A new *Eliomys* from the Late Miocene of Spain and its implications for the phylogeny of the genus

SAMUEL MANSINO, ANTONIO GARCÍA-ALIX, FRANCISCO J. RUIZ-SÁNCHEZ, and PLINIO MONTOYA

Mansino, S., García-Alix, A., Ruiz-Sánchez, F.J., and Montoya, P. 2015. A new *Eliomys* from the Late Miocene of Spain and its implications for the phylogeny of the genus. *Acta Palaeontologica Polonica* 60 (3): 577–588.

In this paper, we describe a previously unknown species of the glirid *Eliomys* from the Late Miocene and Early Pliocene Cabriel, Alcoy and Granada basins of southeastern Spain. *Eliomys yevesi* sp. nov. is characterized by its relative small size, narrow lingual wall and common presence of two centrolophs in the upper molars, and well-developed centrolophids in the lower molars. The new species is the probable ancestor of *E. intermedius*, which in turn represents the ancestor of the extant *E. quercinus*. According to its morphologic and biometric features, the origin of *E. yevesi* sp. nov. is likely to be found in some population of *E. truci* from the Late Miocene. Based on these affinities, we propose the lineage *E. truci*–*E. yevesi* sp. nov.–*E. intermedius*–*E. quercinus*, in which there is a trend towards the development of centrolophs, as well as the reduction of accessory crests.

Key words: Mammalia, Rodentia, Gliridae, *Eliomys*, Miocene, Spain.

Samuel Mansino [samuel.mansino@uv.es] and Plinio Montoya [plinio.montoya@uv.es], Departament de Geologia, Universitat de València, 46100 Burjassot, Spain.
Antonio García-Alix [agalix@ugr.es], Instituto Andaluz de Ciencias de la Tierra (IACT-CSIC-UGR), Consejo Superior de Investigaciones Científicas, Universidad de Granada, Avenida de las Palmeras n° 4 18100 Armilla, Granada, Spain.
Francisco J. Ruiz-Sánchez [francisco.ruiz@uv.es], Departament de Geologia, Universitat de València, 46100 Burjassot, Spain; and Museu Valencià d'Història Natural, L'Hort de Feliu, P.O. Box 8460, Alginet, Valencia, 46018, Spain.

Received 31 July 2013, accepted 21 February 2014, available online 28 February 2014.

Introduction

External, genetic and some morphometric characters of the skull distinguish at least three extant species of the genus *Eliomys* (Filipucci et al. 1988a, b; Krystufek and Kraft 1997; Holden 2005), including the garden dormouse *Eliomys quercinus* (Linnaeus, 1766), the Asian dormouse *E. melanurus* Wagner, 1839 (type species) and the Maghreb garden dormouse *E. munbyanus* Pomel, 1856. Its biogeographic range comprises Western Europe, where it is widespread, as well as scattered populations across Central, Eastern, and Southeast Europe, Turkey, and the north of Africa. In addition, fossil representatives of the genus include *E. assimilis* Mayr, 1979 and *E. reductus* Mayr, 1979 from Germany, and *E. lafarguei* Aguilar, Michaux, and Lazzari, 2007 from France, all them from the Late Miocene, as well as *E. truci* Mein and Michaux, 1970 from the Late Miocene–Pliocene, and *E. intermedius* Friant, 1953 from the Pliocene and Pleistocene, both of Western Europe.

Eliomys truci, *E. intermedius*, and the extant *E. quercinus* have been proposed to form part of a single phylogenetic lineage, following first a cladogenetic pattern of evolution, based on the coexistence of *E. truci* and *E. intermedius* during the Early–Late Pliocene (Adrover 1986), before culminating in the anagenetic replacement of *E. intermedius* by *E. quercinus* during the Pleistocene (Chaline 1972; Castillo 1990). However, this picture is made more complex by the appearance of an additional, intermediate form (*E.* aff. *intermedius*) sharing features with both *E. truci* and *E. intermedius*, in the Mio-Pliocene of the Granada Basin of southern Spain (García-Alix et al. 2008a). Here, we provide new information on the evolutionary history of the genus by describing new Mio-Pliocene material from rich localities with the Cabriel (Venta del Moro and La Bullana) and Alcoy basins of southeastern Spain, which, together with *E.* aff. *intermedius* from the Granada Basin, we refer it to the new species *Eliomys yevesi* sp. nov.

Institutional abbreviations.—DEPUG, Departamento de Estratigrafía y Paleontología of the University of Granada, Spain; MGUV, Museum of Geology of the University of Valencia, Spain.

Other abbreviations.—L, length; W, width; see Table 1 for locality name abbreviations.

http://dx.doi.org/10.4202/app.00014.2013

Material and methods

Nomenclature and measurement methods follow Daams (1981) and Freudenthal (2004). Measurements are in millimetres and were taken on a Leica MZ7_5 binocular microscope by means of displacement of a mechanical stage, connected to Sony Magnescale measuring equipment. Photographs were taken with a HITACHI 4800 scanning electron microscope at the Central Support Facility for Experimental Research (SCSIE) of the University of Valencia. The specimens from Venta del Moro, La Bulla and Alcoy are kept at the MGUV, and labelled according to locality, level and, where applicable, year of collection (Table 1).

To determine its affinities, we directly compared our material with fossil collections from Huétor Tájar, Tollo de Chiclana, Moreda, Bélmez-1, Cañada Castaños, Gorafe-2 and 5, Botardo-C, Negratín-1, Calicasas-3B, Purcal-4, 23, 24A, and 25, and Otura-1, housed at the DEPUG (see SOM, Supplementary Online Material available at http://app.pan.pl/SOM/app60-Mansino_etal_SOM.pdf). In addition to these direct comparisons, we took into account published data contained from the localities of Balaruc 2, Layna, Caravaca, Crevillente 1, 3, 5, and 6, Tortajada A and C, and Masada del Valle 2 (all in Weerd 1976), as well as Orrios 3, Sete, Arquillo 3, Villalba Alta, Hautimagne, Los Mansuetos, and Aljezar B (Adrover 1986). Finally, we performed a phylogenetic analysis of the genus using the implicit enumeration option of the phylogenetic software package TNT (Goloboff et al. 2003, 2008). All of the characters included in this analysis are listed in the Appendix 1.

Table 1. Locality abbreviations. Square brackets denote modifiers indicating particular levels (e.g., C, D) or years of collection.

Number of acronym	Name [levels/year of collection]
MGUV ABS-3A	Alcoi Barranc Sud 3A
MGUV AC-0	Alcoi Cristian 0
MGUV AF-1	Alcoi Forn 1 [2006, 2007]
MGUV AL2	Alcoi 2 [C, D]
MGUV LB-2B	La Bullana 2B
MGUV VVm	Venta del Moro [A–D]
DEPUG CLC-3B	Calicasas 3B
DEPUG OUT-1	Otura 1
DEPUG PUR	Purcal [4, 23, 23A, 25]
DEPUG TCH	Tollo de Chiclana [1B, 3, 13]

