A new species of glirid rodent *Vasseuromys* from the Aragonian (Miocene) of the Ebro Basin (north-eastern Spain)

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We describe a new species of *Vasseuromys* from the locality of Pico del Fraile 2 (PF2) in the Ebro Basin of northeastern Spain, which has yielded a fauna comprising several rodents and insectivores (*Eumyarion* cf. *weinfurteri*, *Megacricetodon* cf. *primitivus*, *Democricetodon* aff. *hispanicus*, *Spermophilinus* cf. *besana*, *Microdyromys* cf. *legidensis*, *Galerix* sp., and Lagomorpha indet.) indicative of Aragonian zones C or D. *Vasseuromys cristinae* sp. nov. differs from other *Vasseuromys* species in the constant presence of four extra ridges on the lower molars, one of them being connected to the posterolophid in the posterior valley, as well as three extra ridges on the upper molars, with none of them located outside the trigone. Morphological comparisons of this new taxon to other *Vasseuromys* species from the western Mediterranean area allow the reconstruction of their phylogenetic interrelationships during the Early and Middle Miocene of Europe, suggesting that *V. cristinae* sp. nov. is a descendant of *V. autolensis*.

Key words: Mammalia, Rodentia, Gliridae, *Vasseuromys*, systematics, Miocene, Ebro Basin, Spain.

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Introduction

We describe *Vasseuromys cristinae* sp. nov. from Pico del Fraile 2 (PF2) in the western Ebro Basin of northeastern Spain. *Vasseromys* Baudelot and de Bonis, 1966 is uncommon in the European Early and Middle Miocene fossil record, and was originally erected based on material from the localities of Laugnac and Moissac I (France, Lower Miocene) in order to distinguish glirid rodents of medium size marked by concave occlusal surfaces and a tendency for the molar cusps to form longitudinal walls.

The genus comprises seven species: *Vasseuromys autolensis* (Cuenca, 1985), *V. priscus* de Bonis, 1973, *V. duplex* Ünay, 1994, *V. rugosus* Baudelot and de Bonis, 1966, *V. bacchius* (Martínez Salanova, 1987), *V. elegans* Wu, 1993, and *V. pannonicus* (Kretzoi, 1978). While six out of these seven species occur in Europe, *V. duplex* has only been found in Anatolia, Turkey (Ünay 1994). The fossil record of *V. autolensis* (Cuenca 1985) and *V. bacchius* (Martínez-Salanova 1987) is restricted to Spain, whereas *V. elegans* and *V. pannonicus* have only been reported from Central Europe (Kretzoi 1978; Daxner-Höck and de Bruijn 1981; Wu 1993). The other European species, *V. priscus* and *V. rugosus*, have a wider geographic range, extending to both southwestern and Central Europe (de Bonis 1973; Álvarez-Sierra et al. 1991; Wu 1993).

Until now, the oldest European record of *Vasseuromys* is represented by *V. autolensis* from the Ebro Basin. Its sudden appearance in the Early Miocene is considered to be the result of a dispersal event, as also suggested by the composition of the latest Oligocene faunas of Western Europe (Agustí et al. 2001). Another species, *V. moyai*, was reported from older deposits correlating with zone MP 25 at the Spanish locality of Sineu (Hugueney and Adrover 1990). How-

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ever, Freudenthal and Martín-Suárez (2007a) referred this taxon to *Oligodyromys,* following Hugueney and Adrover (1990), who thought it to be derived from a species close to *Oligodyromys planus*.

While it seems that *Vasseuromys* occurred simultaneously in Anatolia and SW Europe, the Palaeogene history of glirids in Anatolia is still largely unknown (Ünay 1994), and a potential Asiatic origin of *Vasseuromys* can therefore not be ruled out.

The temporal range of the genus extends from the Early to the Late Miocene (zones MN1 to MN11). In zones MN4 to MN10 its fossil record is scarce and, so far, restricted to *V.* aff. *elegans* from the localities of Erkertshofen 2 and Petersbuch 2 (Wu 1993), as well as *V.* aff. *elegans*, *V.* aff. *priscus*, and *Vasseuromys* sp. from Blanquatère 1 (Aguilar and Lazzari 2006). Furthermore, in the area of the Bardenas Reales (Ebro Basin, Spain), where locality PF2 is located, new data demonstrate its occurrence near the Ramblian/Aragonian boundary (Ruiz-Sánchez et al. 2010).

