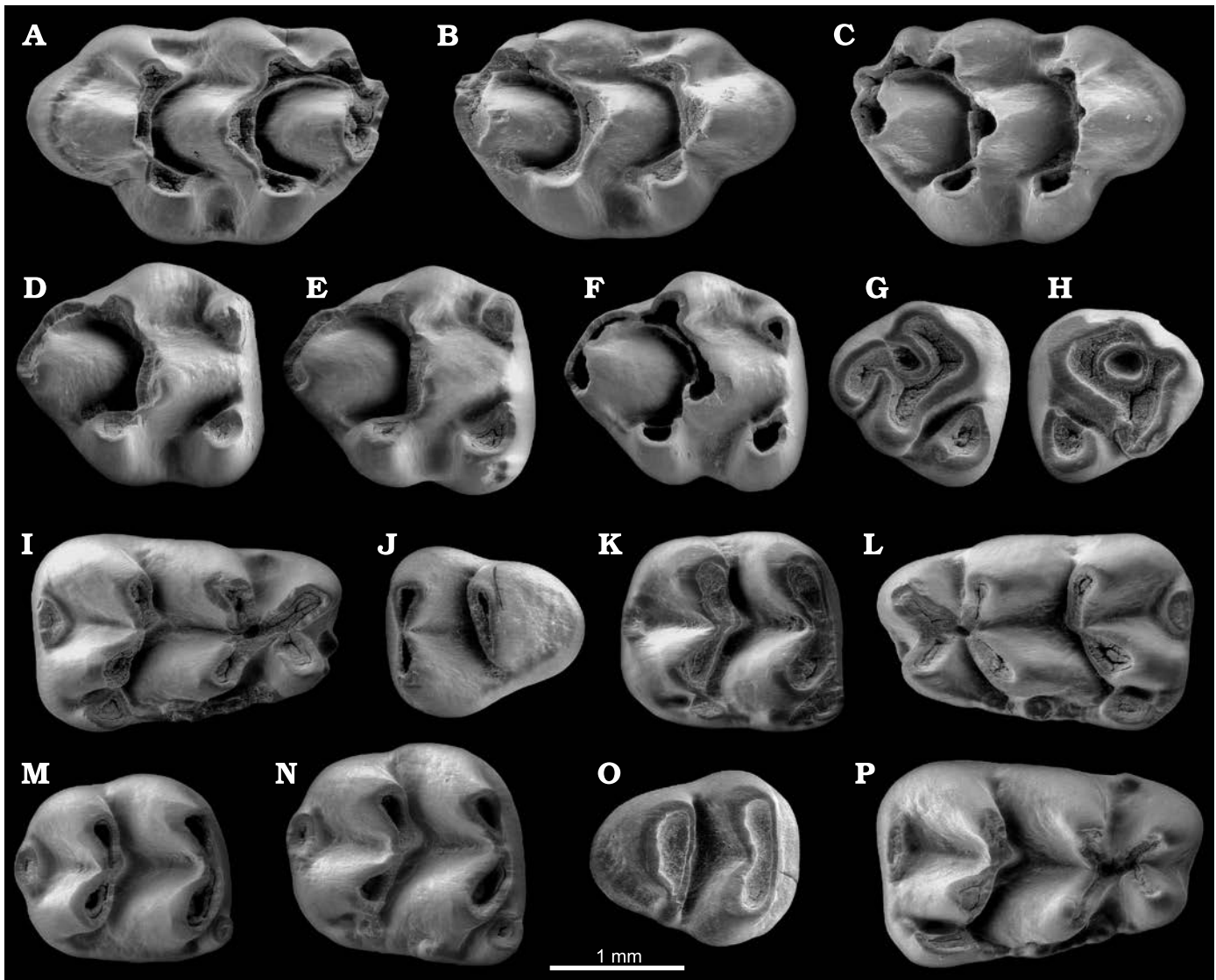
Fig. 3. Upper and lower dentition of the murid rodent *Paraethomys baeticus* sp. nov. from Baza-1, early Pliocene, Guadix-Baza Basin, Spain, in occlusal view. **A**. BA1-2001-R7/2, left M1 (holotype). **B**. BA1-2001-R7/5, right M1. **C**. BA1-2001-R7/16, right M1. **D**. BA1-2001-R7/22, right M2. **E**. BA1-2001-R7/24, right M2. **F**. BA1-2001-R7/25, right M2. **G**. BA1-2001-R8/20, right M3. **H**. BA1-2001-R8/17, left M3. **I**. BA1-2001-R7/32, right m1. **J**. BA1-2001-R8/12, left m3. **K**. BA1-2001-R7/62, right m2. **L**. BA1-2001-R7/43, left m1. **M**. BA1-2001-R7/73, right m2. **N**. BA1-2001-R7/78, right m2. **O**. BA1-2001-R8/3, right m3. **P**. BA1-2001-R7/48, right m1.

1984 *Paraethomys* cf. *meini* (Michaux, 1969); Ruiz Bustos et al. 1984: 236, pl. 2: 7, 8.

1988 *Paraethomys meini* (Michaux, 1969); Martín-Suárez 1988: 80, pl. 1: 14.

1993 *Paraethomys anomalus* Bruijn, Dawson, and Mein, 1970; Adrover et al. 1993: 74, pl. 11: 1–5.

2008 *Paraethomys* aff. *abaigari* Adrover, Mein, and Moissenet, 1988; García-Alix et al. 2008a: 195, pl. 3: AE–AJ.

2013 *Paraethomys* aff. *abaigari* Adrover, Mein, and Moissenet, 1988; Mansino et al. 2013: 271, pl. 3: 18–23.

2015 *Paraethomys* aff. *abaigari* Adrover, Mein, and Moissenet, 1988; Mansino et al. 2015a: 560, pl. 3: E–I.

2015 *Paraethomys* aff. *abaigari* Adrover, Mein, and Moissenet, 1988; Mansino et al. 2015b: 280, pl. 3: 18–22.

2017 *Paraethomys* aff. *abaigari* Adrover, Mein, and Moissenet, 1988; Piñero et al. 2017a: e1338294-9, pl. 5: M–R.