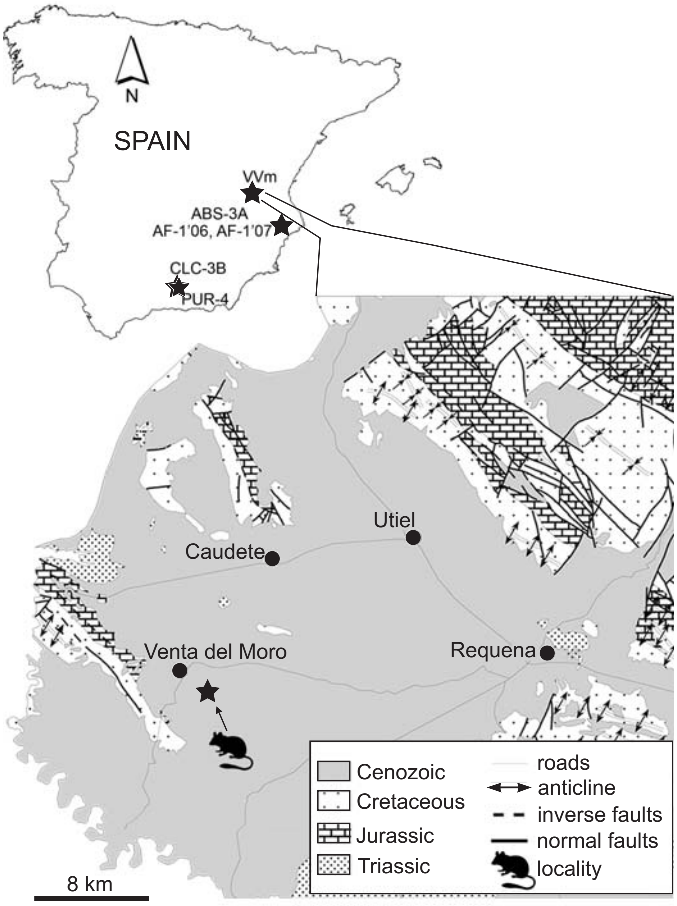

Fig. 1. Location of the Venta del Moro, Alcoy, Purcal, and Calicasas sites (stars) that have yielded specimens of *Eliomys yevesi* sp. nov. The dormouse symbol indicates the location of Venta del Moro, the type locality of *E. yevesi*. Abbreviations: ABS-3A, Alcoi Barranc Sud 3A; AF-1, Alcoi Forn 1; CLC-3B, Calicasas 3B; PUR-4, Purcal 4; VVm, Venta del Moro.

Geological setting

The material described here was recovered from lacustrine and palustrine sediments belonging to the Villatoya-Venta del Moro Formation (Robles 1970; Montoya et al. 2006) exposed at Venta del Moro (VVm) and La Bullana 2B (LB-2B), both situated in the Cabriel Basin of southeastern Spain (Robles 1970; Morales 1984; Montoya et al. 2006), as well as the localities of Alcoi Forn 1'06 (AF-1'06), Alcoi Barranc Sud 3A (ABS-3A), Alcoi Cristian 0 (AC-0), and Alcoi 2 (AL2-C and AL2-D), all of them located in the west margin of the lacustrine Basin of Alcoy (southeastern Spain). At Venta del Moro, specimens were collected from several levels, previously referred to as VM-A, B, C, BC, and D by Montoya et al. (2006). The latter are here labeled as VVm-A, VVm-B, VVm-BC, VVm-C, and VVm-D, respectively, to distinguish the specimens housed at the University de Valencia from previously collected material from the same locality housed at the Museo Nacional de Ciencias Naturales, Madrid (Montoya et al. 2006).

The age of the fossiliferous levels of Venta del Moro, has recently been dated to 6.23 Ma, or latest Miocene (late Turolian–late Messinian), based on their faunal assemblage and magnetostratigraphic data (magnetochron C3An; Gibert et al. 2013). This age estimate is confirmed by the presence of *Apocricetus alberti* Freudenthal, Mein, and Martín Suárez, 1998, *Ruscinomys schaubi* Villalta and Crusafont, 1956, *Paraethomys meini* (Michaux, 1969) and *Apodemus gudrunae* van de Weerd, 1976 (Freudenthal et al. 1998; Sesé 2006a; García-Alix et al. 2008a). This faunal association is consistent with the *Apodemus gudrunae* Assemblage Zone in the Guadix Basin (Minwer-Barakat et al. 2012). The presence of *Stephanomys dubari* Aguilar, Michaux, Bachelet, Calvet, and Faillat, 1991, in the localities of Venta del Moro (Montoya et al. 2006) differs from late Turolian (late Messinian) sites in the Teruel Basin, such as the locality of Arquillo 4, which instead yields *S. ramblensis* van de Weerd, 1976 (Mein et al. 1990; Adrover et al. 1993).

Stephanomys dubari Aguilar, Michaux, Bachelet, Calvet and Faillat, 1991, *Apodemus gorafensis* Ruiz-Bustos, Sesé, Dabrio, Peña, and Padial, 1984*, Occitanomys alcalai* Adrover, Mein, and Moissenet, 1988, and *Paraethomys meini* (Michaux, 1969) typically appear together in the latest Turolian–earliest Ruscinian localities of southern Spain (late Messinian–early Zanclean; García-Alix et al. 2008b, c). These taxa are present at PUR-4, CLC-3B, AF-1'06, AF-1'07, and LB-2B, but *Occitanomys alcalai* and *Apodemus gorafensis* are absent in ABS-3A, which has yielded few micromammal remains. By contrast, *Apocricetus barrierei* (Mein and Michaux, 1970), an indicator of early Ruscinian (Zanclean) age (Freudenthal et al. 1998; Sesé 2006a; García-Alix et al. 2008a) is present at ABS-3A, PUR-4, CLC-3B AF-1'07, and LB-2B, yet absent at AF-1'06, which has yielded over a hundred specimens. The localities of PUR-4 and CLC-3B are within the *Apocricetus barrierei* Assemblage Zone (earliest Ruscinian–earliest Zanclean) of the Granada Basin (García-Alix et al. 2008c).

Eliomys intermedius is a typically Ruscinian taxon (Sesé 2006a). The presence of *Apodemus* cf. *gorafensis*, *Occitanomys* cf. *alcalai*, *Paraethomys meini*, and *Stephanomys cordii* at AC-0 place this locality in the Early Ruscinian (MN14). The faunal lists of AL2-C and AL2-D, which include *Trilophomys* cf. *castroi*, *Blancomys* sp., *Stephanomys cordii*, *Paraethomys meini*, *Paraethomys* aff. *abaigari*, *Ruscinomys* cf. *lasallei*, and *Apocricetus* cf. *angustidens* suggest also an early Ruscinian age (Mansino et al. 2013). However, the presence of two species of *Paraethomys*, the more developed crests of *Stephanomys cordii*, and the presence of *Apocricetus* cf. *angustidens* instead of *A. barrierei* indicate a younger age for these localities than for AC-0.

Systematic paleontology

Order Rodentia Bowdich, 1821

Family Gliridae Muirhead, 1819

Subfamily Dryomyinae de Bruijn, 1967

Genus *Eliomys* Wagner, 1840

Type species: *Eliomys melanurus* Wagner, 1840; extant, Sinai Peninsula, Egipt.

Eliomys yevesi sp. nov.

Fig. 2A–L.

1953 *Eliomys* aff. *intermedius*; Friant 1953: pl. 4: 9–19.
2008 *Eliomys* aff. *intermedius*; García-Alix et al. 2008a: 24–25.

Etymology: Dedicated to José María Yeves and his family, owners of the "Hostal Ventamorino", for their friendly hospitality during the many summer campaigns in Venta del Moro.

Holotype: Right M1, VVmA-25.

Type locality: Venta del Moro A, Cabriel Basin, Spain; coordinates: 39º 28' 29.12" N, 1º 20' 40.38" W.

Type horizon: Villatoya-Venta del Moro Formation, MN13, late Turolian (Late Miocene, 6.23 Ma).