While the micromammal fauna of PF2 will be described elsewhere, the preliminary mammal fauna list includes *Eumyarion* cf. *weinfurteri* (Schaub and Zapfe, 1953), *Megacricetodon* cf. *primitivus* (Freudenthal, 1963), *Democricetodon* aff. *hispanicus* Freudenthal, 1967, *Spermophilinus* cf. *besana* Cuenca, 1988, *Microdyromys* cf. *legidensis* Daams, 1981, *Galerix* sp., and Lagomorpha indet. The association of *Megacricetodon* cf. *primitivus* and *Eumyarion* cf. *weinfurteri* allows the dating of PF2 to Aragonian zone C or lower zone D, straddling the MN4/MN5 boundary, and thus the Lower–Middle Miocene (Daams and Freudenthal 1988; Van der Meulen and Daams 1992).

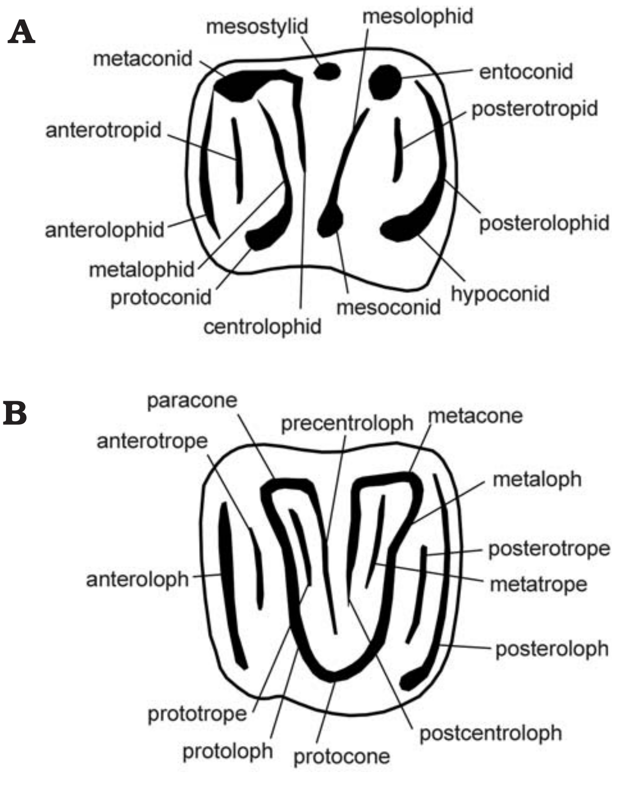

Fig. 1. Nomenclature of the cheek teeth, after Freudenthal (2004). **A**. Lower molars. **B**. Upper molars.

Institutional abbreviations.—SCSIE(UV), Servei Central de Suport a la Investigació Experimental de la Universitat de València, Burjassot, Spain; UPV/EHU, Universidad del País Vasco/Euskal Herriko Unibertsitatea, Bilbao, Spain.

Other abbreviations.—ATNTS, Astronomically tuned Neogene time scale; dP4, P4, M1, M2, and M3, upper teeth; L, length; MN, European Neogene land mammal units; PF2, Pico del Fraile locality 2 (Ebro Basin); p4, m1, m2, and m3, lower teeth; W, width.

Material and methods

Fossils were collected during the field seasons of 2004–2006, and are kept in the Department of Stratigraphy and Palaeontology of the University of the Basque Country (UPV/EHU) with the field label PF2-. The nomenclature used in the descriptions of the teeth and the measurement method are that of Freudenthal (2004) (Fig. 1). Measurements are in tenths of 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. Concavity profiles of the occlusal surfaces of 12 specimens (three m1, four m2, three M1, and two M2) of *V. cristinae* sp. nov. in anterior and posterior view were drawn with a camera lucida mounted on a Wild M5 binocular microscope at 40× magnification, following Freudenthal and Martín-Suárez (2007b).

Geological setting

The section at Pico del Fraile belongs to the Tudela Formation, and includes the youngest sediments preserved in the western part of the Ebro Basin (Fig. 2) in the region of the Bardenas Reales de Navarra (Larrasoaña et al. 2006). The formation has been divided into five lithostratigraphic units according to the predominance of distal alluvial (Units 1 and 4), palustrine (Unit 3), and lacustrine (Units 2 and 5) sedimentary facies (Larrasoaña et al. 2006), with the Pico del Fraile section spanning the uppermost part of Unit 3, Unit 4, and the lowermost part of Unit 5 (Larrasoaña et al. 2006) (Fig. 3).