2019 *Paraethomys* aff. *abaigari* Adrover, Mein, and Moissenet, 1988; Piñero and Agustí 2019: 308, pl. 11: I–M, pl. 12: F, M.

Etymology: From Latin masculine adjective *baeticus* [ba.e'ti.cus], in reference to the Roman province Baetica, partially corresponding to modern Andalusia, the place of the type locality.

Type material: Holotype: BA1-2001-R7/2, isolated left M1. Paratypes: 25 M1 (BA1-2001-R7/1, BA1-2001-R7/3–16, BA1-2018-R1/1–5, IPS 89269, IPS89270, IPS89272, IPS89273, IPS89274), 28 M2 (BA1-2001-R7/17–31, BA1-2018-R1/6, IPS89275–89286), 12 M3 (BA1-2001-R8/17–20, BA1-2018-R1/8, IPHES-Bz-1-R8/22, IPS89287, IPS89288, IPS89292–89295), 37 m1 (BA1-2001-R7/32–54, BA1-2018-R1/9–12, IPS8297–82306), 44 m2 (BA1-2001-R7/55–81, BA1-2018-R1/13–16, BA1-2018-R1/18, IPS89308–89319), 27 m3 (BA1-2001-R8/1–16, BA1-2001-R8/21, BA1-2018-R1/19–21, IPS89320, IPS89323, IPS89325–89329). All from type locality and horizon.

Type locality: Baza-1 (37º29'00''N and 2º47'05''W), Guadix-Baza Basin, Granada Province, Andalusia, Spain (Piñero et al. 2017a; Ros-Montoya et al. 2017).

Type horizon: *Paraethomys baeticus* Zone (previously referred as *Par-*

aethomys aff. *abaigari* Zone by Piñero et al. 2018), 4.6–4.3 Ma, Baza Formation, early Ruscinian, early Pliocene.

Diagnosis.—Medium-sized species of *Paraethomys* with marked longitudinal connections both in upper and lower molars, but incomplete stephanodonty. Teeth intermediate in size between the small-sized *Paraethomys meini* and the large-sized *Paraethomys abaigari* and *Paraethomys jaegeri*. M1 and, to a lesser extent, M2 with posterior spurs on t1 and t3 directed towards the t4–t5 and t5–t6 intersections, respectively. M1 with high t6–t9 and low t4–t8 connections and small t12. t9 and t12 absent in M2. Regular presence of a funnel between the anteroconid and the protoconid-metaconid in m1, as well as absent or greatly reduced tma, moderate labial cingulum with large posterior accessory cuspid, and longitudinal spur.

Paraethomys baeticus sp. nov. differs from *Paraethomys meini* in: larger size (Fig. 4); M1 with higher frequency of distal spurs on t1 and t3, somewhat stronger connection between t6 and t9, and mostly smaller t12; complete absence of t9 on M2; higher frequency of occurrence of longitudinal spur on m1. Differences with *Paraethomys abaigari* are mainly biometrical, *P. baeticus* sp. nov. being on average smaller than *P. abaigari* (Fig. 4). Distinct from *Paraethomys jaegeri* in: smaller size (Fig. 4); molars relatively narrower; M1 and M2 with less developed distal spurs on t1 and t3. Distinguishable from *Paraethomys belmezensis* in: better developed connections among cusps in the molars; M1 with t6 connected to the t9; larger t3 on M2; m1 with absent or greatly reduced tma. Differing from *Paraethomys balearicus* in: lower-crowned molars; complete absence of t9, and t1 and t3 never connected on M2; complete absence of a funnel between the posterior accessory cuspid and hypoconid, and lower accessory labial cuspids on m1. Distinct from *Paraethomys lissasfensis* Geraads, 1998 in: larger size; M1 with high t2–t3 connection.

Measurements.—See Table 1 and SOM 1: table S1.

Description.—*Paraethomys baeticus* sp. nov. from Baza-1 was first described in detail by Piñero et al. (2017a), who referred it as *Paraethomys* aff. *abaigari*. Subsequent sampling in that site has made it possible to enlarge the original sample attributable to that species. On the basis of the original and new teeth we emend the description as follows:

The M1 (n = 26) is antero-posteriorly elongate, wider posteriorly than anteriorly. The t1 is somewhat displaced

Table 1. Measurements (in mm) of the teeth of *Paraethomys baeticus* sp. nov. from Baza-1, early Pliocene, Guadix-Baza Basin, Spain. σ, standard deviation.

Element	Length					Width				
	N	min	mean	max	σ	N	min	mean	max	σ
M1	19	2.47	2.61	2.76	0.086	21	1.68	1.76	1.84	0.049
M2	26	1.79	1.92	2.03	0.052	28	1.65	1.73	1.85	0.043
M3	10	1.25	1.32	1.42	0.056	12	1.18	1.28	1.40	0.060
m1	33	2.24	2.40	2.57	0.079	34	1.38	1.53	1.69	0.069
m2	39	1.64	1.74	1.86	0.057	42	1.44	1.57	1.68	0.069
m3	26	1.39	1.50	1.63	0.053	26	1.21	1.33	1.43	0.047

backwards with respect to the t3. The union between t2 and t3 is higher than the union between t1 and t2. There is neither a t1bis nor a t2bis. A round and low extra cusp between the t2 and t3 is present in one specimen (BA1-2001-R7/15; SOM 2: fig. S1D). All the teeth have a distal spur on the t1 connected basally to the t4–t5 intersection. A distal spur on t3 directed to the t5–t6 intersection is also present. It lies on the valley between the t5 and t6 in eight out of 25 cases in which this part of the tooth is well preserved (BA1-2001-R7/1, BA1-2001-R7/5, BA1-2001-R7/11, BA1-2001-R7/15, BA1-2018-R1/1, BA1-2018-R1/2, IPS89272, IPS89273; Fig. 3B; SOM 2: fig. S1D, E, J, K, L). The t4–t6, t9, t8 are united, the connection between t4 and t8 being much lower than the rest. The t6–t9 connection is high. There is a small or medium-sized t12 in all the specimens. There are three major roots (one anterior, one posterior and one lingual).