Material.—Venta del Moro: 2 p4 (VVmA-42, 43), 12 m1, m2 (VVmA-1–11, 32), 6 m3 (VVmA-33–38), 1 dP4 (VVmA-44), 3 P4 (VVmA-39–41), 12 M1, M2 (VVmA-16, 21–31), 8 M3 (VVmA-12–15, 17–20); 1 m1, m2 (VVmB-1). VVmBC: 2 m1, m2 (VVmBC-1, 2), 1 m3 (VVmBC-5), 1 M1, M2 (VVmBC-3), 1 M3 (VVmBC-4); 1 m3 (VVmC-1); 2 M1, M2 (VVmD-1, 2). Alcoi Barranc Sud 3A, MN14: 1 m1, m2 (ABS3A-38). Alcoi Forn, MN13-MN14: 1 m1, m2 (AF1'06-190), 1 m3 (AF1'06-187); 1 M1, M2 (AF1'07-36). Purcal 4, MN14: 1 p4 (PUR-4 871), 12 m1, m2 (PUR-4 872–883), 3 m3 (PUR-4 884–886), 1 dP4 (PUR-4 887), 1 P4 (PUR-4 888), 2 M1, M2 (PUR-4 889, 890), 3 M3 (PUR-4 891–893). Calicasas 3B, MN14: 1 m3 (CLC-3B 67), 2 M1, M2 (CLC-3B 68, 69), 1 M3 (CLC-3B 70).

Diagnosis.—Size intermediate between *Eliomys truci* and the youngest *E. intermedius*; sub-quadrangular m1, m2, usually with a posterotropid and a well-developed centrolophid; no posterotropid on m3; common presence of both centrolophs in the upper molars; posteroloph and endoloph usually connected.

Differential diagnosis.—Eliomys yevesi differs from *E. assimilis* in the more quadrangular shape of m1, m2, less reduced m3, and the absence of any accessory crests in the upper molars; from *E. reductus* in its bigger size, more quadrangular shape of the lower molars, discontinuous endolophid, and common presence of posterotropid; and from *E. lafarguei* in its bigger size, long centrolophid on m1, m2, discontinuous endolophid, the presence of a centrolophid on many m3, and the common presence of postcentrolophs in the upper molars.

Eliomys yevesi ranges in size from the biggest specimens of *E. truci* to the smallest ones of *E. intermedius*. It differs from *E. truci* in more frequently showing centrolophs in the upper molars, as well as the presence of well-developed postcentrolophs, reaching half the width of the tooth or more, in some specimens (Fig. 2G). *E. yevesi* further differs from *E. intermedius* in the subquadrangular shape (Fig. 2B, C, N, R) and lower and narrower lingual wall of the upper molars (Fig. 2F, G). A long centrolophid connected to the metalophid is present in all but one m1, m2 of *E. yevesi*, whereas in *E. intermedius* it is short in 27 out of 106 specimens. In addition, the posterotropid is more frequent and usually longer in *E. yevesi* than in *E. intermedius* (27 out of 29 m1, m2 of *E. yevesi*; 80 out of 107 of *E. intermedius*). In the upper molars, the two centrolophs are usually slightly longer and occur somewhat more frequently in *E. intermedius* (97 out of 165, 58.78%, compared to 17 out of 36, 47.22%, in *E. yevesi*).

Eliomys yevesi differs from the extant *E. quercinus* in its smaller size, but resembles the latter in the absence of accessory crests in the upper molars and an anteroloph-protoloph connection, as well as the frequent presence of two centrolophs. Two subspecies of *E. quercinus* with distinct m1, m2 morphologies occur in the Iberian Peninsula: *E. q. lusitanicus*, which differs from *E. yevesi* in the absence of a centrolophid; and *E. q. quercinus*, which differs from *E. yevesi* in the absence of accessory crests in the lower molars, a continuous endolophid on m1, m2 and in having a small centrolophid.

Measurements.—See Table 2.

Description.—*Material from Venta del Moro*: *p4*: The occlusal outline of this tooth is subtriangular. The protoconid and the large anterolophid create a high, triangular anterior complex, which is separated from the metaconid by a narrow furrow. One specimen (VVmA-42; Fig. 2A) has a short centrolophid. The mesoconid and entoconid are connected by the mesolophid, and separated from the anterior complex by a deep valley. The mesoconid and hypoconid are separated. There is no posterotropid. The posterolophid is high and curved. There are two fused roots.

m1, m2: The occlusal outlines of these teeth are sub-quadrangular. The anterolophid is connected to the protoconid in 6 out of 14 specimens (4 out of 12 from VVm-A, the only specimen from VVm-B and 1 out of 2 from VVm-BC). One specimen (Fig. 2C) has a vestigial anterotropid. Most molars show a connection between the metalophid and the metaconid, whereas the metaconid and entoconid are separated. The centrolophid is usually long and sometimes connected to the metalophid. The posterotropid is long in 10 specimens (9 out of 12 from VVm-A, 1 out of 2 from VVm-BC), short in three (one specimen from VVm-A, the only specimen from VVm-B and 1 of 2 from VVm-BC) and absent in another two (both from VVm-A). The hypoconid is large. There are three roots.

m3: The occlusal outline of this tooth is sub-trapezoidal. The anterolophid is usually separated from the protoconid. The metalophid is sometimes connected to the metaconid. There are no accessory crests. Where present, the centrolophid is not connected to the metalophid. In 1 out of 13 m3, the mesolophid does not reach the entoconid (Fig. 2D). The posterolophid is continuous.

dP4: Known only from a single, extremely worn molar. No features of the occlusal surface can be observed.

P4: The occlusal outline of this tooth is triangular. The paracone and metacone are higher than the protocone. The anteroloph is short, low and connected, at a low level, to the paracone. The protoloph is clearly discontinuous in 1 out of 4 specimens, whereas the remainder shows just a constriction in the central part of this crest. Two specimens present a well-developed precentroloph, and a further one a postcentroloph, which is not connected to the metacone (Fig. 2E). The metaloph is high and continuous. The posteroloph is low and lingually connected to the protocone; discontinuous in two specimens, and not connected to the endoloph in another one (Fig. 2E). The roots are not preserved in any of the specimens.

Table 2. Measurements (in mm) of the (pre-)molars of *Eliomys yevesi* sp. nov. from Venta del Moro and Alcoy, and of *Eliomys intermedius* from Alcoy and La Bullana. n, number of measurable specimens. Repository numbers of the measured specimens are available in Appendix 2.

Element	Species	Locality	Length Width	n	Min.	Max.	Mean
p4	*E. yevesi*	VVm-A	L	2	1.05	1.06	1.06
			W	2	0.95	1.03	0.99
m1, m2	*E. yevesi*	VVm-A	L	11	1.10	1.22	1.16
			W	11	1.14	1.47	1.30
	E. yevesi	VVm-B	L	1	–	–	1.06
			W	1	–	–	1.24
	E. yevesi	VVm-BC	L	2	1.12	1.19	1.16
			W	2	1.30	1.40	1.35
	E. yevesi	ABS-3A	L	1	–	–	1.30
			W	1	–	–	1.45
	E. yevesi	AF-1’06	W	1	–	–	1.46
	E. intermedius	AL2-C	W	1	–	–	1.61
	E. intermedius	AL2-D	L	1	–	–	1.56
			W	1	–	–	1.71
	E. intermedius	LB-2B	L	2	1.42	1.51	1.47
			W	2	1.50	1.77	1.64
m3	*E. yevesi*	VVm-A	L	6	0.95	1.12	1.03
			W	6	1.06	1.23	1.16
	E. yevesi	VVm-BC	L	2	–	–	1.01
			W	1	–	–	1.17
	E. intermedius	AC-0	L	1	–	–	1.31
			W	1	–	–	1.41
	E. intermedius	AL2-D	L	1	–	–	1.34
			W	1	–	–	1.54
D4	*E. yevesi*	VVm-A	L	1	–	–	0.75
			W	1	–	–	0.78
P4	*E. yevesi*	VVm-A	L	3	0.84	0.87	0.86
			W	3	1.25	1.29	1.27
	E. intermedius	LB-2B	L	1	–	–	1.08
			W	1	–	–	1.48
M1, M2	*E. yevesi*	VVm-A	L	12	1.01	1.22	1.11
			W	11	1.33	1.49	1.41
	E. yevesi	VVm-BC	L	1	–	–	0.99
			W	1	–	–	1.34
	E. yevesi	VVm-D	L	2	1.17	1.22	1.20
			W	2	–	–	1.47
	E. yevesi	AF-1’07	W	1	–	–	1.38
	E. intermedius	AL2-D	L	2	1.38	1.58	1.48
			W	2	1.74	1.95	1.85
	E. intermedius	LB-2B	L	1	–	–	1.25
			W	1	–	–	1.79
M3	*E. yevesi*	VVm-A	L	7	0.85	1.00	0.95
			W	8	1.21	1.37	1.28
	E. yevesi	VVm-C	L	1	–	–	0.96
			W	1	–	–	1.25
	E. intermedius	LB-2B	L	1	–	–	1.27
			W	1	–	–	1.52