PF2 is located at the top of the section in Unit 5, which is composed of grey and ochre mudstone, and grey and beige limestone. The mudstone packages are massive and range from a few centimetres to several metres in thickness, while the limestone beds are up to 2 metres thick, often massive and bioturbated, and contain abundant gastropods, ostracods, charophytes, fish bones, and other fossil fragments. The limestone indicates deposition in a stable fresh water lacustrine system, whereas the mudstone was deposited under palustrine conditions. These facies are similar to those

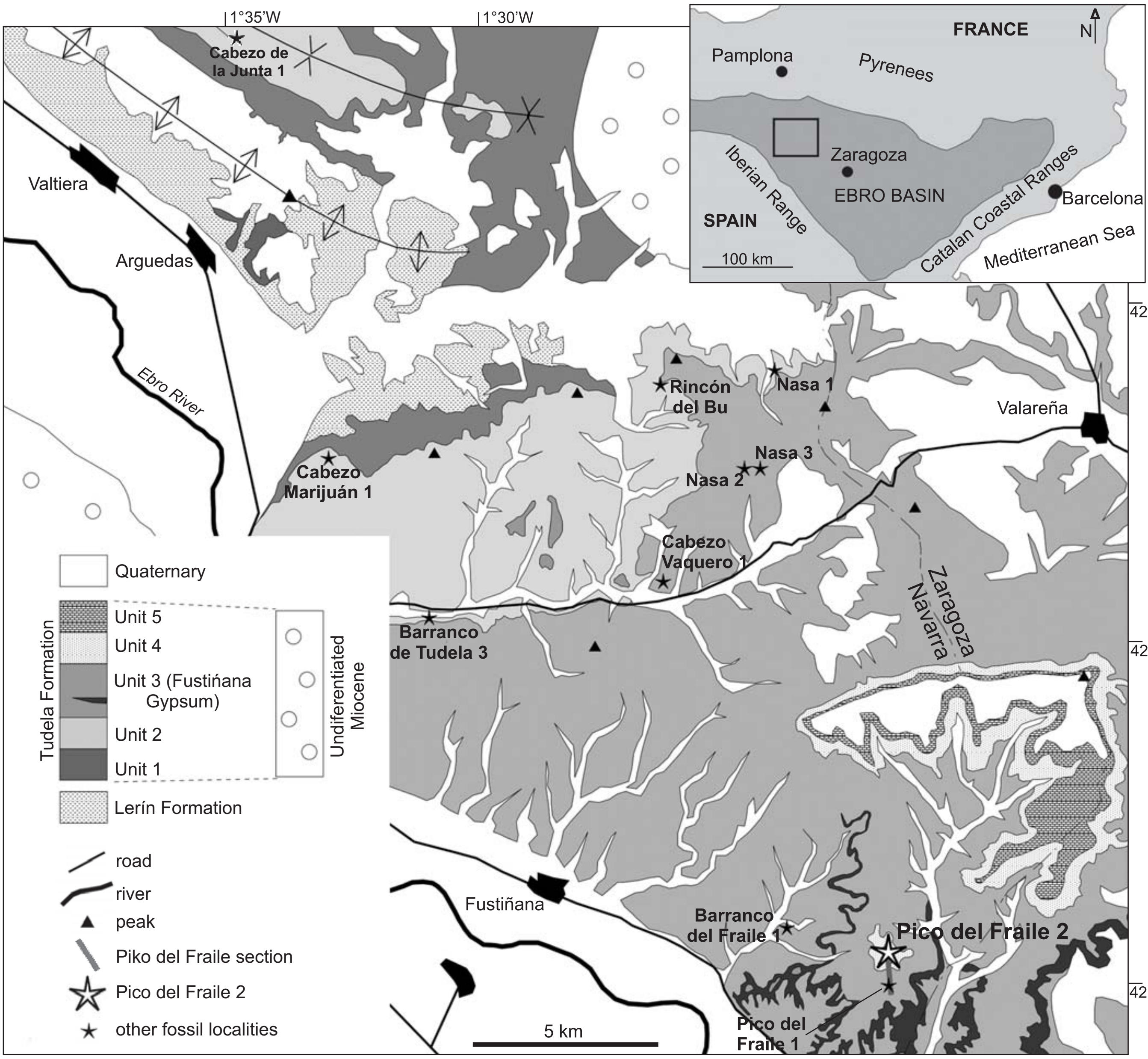

Fig. 2. Geological map of the Lower–Middle Miocene continental sediments of the Tudela Formation exposed in the Bardenas Reales de Navarra area, showing the location of the Pico del Fraile 1 section and Pico del Fraile 2 (PF2). Other fossil localities studied previously by Murelaga (2000) and Murelaga et al. (2004a, b) are also shown. Abbreviations: BF1, Barranco del Fraile 1; BT3, Barranco de Tudela 3; CJ1, Cabezo de la Junta 1; CM1, Cabezo Marijuán 1; CV1, Cabezo Vaquero 1; N1, Nasa 1; N2, Nasa 3; N3, Nasa 3; PF1, Pico del Fraile 1; RB1, Rincón del Bu 1.

described from the Early and Middle Miocene of the central part of the Ebro Basin, when the latter formed an endorrheic depression at the foothills of the Pyrenees, the Iberian Range, and the Catalan Coastal Range (Arenas and Pardo 1999; Alonso Zarza et al. 2002).