The M2 (n = 28) has a nearly rounded occlusal outline, expanded anteriorly and narrower and rounder posteriorly. It has a large, oval or comma-shaped t1. A low posterior spur on the t1 directed towards the t4–t5 intersection is present in 20 out of 28 specimens (Fig. 3E), and absent in the remaining eight (BA1-2001-R7/19, BA1-2001-R7/21, BA1-2001-R7/22, BA1-2001-R7/25, BA1-2001-R7/26, IPS89278, IPS89280, IPS89285; Fig. 3D, F). The small, isolated t3 can be rounded or comma-shaped. It develops a reduced distal spur directed to the t5–t6 intersection in seven out of 28 individuals (BA1-2001-R7/20, BA1-2001-R7/25, BA1-2001-R7/30, BA1-2018-R1/6, IPS89276, IPS89279, IPS89284; see Fig. 3F; SOM 2: fig. S1R, T, Y). The t9 is reduced to a crest connecting t6 and t8. It is slightly inflated only in 14% of specimens (BA1-2001-R7/21, BA1-2001-R7/22, IPS89276, IPS89281; see Fig. 3D; SOM 2: fig. S1U, V). The t4–t5 connection is weak and low. The t4 is connected basally to t8. The t12 is absent. There are three roots (anterior, posterior, and lingual).

In occlusal view, the M3 (n = 12) is subtriangular. The large t1 is isolated. The t3 is absent. The t4–t6, t8 are connected forming a central depression (see Fig. 3G, H). This depression is generally closed, but it is open lingually between t4 and t8 in four specimens (BA1-2001-R8/22, BA1-2018-R1/8, IPS89292, IPS89293; SOM 2: fig. S1AB, AD), and open labially between t6 and t8 in three other teeth (BA1-2001-R8/20, IPS89287, IPS89295; see Fig. 3G; SOM 2: fig. S1AC, AF). Three roots are present (anterior, posterior, and lingual).

The m1 (n = 37) is broader posteriorly than anteriorly. The lingual anteroconid is slightly more anteriorly extended than the labial anteroconid. The protoconid and hypoconid are somewhat displaced posteriorly with respect to the metaconid and entoconid. The tma is absent in 29 specimens (Fig. 3L, P), and greatly reduced and low in the remaining six (BA1-2001-R7/32, BA1-2001-R7/36, BA1-2001-R7/38, BA1-2001-R7/46, BA1-2018-R1/12, IPS89304; see Fig. 3I and SOM 2: fig. S2B). A round islet of enamel between the anteroconid and the protoconid-metaconid complexes is present in 50% of specimens (Fig. 3I, L, P). There is a longitudinal spur (not reaching the protoconid-metaconid
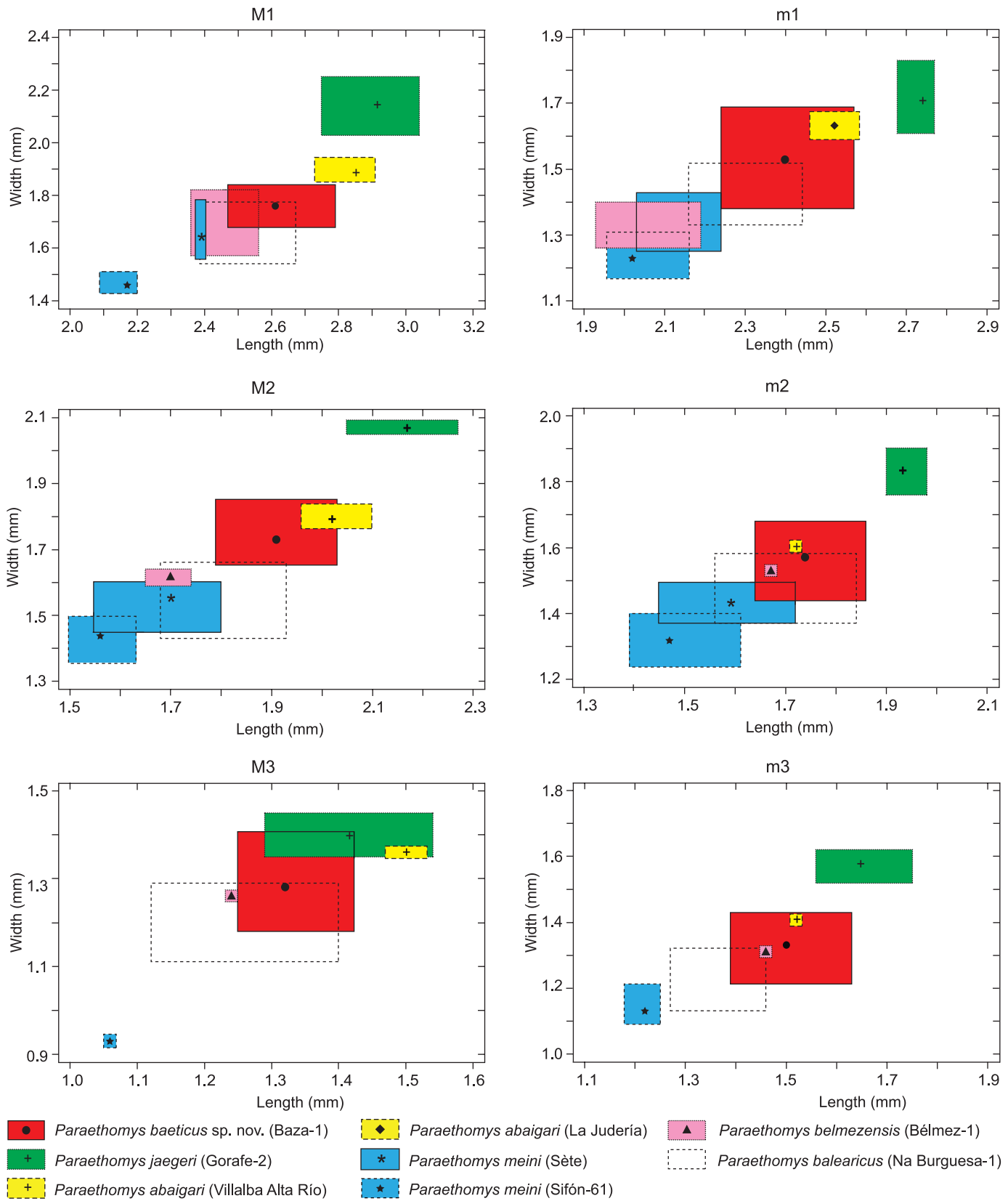
Fig. 4. Ranges of size variation (in mm) in the upper (M1–M3) and lower (m1–m3) teeth of *Paraethomys baeticus* sp. nov. from Baza-1 (type locality; this paper), *Paraethomys jaegeri* from Gorafe-2 (type locality; Montenat and De Bruijn 1976), *Paraethomys abaigari* from Villalba Alta Río (type locality) and La Judería (Adrover et al. 1988), *Paraethomys meini* from Sète (type locality; Michaux 1969; Adrover 1986) and Sifón-61 (Piñero and Agustí 2019), *Paraethomys belmezensis* from Bélmez-1 (type locality; Castillo Ruiz 1992), and *Paraethomys balearicus* from Na Burguesa-1 (type locality; Torres-Roig et al. 2019). Mean sizes are marked by symbols inside the boxes.