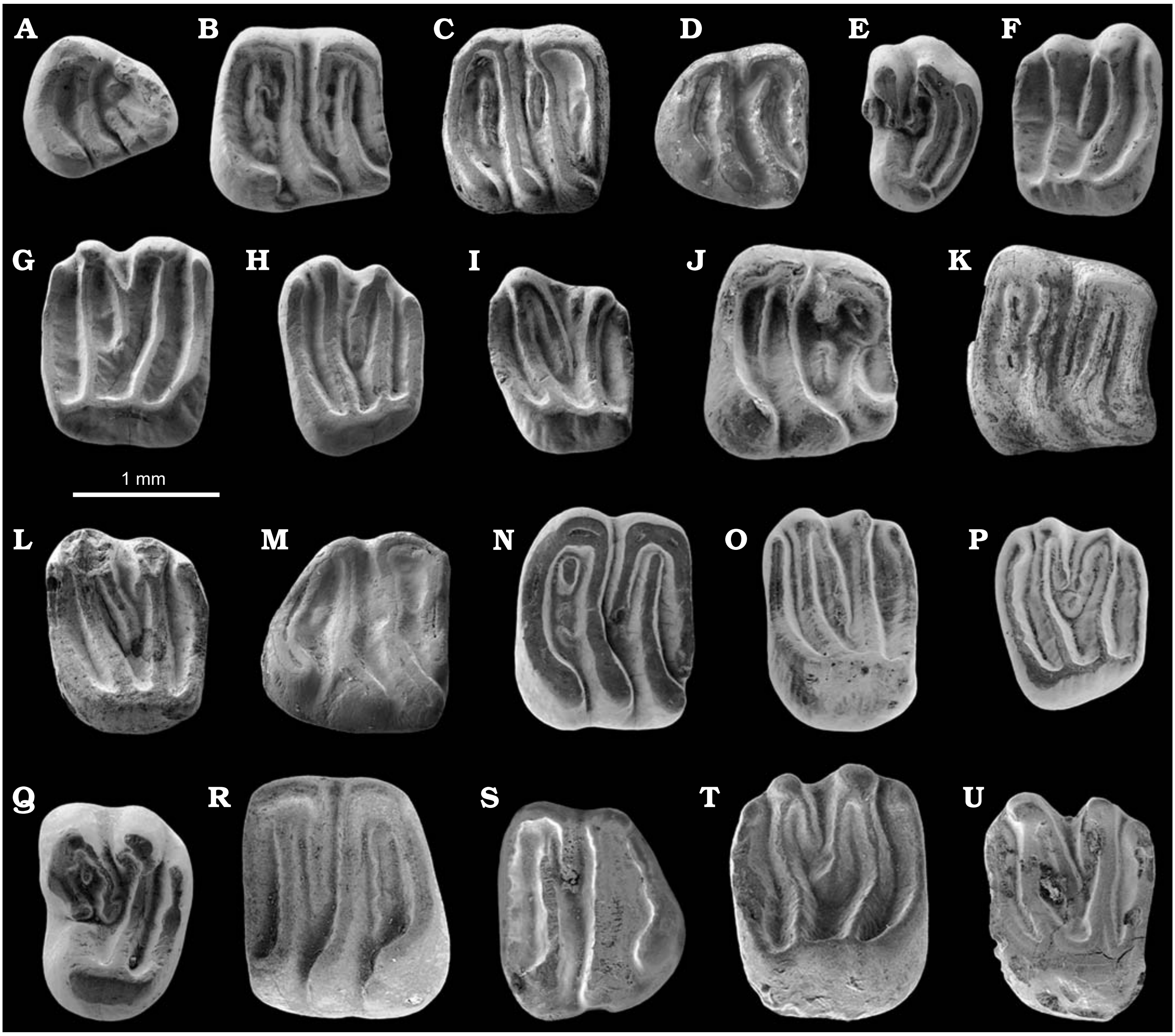

Fig. 2. The glirid mammals *Eliomys yevesi* sp. nov. (A–L) and *Eliomys intermedius* Friant, 1953 (M–U) from Spain, Villatoya-Venta del Moro Formation, Miocene (see Table 1 for locality name abbreviations). **A**. VVmA-42 (MGUV-27256), right p4. **B**. VVmA-1 (MGUV-27215), right m1, m2. **C**. VVmA-6 (MGUV-27220), right m1, m2. **D**. VVmBC-5 (MGUV-27490), right m3. **E**. VVmA-40 (MGUV-27254), left P4. **F**. VVmA-16 (MGUV-27230), right M1, M2. **G**. VVmA-25 (MGUV-27239), right M1, M2. **H**. VVmA-13 (MGUV-27227), left M3. **I**. VVmA-14 (MGUV-27228), left M3. **J**. ABS3A-38 (MGUV-23529), right m1, m2. **K**. AF1'06-190 (MGUV-28334), right m1, m2. **L**. AF1'07-36 (MGUV-28427), left M1, M2. **M**. AC0-88 (MGUV-28551), right m3. **N**. LB2B-176 (MGUV-28727), right m1, m2. **O**. LB2B-241 (MGUV-28727), left M1, M2. **P**. LB2B-177 (MGUV-28728), left M3. **Q**. LB2B-178 (MGUV-28729), left P4. **R**. AL2D-290 (MGUV-28063), left m1, m2. **S**. AL2D-356 (MGUV-28129), left m3. **T**. AL2D-291 (MGUV-28064), right M1, M2. **U**. AL2D-293 (MGUV-28066), left M1, M2.

M1, M2: The occlusal outlines of these teeth are trapezoidal or subrectangular. The anteroloph is separated from the paracone and the protoloph. The paracone and metacone are high and separated. The protoloph and metaloph are continuous, and occasionally sinuous. There is a well-developed precentroloph, which is not connected to the paracone in one of the specimens and reaches the metaloph in another one. Where present, the postcentroloph is short, except in VVmA-29, which has a well-developed crest, and VVmA-25, in which both centrolophs are fused into a central crest (Fig. 2G). The posteroloph is connected to the endoloph. There are three roots.

M3: The occlusal outline of this tooth is trapezoidal. The anteroloph is connected to the protocone. In some specimens, the protoloph and metaloph are sinuous. Both centrolophs are present in 5 out of 8 specimens from VVm-A, and the single tooth from VVm-BC. Two of the specimens from VVm-A bear a long postcentroloph (Fig. 2H). Where present, the precentroloph is usually attached to the paracone, whereas the postcentroloph is connected to the metacone. The endoloph is continuous, except for the single specimen from VVm-BC. There are three roots.