The absolute age of PF2 can be derived with confidence from the results of an earlier magnetostratigraphic study (Larrasoaña et al. 2006). Pico del Fraile 2 is located at the uppermost reversed magnetozone of the Pico del Fraile section, which unambiguously correlates with the lower part of chron C5Br. We therefore estimate an extrapolated age of about 15.8 Ma (Middle Miocene) for PF2.

Systematic palaeontology

Order Rodentia Bowdich, 1821

Family Gliridae Muirhead, 1819

Subfamily Myomiminae Daams, 1981

Genus *Vasseuromys* Baudelot and de Bonis, 1966

Type species: *Vasseuromys rugosus* Baudelot and de Bonis, 1966; Lower Miocene, Laugnac, France.

Original diagnosis (Baudelot and de Bonis 1966, translated from French).—“[A medium-sized glirid having cheek teeth

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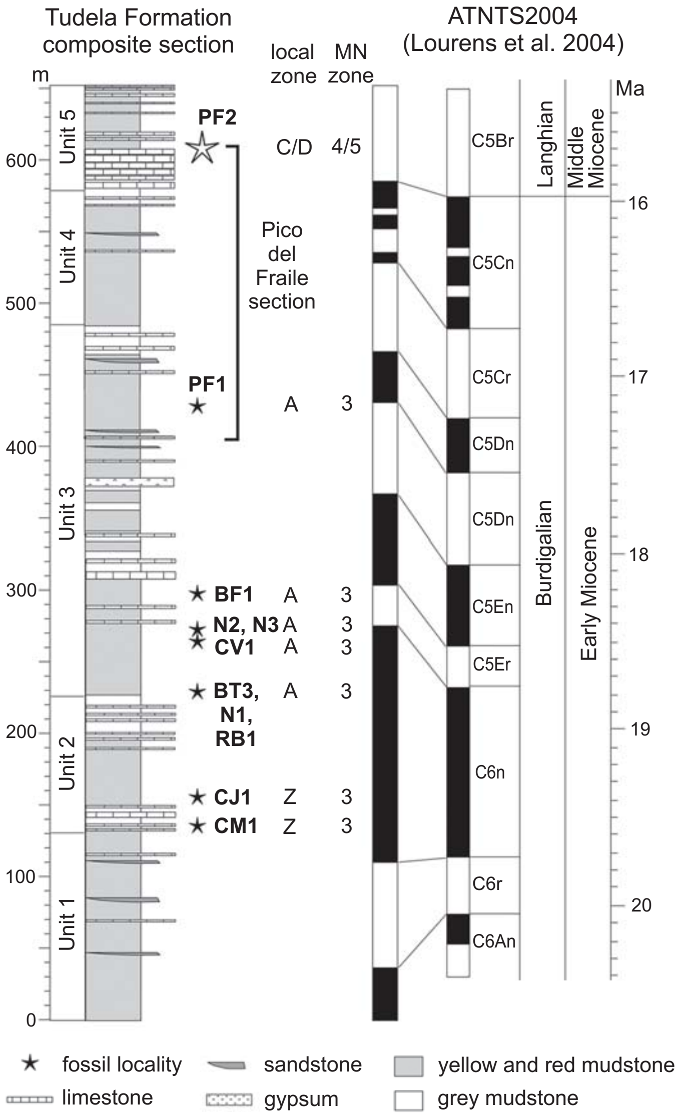

Fig. 3. Composite lithostratigraphic and magnetostratigraphic logs of the Tudela Formation (see Larrasoaña et al. 2006) and their correlation to the ATNTS2004 of Lourens et al. (2004). The position of PF2 is described in this study; for the other fossil localities see Fig. 1, Murelaga (2000) and Murelaga et al. (2004a, b).

with a concave occlusal surface. Lower molars characterised by a centrolophid reaching the labial border and by longitudinal prolongation of the labial cusps, which form a nearly continuous external wall.]"