intersection) in 22 out of 34 individuals (Fig. 3I, P). As wear advances, the longitudinal spur is usually more pronounced (SOM 2: fig. S2A). The labial cingulum is moderately developed. The large, subtriangular posterior accessory cuspid is connected to the labial face of the hypoconid by a low crest in all but two specimens (BA1-2001-R7/47, BA1-2001-R7/51; SOM 2: fig. S2D). There is occasionally another spur in contact with the posterior face of the hypoconid (Fig. 3P). There are up to three other accessory labial cuspids (see SOM 2: fig. S2I). The medium-sized posterior cingulum can be oval (Fig. 3L) or compressed (Fig. 3P). It is transversally elongated and displaced lingually. Two well-developed roots (anterior and posterior) are present.

The m2 (n = 44) displays a rather square occlusal outline, somewhat wider anteriorly than posteriorly. The moderate-sized labial anteroconid can be round or oval, and is connected basally to the weak or moderate labial cingulum. There is a small posterior accessory cuspid in 23 out of 41 specimens preserving this part (Fig. 3K, N). It can be oval (SOM 2: fig. S2R, T), round (Fig. 3N) or subtriangular (Fig. 3K; SOM 2: fig. S2O) and is connected to the hypoconid in most cases. A longitudinal spur not reaching the protoconid-metaconid intersection is discernible in 49% of specimens (Fig. 3K); it is more pronounced as wear advances. The variable posterior cingulum is displaced lingually. It can be small or large, and oval (Fig. 3M, N) or compressed (Fig. 3K; SOM 2: fig. S2O). There are two roots (anterior and posterior).

The m3 (n = 27) has a subtriangular occlusal outline. The labial anteroconid is absent (except for BA1-2001-R8/11, in which it is very low and reduced; SOM 2: fig. S2AE). The posterior complex (hypoconid-entoconid pair) is separated from the protoconid-metaconid pair. The labial cingulum is weak or absent. A much reduced posterior accessory cuspid attached to the labial side of the posterior complex (hypoconid) is present in eight out of 27 specimens (BA1-2001-R8/4, BA1-2001-R8/10, BA1-2001-R8/11, BA1-2001-R8/12, BA1-2018-R1/20, IPS89326, IPS89327, IPS89328; see Fig. 3O; SOM 2: fig. S2Z, AB, AH). Two roots (anterior and posterior) are present.

Stratigraphic and geographic range.—Early Pliocene (MN14) of the Iberian Peninsula: Baza-1, Gorafe-1, Gorafe-A, Gorafe-4 (Guadix-Baza Basin); Purcal-13, Calicasas-5A (Granada Basin); Alcoy-2C, Alcoy-2D, Alcoi Barranc Sud-2, Alcoi Barranc Sud-3, Alcoi Barranc Sud-3A, Alcoi Cristian-0, Alcoi Cristian-0B (Alcoy Basin); Sifón-P (Fortuna Basin); La Bullana-2B, La Bullana-3 (Cabriel Basin); Celadas-1, Celadas-9, La Gloria-4 (Teruel Basin).

Discussion

The material from Baza-1 displays the common traits of the genus *Paraethomys*: union between t6 and t9 in M1, reduced or absent t9 in M2, general absence of tma in m1, weak

or moderate labial cingulum in the lower molars, common presence of a small funnel between the anteroconid complex and the protoconid-metaconid pair in m1, and reduced or absent labial anteroconid in m3.