Material from Alcoy: These specimens from the Alcoy Basin resemble the specimens from Venta del Moro, with the exception of having an anterolophid connected basally with the protoconid, and a metalophid that does not reach the metaconid (both on m1, m2). In the m1, m2 from ABS-3A (Fig. 2J), the centrolophid is not continuous. In the M1, M2 from AF-1'07 (Fig. 2L), the anteroloph and the paracone are connected basally.

Remarks.—*Eliomys yevesi* is a relatively small-sized species, being smaller than Plio-Pleistocene *E. intermedius* and *E. quercinus*, and only slightly larger than the Miocene representatives of the genus (*E. lafarguei*, *E. reductus*, and *E. assimilis*) (Fig. 3). The molars from Venta del Moro and AF-1'07 fall within the range of variation of *E. truci*. However, the specimens from the early Ruscinian localities of PUR-4 and CLC-3B (Granada Basin), and AF-1'06 and ABS-3A (Alcoy Basin), are slightly larger, and intermediate between *E. truci* and *E. intermedius* (Fig. 3).

Morphologically, the present material resembles *E. truci*, but differs in the development of the centrolophs on M1, M2, while the presence of both centrolophs is rare in *E. truci* (5 out of a total of 41 specimens, 12.90%; two specimens from Concud 3 and one each from OTU-1, PUR-23, and Orrios 3), 4 out of 12 specimens *E. yevesi* from VVm-A and VVm-BC (33.33%), and all of the M1, M2 from VVm-D, AF-1'07, CLC-3B, and PUR-4 (except one) have both centrolophs. Moreover, when present, the postcentroloph is usually reduced in *E. truci*, whereas in some M1, M2 of *E. yevesi* from VVm-A it is very well developed, reaching half the width of the molar or more (Fig. 2G). Similarly, *E. truci* never bears two centrolophs on M3, whereas they do occur in 5 out of 8 molars (62.50%) of *E. yevesi* from VVm-A, as well as the only M3 from VVm-C and CLC-3B.

In the upper molars of *E. intermedius*, 79 out of 130 (60.77%) M1, M2 and 18 out of 35 (51.42%) M3 have two centrolophs (Weerd 1976; Adrover 1986; Castillo 1990; García-Alix et al. 2008a). Specimens from both the extant (Castillo 1990) and relatively young fossil (e.g., Casablanca B; García-Alix et al. 2008a) populations of *E. quercinus* generally have two centrolophs, with the anterior one often being longer. Together, these observations support a trend towards better-developed centrolophs within a lineage comprising *E. truci*–*E. yevesi*–*E. intermedius*–*E. quercinus*.

Besides the change in development of the centrolophs, *Eliomys* also shows a trend towards the reduction of the centrolophid and the accessory crests in the lower molars (Castillo 1990; García-Alix et al. 2008a). This observation is borne out by the present data, m1, m2 of *E. yevesi* resemble those of *E. truci* in having a long centrolophid and a well-developed posterotropid. In *E. intermedius*, the centrolophid is still present in 104 out of 106 (98.11%) m1, m2, but in 26 of these specimens (24.53%) it is less than half the width of the molar—with the exception of the material from Sète (n = 30), which always displays a long centrolophid. The centrolophid is even more reduced in *E. quercinus*, where it is short in 8 (61.54%) and absent in 5 (38.46%) out of the 13 studied specimens. A posterotropid is present in 29 out of 30 m1, m2 of *E. truci* (96.67%), 27 out of 29 m1, m2 of *E. yevesi* (93.10%), 80 out of 107 m1, m2 of *E. intermedius* (74.76%), and 1 out of 11 m1, m2 (9.09%) of *E. quercinus* (2 of the 13 specimens studied here are too damaged or worn to observe this character).

Stratigraphic and geographic range.—MN13–14, Late Miocene–Early Pliocene; Cabriel, Granada, and Alcoy basins of southeastern Spain.

Eliomys intermedius Friant, 1953

Fig. 2M–U.

Material.—Alcoi Cristian, MN14: 1 m3 (AC0-88), 1 M1, M2 (AC0-87). Alcoi 2, MN14: 1 m1, m2 (AL2C-97), 1 m3 (AL2C-47); 1 m1, m2 (AL2D-290), 1 m3 (AL2D-356), 3 M1, M2 (AL2D-291-293). La Bullana, MN14: 4 m1, m2 (LB2B-6, LB2B-176, LB2B-242, LB2B-243), 1 m3 (LB2B-179), 1 P4 (LB2B-178), 2 M1, M2 (LB2B-241, LB2B-253), 1 M3 (LB2B-177).

Measurements.—See Table 2.

Description.—*m1, m2*: The occlusal outline of these teeth is trapezoidal or subrectangular. The anterolophid is connected to the protoconid in three specimens, and unconnected in a further three. There is no anterotropid. The metalophid is connected to the metaconid. The centrolophid is long, reaching the metalophid in 3 out of 6 specimens. The metaconid and entoconid are separated. The posterotropid is well developed. The hypoconid is large.

m3: The occlusal outline of this tooth is sub-trapezoidal. The anterolophid and the protoconid are separated. There is no anterotropid. The metalophid is connected to the metaconid. There is a short centrolophid, not connected to the metalophid (Fig. 2S). The metaconid and entoconid are separated. There is no posterotropid.

P4: The occlusal outline of this tooth is subtriangular. There is no anteroloph, and the protoloph is discontinuous. The paracone and metacone are higher than the protocone. There is a well-developed precentroloph and a short postcentroloph. The endoloph is continuous.

M1, M2: The outline of these teeth are subrectangular or trapezoidal. The anteroloph and paracone are connected basally in AC0-87, but not connected in any of the other specimens. In some specimens (especially AC0-97), the protoloph and metaloph are distinctly sinuous. Both centrolophs are usually present. The posteroloph is connected to the endoloph. There are three roots.

M3: The occlusal outline of this molar is trapezoidal. The anteroloph is separated from both protoloph and paracone. There is neither an anterotrope nor a posterotrope. The paracone and metacone are high and separated. The protoloph and metaloph are continuous. Both centrolophs are present and well developed, with the postcentroloph being longer and interrupted (Fig. 2P). The endoloph and posteroloph are connected and continuous.