De Bruijn (1974) recognized for the first time two European *Paraethomys* forms larger than *Paraethomys anomalus* (= *P. meini*), although the author did not define any new species and referred to them as *Paraethomys* sp. 1 and *Paraethomys* sp. 2. The latter, found in Gorafe-2 (Guadix-Baza Basin), represented the largest form and was defined two years later as *P. jaegeri* (see Montenat and De Bruijn 1976). However, *Paraethomys* sp. 1 from Gorafe-1, intermediate in size between *P. meini* and *P. jaegeri*, was not formally defined. Although the measurements were greater, Agustí and Martín-Suárez (1984) assigned the material from Gorafe-1 to *P. meini*. Years later, Adrover et al. (1988) erected *P. abaigari* from Villalba Alta Río (Teruel Basin), a species smaller than *P. jaegeri* and larger than *P. meini*. *Paraethomys* sp. 1 from Gorafe-1 shows features close to those of *P. abaigari* from its type locality, but the teeth are slightly smaller. Similarly, the large-sized *Paraethomys* from Purcal-13, Calicasas-5A (García-Alix et al. 2008a), Alcoy-2C, Alcoy-2D (Mansino et al. 2013), Alcoi Barranc Sud-2, 3, 3A, Alcoi Cristian-0, 0B (Mansino et al. 2015a), La Bullana-2B and 3 (Mansino et al. 2015b), Baza-1 (Piñero et al. 2017a) and Sifón-P (Piñero and Agustí 2019) share their main characteristics with *P. abaigari* from Villalba Alta Río (Adrover et al. 1988): presence of distal spurs on t1 and t3, large t1 with posterior spur in M2, presence of longitudinal spur in m1, moderate labial cingulum, large posterior accessory cuspid and moderate posterior cingulum in m1. However, these samples differ from *P. abaigari* in their size, being slightly smaller than the material from Villalba Alta Río, La Judería and Celadas 6 (Adrover et al. 1988; Mein et al. 1990). As a result, all these collections were determined as *P.* aff. *abaigari* in their respective works (García-Alix et al. 2008a; Mansino et al. 2013, 2015a, b; Piñero et al. 2017a; Piñero and Agustí 2019). Based on morphological similarities, García-Alix et al. (2008a) considered that the material from La Gloria 4 and Celadas 9, originally ascribed to *P. anomalus* by Adrover et al. (1993), also belonged to *P.* aff. *abaigari*. All mentioned collections determined as *P.* aff. *abaigari* are now ascribed to *P. baeticus* sp. nov. *Paraethomys anomalus* from Celadas-1 (Adrover et al. 1993), *P.* cf. *meini* from Gorafe-A (Ruiz Bustos et al. 1984) and *P. meini* from Gorafe-4 (Martín-Suárez 1988) are morphologically very similar to the sample from Baza-1, their size being consistent with *P. baeticus* sp. nov. rather than with *P. meini*.

All samples transferred to *P. baeticus* sp. nov. agree in size with that from the type locality, Baza-1 (see SOM 1: table S2). The same features as those from Baza-1 are observed in the specimens from Celadas-9, La Gloria-4 (Adrover et al. 1993), Gorafe-A (Ruiz-Bustos et al. 1984), Gorafe-1 (De Bruijn 1974), Gorafe-4 (Martín-Suárez 1988), Alcoy-2B, Alcoy-2C (Mansino et al. 2013), Alcoi Barranc Sud-2, 3, 3A, Alcoi Cristian-0, 0B (Mansino et al. 2015a),

La Bullana-3 and La Bullana-2B (except for the presence of a reduced t12 in two M2) (Mansino et al. 2015b). When compared in detail, the teeth from Baza-1 and those from Purcal-13 (García-Alix et al. 2008a) show certain morphological differences: M1 and M2 from Purcal-13 show a lesser development of distal spurs on t1 and t3, and M2 presents a reduced t12 which is absent in M2 from Baza-1. We compared directly the collection from Baza-1 with that from Sifón-P (currently stored at ICP), and found that the specimens from Sifón-P exhibit some traits that can be considered more archaic: moderately lower frequency of distal spurs on t1 and t3, and slightly larger t12 in M1, weaker union between the anteroconid complex and the protoconid-metaconid pair in m1, and better-developed labial cingulum in m3. Moreover, the specimens from Baza-1 are a bit larger, which is coherent with the slightly older age of Sifón-P (Piñero and Agustí 2019).

Morphological features of *P. baeticus* sp. nov. are close to those of *P. abaigari* from Villalba Alta Río (see above). Regarding size, the maximum values of *P. baeticus* sp. nov. from Baza-1 generally match with the minimum values of *P. abaigari* from Villalba Alta Río and La Judería (Adrover et al. 1988) (Fig. 4). However, these collections cannot be ascribed to a single taxon as the overlap is only partial in M2 and the lower teeth. There is no overlap in the measurements of M1 and M3. The average size is smaller in *P. baeticus* sp. nov. than in *P. abaigari* for all the teeth, but differences are especially marked in the case of the M1 (Fig. 4). The slight overlap in size and similarities in morphology can be explained by the probable ancestor-descendant relationship between both species.

The association of a large-sized lineage of *Paraethomys* (*P. baeticus* sp. nov.–*P. abaigari*–*P. jaegeri*) with a small-sized one (*P. meini*) has been reported from a number of Pliocene localities in southwestern Europe (Fig. 5). *Paraethomys meini* and *P. baeticus* sp. nov. coexist at Baza-1 (Guadix-Baza Basin; Piñero et al. 2017a), Celadas-1 and 9, La Gloria-4 (Teruel Basin; Adrover et al. 1993), Purcal-13, Calicasas-5A (Granada Basin; García-Alix et al. 2008a), Alcoy-2C and 2B (Alcoy Basin; Mansino et al. 2013), La Bullana-2B (Cabriel Basin; Mansino et al. 2015b), Alcoi Barranc Sud-2, 3, 3A, Alcoi Cristian-0, 0B (Alcoy Basin; Mansino et al. 2015a), and Gorafe-1 (Guadix-Baza Basin; De Bruijn 1974; this work). The coexistence of *P. abaigari* and *P. meini* has been identified in Villalba Alta Río (Teruel Basin; Adrover et al. 1988). *Paraethomys meini* (or *Paraethomys* cf. *meini*) co-occurs with *P. jaegeri* in Villalba Alta 1 (Teruel Basin; Adrover et al. 1988), Lomas de Casares (Teruel Basin; Mein et al. 1990), La Juliana (Murcia, Spain; Montenat and De Bruijn 1976), Asta Regia 3 (Jerez Basin; Castillo and Agustí 1996), Sète (Hérault, France; Michaux 1969; Adrover 1986), Mont-Hélène (eastern Pyrenees, France; Aguilar et al. 1986), Lo Fournas 13 (southern France; Bachelet 1990), and Perpignan (southern France; Adrover 1986; Bachelet 1990).

Mein et al. (1990) noted that the two abovementioned lineages of *Paraethomys* tend to increase in size through time.

Further observations showed that there is a much more pronounced size increase along the line *P. baeticus* sp. nov.–*P. abaigari*–*P. jaegeri* than in that of *P. meini* (Adrover et al. 1993; García-Alix et al. 2008a; Mansino et al. 2016; Piñero and Agustí 2019). The origin of the large-sized lineage has been discussed in previous works. According to García-Alix et al. (2008a), *P. abaigari* could evolve from *P. meini* or may be an inmigrant taxon. Piñero and Agustí (2019) proposed that *P. baeticus* sp. nov. (referred to therein as *P.* aff. *abaigari*) originated from *P. meini* as the result of an evolutionary process marked by a size increase and better development of distal spurs on t1 and t3 in the upper teeth, occurring during the early Pliocene.

The coexistence of *P. meini* and its descendant lineage can be explained as the result of a branching speciation event that occurred via asymmetric speciation (budding speciation), where an ancestral species gives rise to a new species and both persist after the speciation event (Foote 1996; Stadler et al. 2018: fig. 1ii). This cladogenetic event would have presumably given rise to *P. baeticus* sp. nov., which after branching off from the *P. meini* lineage experienced progressive increase in size and in the development of longitudinal connections along the Pliocene, leading to *P. abaigari* and then to *P. jaegeri* through an anagenetic evolutionary process.

Biochronology and biostratigraphy

The first recorded representative of the genus *Paraethomys* in Europe is *P. meini*, whose stratigraphic range extends from the late Turolian (MN13 unit, late Miocene) to the late Ruscinian (MN15 unit, Pliocene). The first occurrence of this species in Europe is recorded in the Iberian basins of Fortuna (Sifón-61; Agustí et al. 2006; Piñero and Agustí 2019) and Cabriel (Venta del Moro; Mansino et al. 2016) at about 6.2 Ma, prior to the Messinian Salinity Crisis (Garcés et al. 1998, 2001; Gibert et al. 2013) (Fig. 5). The youngest samples of *P. meini* are found in deposits of late Ruscinian age from Spain and France such as Asta Regia 3 (Jerez Basin, Spain; Castillo and Agustí 1996), Tollo de Chiclana 1 (Guadix Basin, Spain; Minwer-Barakat et al. 2005), Layna and Orrios 3 (Teruel Basin, Spain; Adrover 1986), Mont-Hélène (eastern Pyrenees, France; Aguilar et al. 1986) and Sète (Hérault, France; Adrover 1986).

The other European members of the genus *Paraethomys* have been recorded from Pliocene strata. *Paraethomys balearicus* is an endemic species from the earliest Pliocene of Mallorca (Balearic Islands) related to the latest Miocene populations of *P. meini* (see Torres-Roig et al. 2019). *Paraethomys meini* probably dispersed into Mallorca from eastern Iberia during the peak of the Mediterranean desiccation. After being isolated due to the refilling of the Mediterranean Sea at 5.33 Ma, the mainland ancestor started to evolve under insular conditions, resulting in *P. balearicus*. So far it has only been identified in its type locality (Na Burguesa-1),

Biostratigraphic distribution table (Fig. 5):

EPOCH	ELMA	MN Unit	Alcoy Basin biozones	Granada Basin biozones	Teruel Basin biozones	Guadix-Baza Basin biozones
PLIOCENE	LATE RUSCINIAN	MN15	(grey)	Stephanomys donnezani	M. gracilis + M. hajnackensis / Dolomys / Archaic Mimomys	Mimomys hassiacus / Dolomys adroveri / Mimomys davakosi
PLIOCENE	EARLY RUSCINIAN	MN14	Trilo-phomys / Paraethomys baeticus / Apocricetus barrierei	Trilo-phomys / Paraethomys baeticus / Apocricetus barrierei / Celadensia	Trilo-phomys / two Paraethomys + Promimomys / Celadensia	Trilo-phomys / Paraethomys baeticus / Apocricetus barrierei
MIOCENE	LATE TUROLIAN	MN13	Para-ethomys meini	Paraethomys meini	Stephanomys ramblensis	Apodemus gudrunae + Apocricetus alberti

Magnetic polarity (ATNTS 2012), Ma scale and Western European localities (with Paraethomys record):

Magnetic polarity zones (top to bottom): 2An.2r, 2An.3, 2Ar, 3n.1n, 3n.1r, 3n.2n, 3n.2r, 3n.3n, 3n.3r, 3n.4n, 3r (Messinian Salinity Crisis: 5.33 – 5.97), 3An.1n

Ma scale: 3.5, 4.0, 4.5, 5.0, 5.5, 6.0

Western European localities (with Paraethomys record):

- **Sète**
- Layna
- Orrios 3
- Bélmez-1
- Tollo de Chiclana -1
- **Asta Regia 3**
- Gorafe 2*, 3
- Gorafe 5*
- **Mont-Hélène**
- **Villalba Alta 1**
- Arquillo 3
- Zújar 4*
- **VAR-1* / La Judería / CEL-6**
- Aldehuela
- **Gorafe-1*, A*, 4**
- **Alcoy-2C, 2D**
- **Baza-1 / CEL-9 / LG4**
- **PUR-13 / CLC-5A / AC-0, 0B**
- **La Bullana-2B***
- **Alcoi Barranc Sud-2, 3, 3A**
- La Bullana-3*
- Sifón-P*
- Botardo-C*, D*
- Peralejos E
- CLC 3, 4
- PUR-7
- Fuente del Viso*
- Puerto de la Cadena*
- Afournas 1´07
- Sifón-430*
- Na Burguesa-1
- Sifón-413*
- PUR-4*
- Afournas 1´A, 1´06
- PUR-3*
- Bacochas-1
- Negratín-1*
- Pino Mojón
- Rambla de Chimeneas 3
- Dehesas de Guadix*
- Gafares-2B
- Zorreras-3A*
- Arquillo 4
- Sifón-79*
- Crevillente 6
- Sifón-61*
- Venta del Moro*

Biostratigraphic framework and evolution of the Paraethomys in Europe:

Small-sized lineage: Paraethomys meini, Paraethomys belmezensis, Paraethomys balearicus