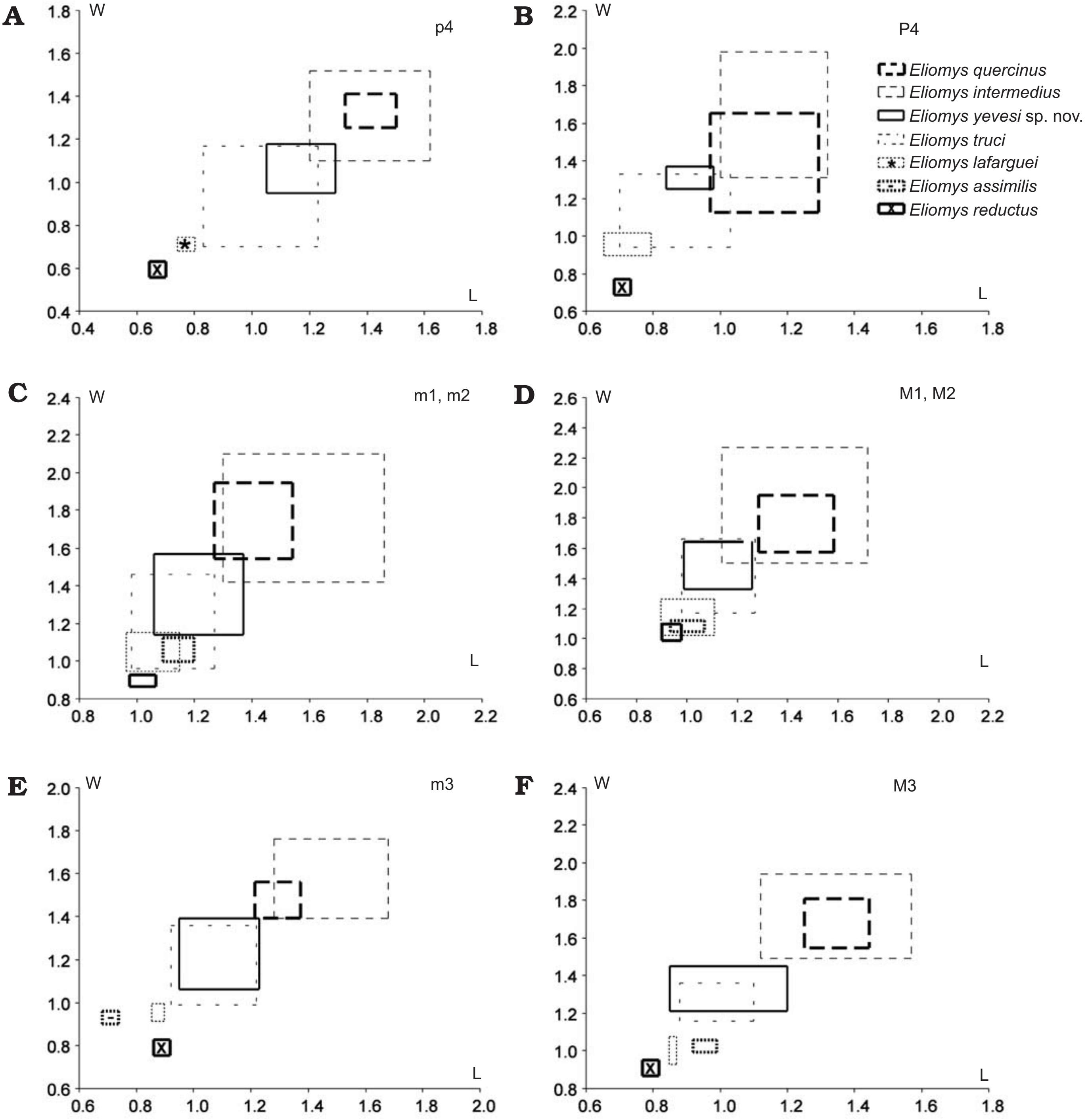

Fig. 3. Comparison of length and width measurements (in mm) of p4 (**A**), P4 (**B**), m1, m2 (**C**), M1, M2 (**D**), m3 (**E**), and M3 (**F**) of *Eliomys truci* from Aljezar B, Hautimagne, Los Mansuetos, Orrios, Sarrión, Sete, Villalba Alta (Adrover 1986), Concud 2 and 3, Concud Barranco de los Calaveros, Los Mansuetos, Masada del Valle 2, 5 and 7, Tortojada A and C (Weerd 1976), DHS-1 and 16, PUR-23, 24, and 25A, OTU-1, TCH-1B and 13 (García-Alix et al. 2008a), Negratín-1 (Minwer-Barakat et al. 2009); Moreda 1A, 1B, Rambla Seca 1 (Castillo 1990) and Puente Minero (Alcalá et al. 1991); *Eliomys yevesi* sp. nov. from VVm-A, B, BC, C, and D, ABS-3A, AF-1'06, AF-1'07, CLC-3B, and PUR-4; *Eliomys intermedius* from Arquillo 3, Sete, Orrios 3, Villalba Alta (Adrover 1986), Escorihuela, Orrios (Weerd 1976), PUR-13, TCH-1 and 1B, TCH3, TCH-13 (García-Alix et al. 2008), Moreda 1A, 1B, Bélmez 1 and Rambla Seca A1 and A2 (Castillo 1990) and Alozaina (Aguilar et al. 1993); *Eliomys quercinus* from Vallparadís and Cal Guardiola (Minwer-Barakat et al. 2011, Baños de Mula (Agustí et al. 1990), Peña de Estebanvela (Sesé 2006b), Valdocarros (Sesé et al. 2011), Sima de los Huesos (Cuenca-Bescós et al. 1997), Bois Roche (Sesé and Villa 2008), Santenay (Chaline 1972); and *Eliomys* aff. *quercinus* from Huétor Tájar 1 and 8.

Remarks.—*Eliomys intermedius* from the Early Pliocene (early Ruscinian–early Zanclean; Mansino et al. 2013) localities of AL2-C and AL2-D is slightly bigger than specimens from the slightly older localities of AC-0 and LB-2B (Table 2), but all of the specimens from these sites fall within the range of *E. intermedius* from Sète, the type locality of the species

(Adrover 1986). The specimens of *E. intermedius* from AC-0, AL2-C, AL2-D, and LB-2B have higher and thicker lingual walls than *E. truci* and *E. yevesi*, sinuous crests, a rounded occlusal outline, and two well-developed centrolophs in the upper molars (M1, M2 from AC-0 and AL2-D, and M3 from LB-2B). These features agree with *E. intermedius.*

Stratigraphic and geographic range.—MN 14, Early Pliocene–early Pleistocene (MQ2) of the Alcoy and Cabriel, and Calatayud-Teruel basins of Spain and the Aquitaine, Paris, and Sud-est basins of France. Other reported occurrences (Bruijn et al. 1970) are dubious.

Discussion

Phylogenetic relationships of *Eliomys*.—Some previous authors (Nadachowski and Daoud 1995) have suggested a relationship of the extant *Eliomys quercinus* with *E. reductus* and *E. assimilis*, both from the German locality of Hammerschmiede (early Vallesian–Tortonian, Late Miocene). However, this is seemingly contradicted by the absence of a clear relationship between *E. reductus, E. assimilis* and the likely ancestor of *E. quercinus*, *E. intermedius* (Daams and de Bruijn 1995).

An alternative hypothesis groups *E. reductus* with *E. lafarguei* from Lo Fournas 6C and Lo Fournas 16M (Vallesian–Tortonian, Late Miocene), based on the presence of a continuous endolophid and a trend towards larger size and reduced postcentrolophs, which commonly occurs in glirids (Aguilar et al. 2007). This relationship is further supported by m1, m2 being longer than wide in these two taxa (albeit only slightly so in *E. lafarguei*) and showing a tendency towards a shortening of the centrolophid. The latter is isolated in the holotype of *E. reductus*, an m2, and shows a low connection with the metaconid in the m1, whereas in *E. lafarguei* the centrolophid is absent or greatly reduced on m2, and variably isolated or connected to the metaconid at a low level on m1. By contrast, in *E. truci*, *E. yevesi*, *E. intermedius*, and *E. quercinus* these teeth are wider than longer, and the centrolophid is usually connected to the metaconid.

Based on these observations, we agree with Aguilar et al. (2007) in recognizing two distinct lineages within *Eliomys*, comprising *E. lafarguei–E. reductus*, and *E. truci–E. yevesi–E. intermedius–E. quercinus*, respectively. The former lineage may also include *Eliomys* sp. A from the early Turolian of Tortajada A (Teruel, Spain; Weerd 1976), based on its possible relationship with *E. lafarguei* (Aguilar et al. 2007). On the other hand, details of the morphology of *E. assimilis*, which has an accessory crest on M1, M2 suggest that this species does not form part of either of the two main lineages. These observations are confirmed by the results of our cladistic analysis (Fig. 4, Table 3).