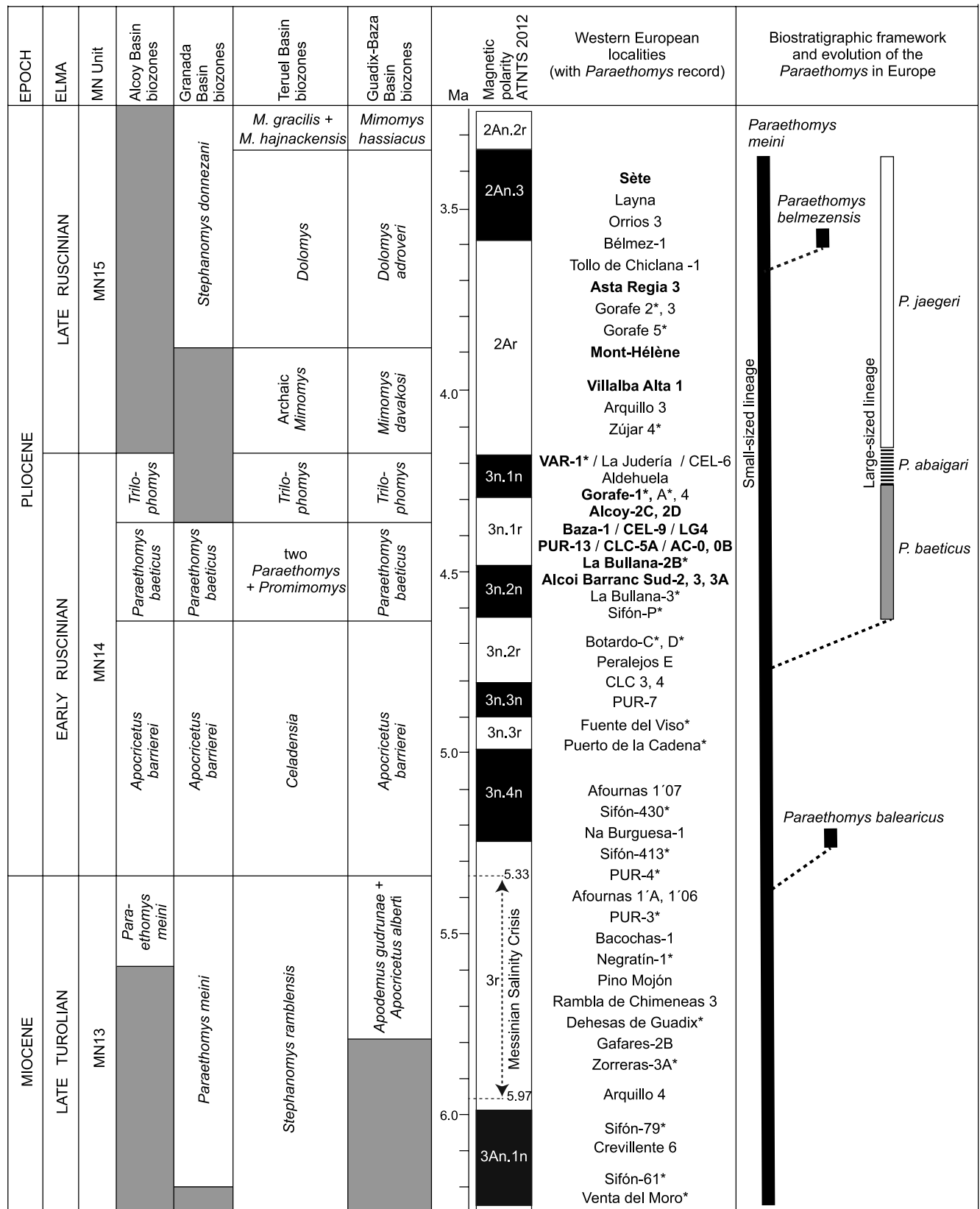Large-sized lineage: P. jaegeri, P. abaigari, P. baeticus

Fig. 5. Biostratigraphic distribution and evolution of the European *Paraethomys* species, showing their chronological ranges. The localities marked with an asterisk are calibrated with paleomagnetic data (Opdyke et al. 1997; Martín-Suárez et al. 1998, 2000; Oms et al. 1999; Gibert et al. 2013; Garcés et al. 1998, 2001; Hüsing et al. 2010; Mansino et al. 2015b; Piñero et al. 2017b, 2018). The sites with two species of *Paraethomys* in coexistence are in bold. Abbreviations: AC, Alcoi Cristian; ATNTS, Astronomically Tuned Neogene Time Scale; CEL, Celadas; CLC, Calicasas ELMA, European Land Mammal Ages; LG, La Gloria (Adrover et al. 1993); *M.*, *Mimomys*; MN, Mammal Neogene; *P.*, *Paraethomys*; PUR, Purcal; VAR, Villalba Alta Río.

suggesting that this species became extinct soon after its arrival on the island (Torres-Roig et al. 2019).

Paraethomys belmezensis is only known from the Pliocene fissure filling of Bélmez-1 (late Ruscinian, MN15) in Córdoba (southern Spain) (Castillo Ruiz 1992). This species is related to *P. meini* (Castillo Ruiz 1992), and probably represents an endemic divergence from this latter taxon.

Paraethomys baeticus sp. nov. is usually associated to taxa considered to be typical of the early Ruscinian continental stage (MN14), such as the cricetid *Apocricetus barrierei*, and the murids *Stephanomys cordii* and *Castillomys gracilis* (Mein 1975; Fejfar and Heinrich 1990; García-Alix et al. 2008b; Minwer-Barakat et al. 2012; Piñero and Agustí 2019). The oldest known evidences of *P. baeticus* sp. nov. are those of the levels of Sifón-P (Piñero and Agustí 2019) and La Bullana-3 (Mansino et al. 2015b), in the later part of the early Ruscinian. This species has an exclusively MN14 distribution (Adrover et al. 1993; García-Alix et al. 2008b; Mansino et al. 2013, 2015a, b; Piñero et al. 2017a; Piñero and Agustí 2019), evolving into *P. abaigari* during the late early Ruscinian (Adrover et al. 1988; Mein et al. 1990) (Fig. 5). Thus, *P. baeticus* sp. nov. is useful for establishing divisions within the early Ruscinian, and becomes a characteristic taxon for the early Pliocene in the terrestrial record of the Iberian Peninsula.

In terms of magnetostratigraphy, Sifón-P was assigned to C3n.2n, at about 4.6 Ma (Garcés et al. 2001). La Bullana-3 and La Bullana-2B were preliminarily correlated with C3n.4n (5.235–4.997 Ma) and C3n.3r (4.997–4.896 Ma), respectively (Mansino et al. 2015b). Botardo-D represents one of the youngest localities in which two *Paraethomys* species are not yet distinguished (Piñero and Agustí 2020). However, La Bullana-3 and 2B reported two coexisting *Paraethomys* species, which suggests a younger age than Botardo-D, a locality included in C3n.2r (4.799–4.631 Ma) (Piñero et al. 2018; Piñero and Agustí 2020). In addition, the occurrence of the gerbil *Debruijnimys* cf. *julii* in La Bullana-2B is a further argument to indicate an older age than Botardo-D, where *Debruijnimys* sp., ancestor of *D. julii*, is present (Piñero and Agustí 2020). This inconsistency in the magnetostratigraphic correlations is best explained if the normal interval identified at La Bullana-3 corresponds to the younger C3n.2n (4.631–4.493 Ma), and La Bullana-2B to C3n.1r (4.493–4.300 Ma). The origin of *P. baeticus* sp. nov. has to be placed sometime between the deposition of Botardo-D and Sifón-P, roughly 4.6 Ma. The youngest evidences of *P. baeticus* sp. nov. are those from Gorafe-1 (De Bruijn 1974), Gorafe-A (Ruiz-Bustos et al. 1986), Alcoy-2C and Alcoy-2D (Mansino et al. 2013). Both Gorafe-1 and Gorafe-A were included in the base of C3n.1n (Piñero et al. 2018), at about 4.30 Ma. Thereby, *Paraethomys baeticus* sp. nov. is recorded in the time span between ca. 4.6 and 4.3 Ma (Fig. 5).

Paraethomys abaigari has only been identified in the Teruel Basin at the localities of Villalba Alta Río-1, Celadas-6 and La Judería (Adrover et al. 1988; Mein et al. 1990). The stratigraphic range of this species is restricted to a short interval at the top of the MN14 unit, so it represents an excellent indicator of the end of the early Ruscinian (Fig. 5).

The first occurrence of *P. jaegeri* is attested at the base of the Zújar section, in the site of Zújar-4 (~4.19 Ma), Guadix-Baza Basin (Oms et al. 1999; Agustí et al. 2001; Piñero et al. 2018). This locality also recorded the first occurrence of the arvicolid *Mimomys* in the Guadix-Baza Basin, which marks the onset of the MN15 unit (late Ruscinian). The stratigraphic record of *P. jaegeri* extends over the late Ruscinian (Montenat and De Bruijn 1976; Adrover 1986; Aguilar et al. 1986; Martín-Suárez 1988; Bachelet 1990; Mein et al. 1990; Castillo and Agustí 1996; Agustí et al. 2001; Piñero et al. 2018). The latest populations of *P. jaegeri* are found in Asta Regia 3 (Castillo and Agustí 1996), Mont-Hélène (Aguilar et al. 1986) and Sète (Adrover 1986), where this species co-occurs with the latest representatives of *P. meini*. All evidences indicate that *P. jaegeri* vanished at the same time as *P. meini* towards the end of the Ruscinian (Fig. 5), which involved the disappearance of the genus *Paraethomys* from Europe. The youngest locality assigned to the MN15 in southern Spain is Tollo de Chiclana-1B, where the arvicolid *Mimomys hassiacus* is recorded (Minwer-Barakat et al. 2008). In this locality, despite the abundance of micromammal remains, *Paraethomys* is not identified (Minwer-Barakat et al. 2005). Therefore, this genus must have disappeared at some moment slightly before the Ruscinian/Villanyian boundary.

In the Neogene basins of the Iberian Peninsula, there is a rich and continuous record of rodents. In this context, a significant number of biostratigraphic schemes have been proposed for the upper Miocene and lower Pliocene (Mein et al. 1990; García-Alix et al. 2008b; Mansino et al. 2017; Piñero et al. 2018; among others). Within the lower Ruscinian, the first record of two coexisting *Paraethomys* species marks the lower limit of different local correlatable biozones in four different basins, whereas the first presence (or first regular presence) of *Trilophomys* marks their upper limit. Such is the case of the *Paraethomys* aff. *abaigari* Zone from the basins of Granada (García-Alix et al. 2008b), Alcoy (Mansino et al. 2017), and Guadix-Baza (Piñero et al. 2018), as well as the Two *Paraethomys* + *Promimomys* Zone from the Teruel Basin (Mein et al. 1990). The lower limit of all these biozones is indeed marked by the first occurrence of *P. baeticus* sp. nov., which coexists with *P. meini*. Therefore, the biozones previously named "*P.* aff. *abaigari*", should now be called "*Paraethomys baeticus*" Zone (Fig. 5). This highlights the biochronological and biostratigraphic value of the new species.

Conclusions

We erect a new murine species, *Paraethomys baeticus* sp. nov., from the early Pliocene of Spain, based on material from Baza-1 (Guadix-Baza Basin, SE Spain). Its distribution range includes southern and eastern Iberian Peninsula

(basins of Granada, Guadix-Baza, Fortuna, Alcoy, Cabriel, and Teruel). This species would have diverged from the small-sized *Paraethomys meini* through asymmetric speciation. Morphological and biostratigraphic evidence suggests that the novel species is the first representative of the large-sized phyletic lineage *P. baeticus* sp. nov.–*P. abaigari–P. jaegeri*, which is characterized by an increase of size and a progressive development of longitudinal connections in the molars along the Pliocene. *Paraethomys baeticus* sp. nov. represents an excellent biostratigraphic marker of the upper part of the MN14 unit (lower Ruscinian continental stage), as well as a characteristic species for the early Pliocene in the continental record of the Iberian Peninsula. Its oldest records are those from Sifón-P and La Bullana-3 (at about 4.6 Ma), whereas the last appearances before it evolves into *P. abaigari* are recorded in Gorafe-1 and Gorafe-A (at about 4.3 Ma). This new species can contribute significantly to the establishment of a more precise biostratigraphic scheme for the Neogene in the entire Iberian Peninsula.

Acknowledgements

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