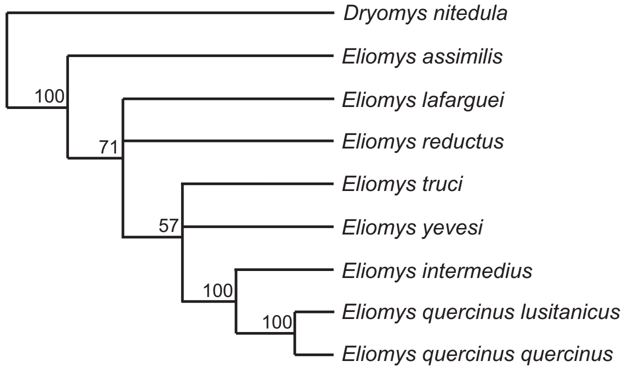

Fig. 4. 50% majority rule consensus of the seven most parsimonious trees (L = 21, retention index = 0.619, consistency index = 0.619) resulting from the phylogenetic analysis. Numbers next to clades indicate the percentage of most parsimonious trees in which the clade was recovered. The extant glirid *Dryomys nitedula*, a form closely related to *Eliomys*, was chosen as outgroup.

Evolutionary process.—The oldest record of *Eliomys* is *E. truci* from the Middle Miocene of Solera (late Aragonian–early Tortonian; Daams and Freudenthal 1988). However, the identity of this material has been questioned (García-Alix et al. 2008a), thus possibly reducing the earliest occurrence of the genus to *E. truci* from the Late Miocene (early Vallesian–Tortonian) of Pedregueras 2A (Daams and Freudenthal 1988). Several members of the genus co-occur during the Miocene (Fig. 5), which may imply cladogenetic evolution. Thus, Adrover (1986) suggested *E. truci*, including its ancestor *Eliomys* sp. I from Viveros de Pinos (Teruel Basin, north-central Spain; early Turolian–Tortonian), and *Eliomys* sp. II from Aljezar B (Teruel Basin, middle Turolian, Tortonian), to be descendants of an older, yet unknown species of the same genus. A similar logic applies to *E. truci* on the one hand, and *E. yevesi–E. intermedius* on the other. Both of these lineages co-existed during the Ruscinian (Zanclean) and the earliest Villanyan (Piacenzian), as is evident at Orrios-3, Sète, Sarrión, Villalba Alta (Adrover 1986), La Gloria 4, Escorihuela (Mein et al. 1990), Moreda-1A, 1B, Rambla Seca 1 (Castillo 1990), TCH-1B and TCH-13 (García-Alix et al 2008a).

Until the first occurrence of *E. quercinus* in the earliest Pleistocene locality of Almenara-Casablanca 1 (Agustí et al. 2011), the only representative of *Eliomys* during the latest Pliocene and early Pleistocene was *E. intermedius* (García-Alix et al. 2008a).

Table 3. Cladistic data matrix for *Eliomys*, including lower (1 to 4) and upper (5 to 8) molar dental characters.

Species	1	2	3	4	5	6	7	8	9	10
Eliomys assimilis	2	0	0	1	1	2	2	1	0	0
Eliomys reductus	2	1	0	0	1	2	0	0	0	0
Eliomys lafarguei	1	1	0	1	0	1	0	0	0	0
Eliomys truci	0	0	0	1	1	1	0	0	0	1
Eliomys yevesi	0	0	0	1	1	2	2	0	0	1
Eliomys intermedius	0	0	0	1	1	2	2	0	0	2
Eliomys quercinus quercinus	0	1	0	0	0	2	2	0	0	2
Eliomys quercinus lusitanicus	0	0	0	1	0	2	2	0	0	2
Dryomys nitedula	1	1	1	1	1	2	2	1	1	0

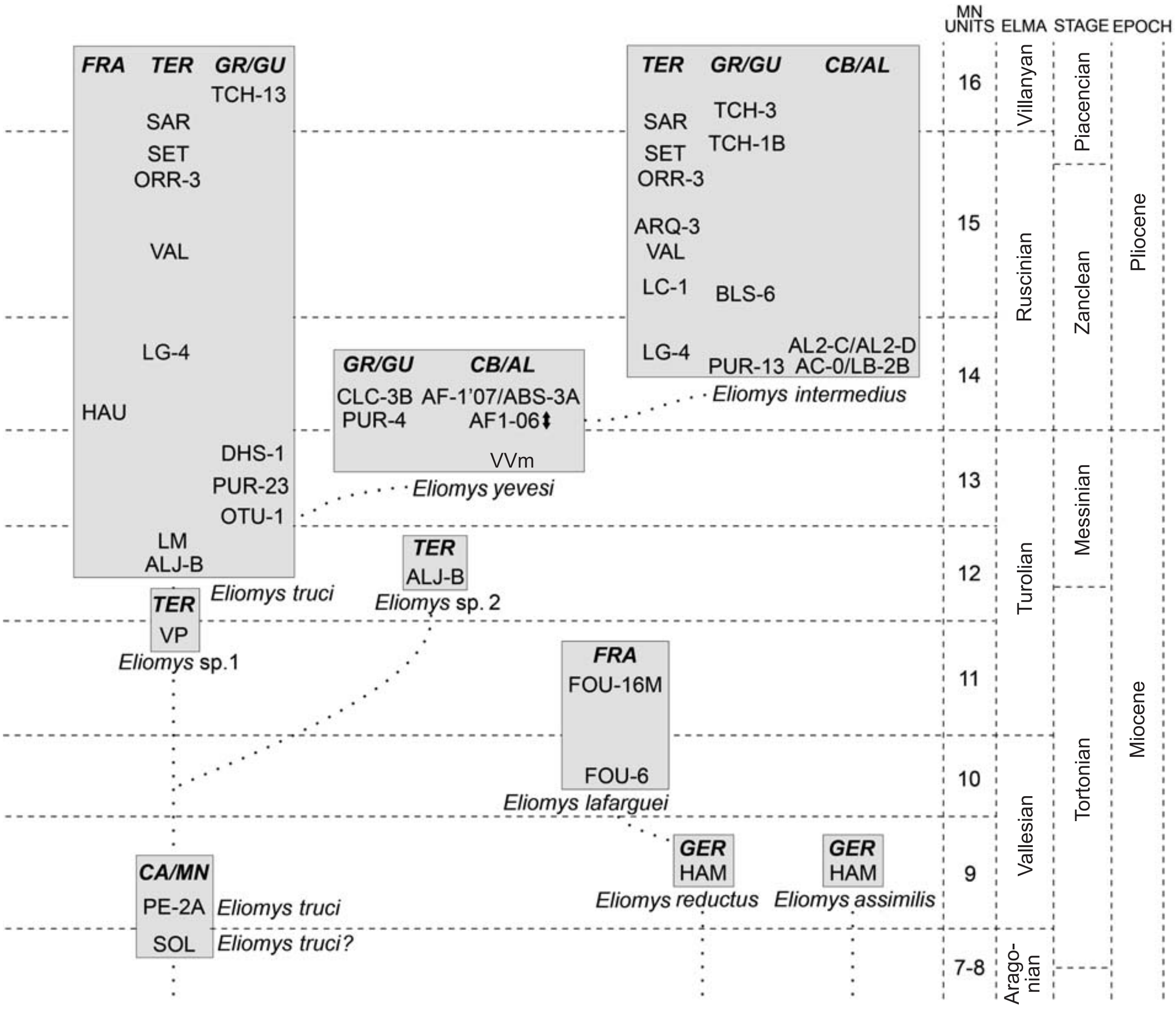

Fig. 5. Early Vallesian (early Tortonian) to early Villanyan (Piacenzian) stratigraphic distribution and proposed phylogenetic relationships of the genus *Eliomys* (modified from García-Alix et al. 2008a). Abbreviations: ABS, Alcoi Barranc Sud; AC, Alcoy Cristian; AF, Alcoi Forn; AL, Alcoy; ALJ, Aljezar; ARQ, Arquillo; BLS, Barranco de Blas; CA/MN, Calatayud-Montalbán Basin; CB/AL, Cabriel and Alcoy Basins; CLC, Calicasas; DHS, Dehesa; ELMA, European Land Mammal Age; FOU, Lo Fournas; FRA, France; GER, Germany; GR/GU, Granada and Guadix Basins; HAU, Hautimagne; Ham, Hammerschmiede; LB, La Bullana; LC, Lomas de Casares; LG, La Gloria; LM, Los Mansuelos; MN, Mammal Neogene Units; ORR, Orrios; OTU, Otura; PE-2A, Pedregueras 2A; PUR, Purcal; SAR, Sarrión; SET, Sète; SOL, Solera; TCH, Tollo de Chiclana; TER, Teruel Basin; VAL, Villaba Alta; VVm, Venta del Moro; VP, Viveros de Pino. The double-headed arrow indicates the range of uncertainty.

In contrast to the earlier process of cladogenesis, several authors have hypothesized that *E. quercinus* may have arisen from *E. intermedius* through a process of anagenetic evolution (Chaline 1972; Castillo 1990; García-Alix et al. 2008a), involving a reduction in size and a trend towards an unconnected anteroloph and protoloph (Castillo 1990). Extant *E. quercinus* comprises at least eight subspecies, two of which are found in the Iberian Peninsula (Moreno Garrido 1984), the smaller *E. quercinus quercinus*, which inhabits relatively open environments and is characterized by slightly sinuous crests, a continuous endolophid, a small centrolophid, and no accessory crests; and the larger *E. quercinus lusitanicus*, which lives in more closed environments, and is marked by more distinctly sinuous crests, accessory crests, and the absence of both the endolophid and the centrolophids. In the latter two features, *E. quercinus lusitanicus* resembles *E. intermedius*, which even led to the suggestion that the latter should be regarded as a subspecies of *E. quercinus* (Martín-Suárez 1988).

In summary, it therefore seems that the lineage including *E. truci*, *E. yevesi*, and *E. intermedius*, and the extant *E. quercinus* originated and diversified through cladogenesis during the Late Miocene, and Early Pliocene, but then switched to a process of anagenetic evolution during the Late Pliocene and Pleistocene.

Conclusions

Based on new fossil material from the Alcoy and Cabriel basins of southeastern Spain, as well as material from the Granada Basin previously referred to *E.* aff. *intermedius*, we erect the new species *Eliomys yevesi* sp. nov., similar in size or slightly larger than *E. truci*. *E. yevesi* generally resembles *E. truci* in terms of its morphology, but differs in having better and more frequently developed centrolophs in the upper molars, similar to *E. intermedius*. Based on its size and morphology, we consider the most probable origin of the new species a Late Miocene population of *E. truci* (Fig. 5), likely an ecomorphotype characterized by well-developed centrolophs in the upper molars, and both a long centrolophid and a well-developed posterotropid in the lower molars. *E. yevesi* thus likely forms part of a lineage comprising *E. truci*–*E. yevesi*–*E. intermedius*–*E. quercinus* (to the exclusion of other members of the genus, such as *E. assimilis* and *E. reductus*; Fig. 4), which is characterized by a trend towards the reduction of accessory crests in the lower molars, as well as the development of centrolophs. This arrangement is complemented by a second lineage including *E. reductus* and *E. lafarguei*, marked by an increase in size, a gradual reduction of the postcentroloph and centrolophid, and a trend towards a more quadrangular occlusal outline (lower length-width ratio).

Acknowledgments

We thank Elvira Martín-Suárez (Universidad de Granada, Spain) for her comments, Sacramento Moreno (Doñana Biological Station, Sevilla, Spain) for providing a picture of the occlusal surface of the molars of *Eliomys quercinus quercinus*, Héctor Botella (Universidad de València, Spain) for his help with the cladistic analysis, and Mattijhs Freudenthal (Universidad de Granada, Spain), an anonymous reviewer, and editor Felix G. Marx (University of Otago, New Zealand), for their useful comments and criticism. The field work at Venta del Moro was approved and supported, from 1995 onwards, by the Conselleria de Cultura of the Generalitat Valenciana, with the permission of the Ministerio de Fomento and the Administración de infraestructuras ferroviarias. This investigation was supported by projects GV06/304 and GVPRE/2008/320 of the Valencian Government, CGL2011-25754 of the Spanish Ministry of Economy and Competitiveness, and RNM 8011 of the Junta de Andalucía.

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Appendix 1

Dental characters included in the cladistic analysis.

Lower molars: 1, Average value of length/width ratio of m1, m2: (0) always less than 1, molars are clearly wider than long; (1) variably above or below 1, molars are sub-quadrangular to sub-rectangular in occlusal outline; (2) always higher than 1, molars are clearly longer than wid. 2, Endolophid: (0) always discontinuous; (1) continuous in some specimens. 3, Anterotropid: (0) always absent; (1) present in some specimens. 4, Posterotropid: (0) always absent; (1) present in some specimens. 5, Centrolophid: (0) absent or short (less than half the width of the molar); (1) usually long (half the width of the molar or longer).

Upper molars: 6, Presence of both centrolophs on M1, M2: (0) absent; (1) rare (less than 30%); (2) common (30% or higher). 7, Presence of both centrolophs on M3: (0) absent; (1) rare (less than 30%); (2) common (30% or higher). 8, Presence of an accessory crest in the upper molars: (0) absent; (1) present in some specimens. 9, Presence of two accessory crests in some upper molars; (0) absent; (1) present in some specimens. 10, Size: (0) clearly smaller on average than *E. truci*, with some dental elements out of the size range of this species (see Fig. 3); (1) equal or largely the same as *E. truci*; (2) clearly bigger on average than *E. truci*, with some dental elements out of the size range of this species. See Table 3 for the resulting data matrix.

Appendix 2

Repository numbers of the specimens listed in Table 1.

p4: VVmA-42 (MGUV-27256), VVmA-43 (MGUV-27257).

m1/m2: VVmA-1 to VVmA-11 (MGUV-27215 to MGUV-27225); VVmB-1 (MGUV-27405); VVmBC-1 (MGUV-27487) and VVmBC-2 (MGUV-27488); ABS3A-38 (MGUV-23529); AF1’06-190 (MGUV-28334); LB2B-176 and LB2B-242 (MGUV-28727 and MGUV-28793); AL2D-290 (MGUV-28063); AL2C-97 (MGUV-28924).

m3: VVmA-33 to VVmA-38 (MGUV-27247 to MGUV-27252); VVmC-1 (MGUV-27487); VVmBC-5 (MGUV-27490); LB2B-179 (MGUV-28730); AF1’06-187 (MGUV-28331); AC0-88 (MGUV-28551); AL2C 97 (MGUV-28924); AL2D-356 (MGUV-28129).

D4: VVmA-44 (MGUV-27258).

P4: VVmA-39 to VVmA-41 (MGUV-27253 to MGUV-27255); LB2B-178 (MGUV-28729).

M1/M2: VVmA-16 (MGUV-27230); VVmA-21 to VVmA-31 (MGUV-27235 to MGUV-27245); VVmBC-3; VVmD-1 and VVmD-2 (MGUV-27543 and MGUV-27544); AF1’07-36 (MGUV-28427); AC0-87 (MGUV-28550); LB2B-241 (MGUV-28792); AL2D-291 (MGUV-28064); AL2D-293 (MGUV-28066).

M3: VVmA-12 to VVmA-15 (MGUV-27226 to MGUV-27229); VVmA-17 to VVmA-20 (MGUV-27231 to 27234); VVmBC-4 (MGUV-27489, LB2B-177 (MGUV-28728).