Emended diagnosis (de Bonis 1973).—The original diagnosis was later emended by adding that the upper molars have an endoloph.

Vasseuromys cristinae sp. nov.

Fig. 4.

Etymology: Named after Cristina Marzo, stepdaughter of the first author.

Holotype: PF2-81, isolated left m1.

Type locality : Pico del Fraile 2 (PF2), Ebro Basin, Spain.

Type horizon: 15.8 Ma, Lower–Middle Aragonian, Middle Miocene.

Referred material.—2 p4 (PF2-103; PF2-104), 8 m1 (PF2-81; PF2-82; PF2-84; PF2-85; PF2-86; PF2-87; PF2-108; PF2-109), 7 m2 (PF2-89; PF2-90; PF2-91; PF2-92; PF2-93; PF2-94; PF2-95), 5 m3 (PF2-97; PF2-98; PF2-99; PF2-100; PF2-101), 1 dP4 (PF2-80), 2 P4 (PF2-78; PF2-79), 11 M1 (PF2-61; PF2-63; PF2-64; PF2-65; PF2-66; PF2-68; PF2-69; PF2-70; PF2-72; PF2-74; PF2-113), 4 M2 (PF2-62; PF2-67; PF2-71; PF2-73), 3 M3 (PF2-76; PF2-77; PF2-111).

Diagnosis.—Medium-sized species of *Vasseuromys.* Lower molars with four extra ridges: anterotropid, extra ridge between metalophid and centrolophid, second centrolophid, and posterotropid; metalophid mostly connected to the metaconid, and mesolophid to the entoconid; posterotropid connected to posterolophidł M1–2 with incomplete endoloph; M1–2 without extra ridges outside the trigone and three on the inside (prototrope, metatrope, and medium-sized and elongated mesostyle between pre- and postcentroloph).

Differential diagnosis.—*Vasseuromys cristinae* sp. nov. differs from *V. autolensis*, *V. priscus*, *V. rugosus*, *V. bacchius*, *V. elegans*, and *V. pannonicus* in: presence of four extra ridges on m1–3; posterotropid always single; differs from *V. duplex* in: single anterotropid; posterotropid connected to the posterolophid; differs from *V. bacchius* and *V. pannonicus* in: metalophid connected to the metaconid; differs from *V. priscus* and *V. rugosus* in: higher frequency of specimens with a mesolophid–entoconid connection; differs from *V. autolensis*, *V. priscus*, *V. duplex,* and *V. pannonicus* in: constant presence of three extra ridges inside the trigone on M1–2; differs from *V. autolensis*, *V. priscus*, *V. bacchius,* and *V. rugosus* in: much higher frequency of M1–2 with anteroloph and posteroloph connected to the paracone and metacone, respectively; differs from *V. pannonicus* in: presence of divided paracone on M1–2; differs from *V. rugosus*, *V. bacchius,* and *V. pannonicus* in: M2 with long prototrope connected to the precentroloph; differs from *V. bacchius* in: anteroloph of M3 connected to the paracone; differs from *V. autolensis* in: lower frequency of anterotrope on M3 (33% vs. 65%); differs from all other species of *Vasseuromys* in: complete absence of endoloph on M1–2. With respect to size, *V. cristinae* sp. nov. is smaller than *V. bacchius*, larger than *V. duplex* and *V. elegans*, and similar to the remaining members of the genus (Figs. 5, 6).

Measurements.—See Table 1.

Description

p4.—The anterolophid is connected to the protoconid. The centrolophid is long and connected to an external wall along the labial border of the tooth (n = 1), or of medium size and not connected to this external wall (n = 1). The labial cusps are elongated anteriorly. The prominent ectolophid is interrupted between the mesolophid and the posterolophid. One out of two specimens has a posterior branch of the hypoconid, forming a tiny valley with the posterolophid behind the hypoconid (Fig. 4A). Both specimens have an extra ridge between the

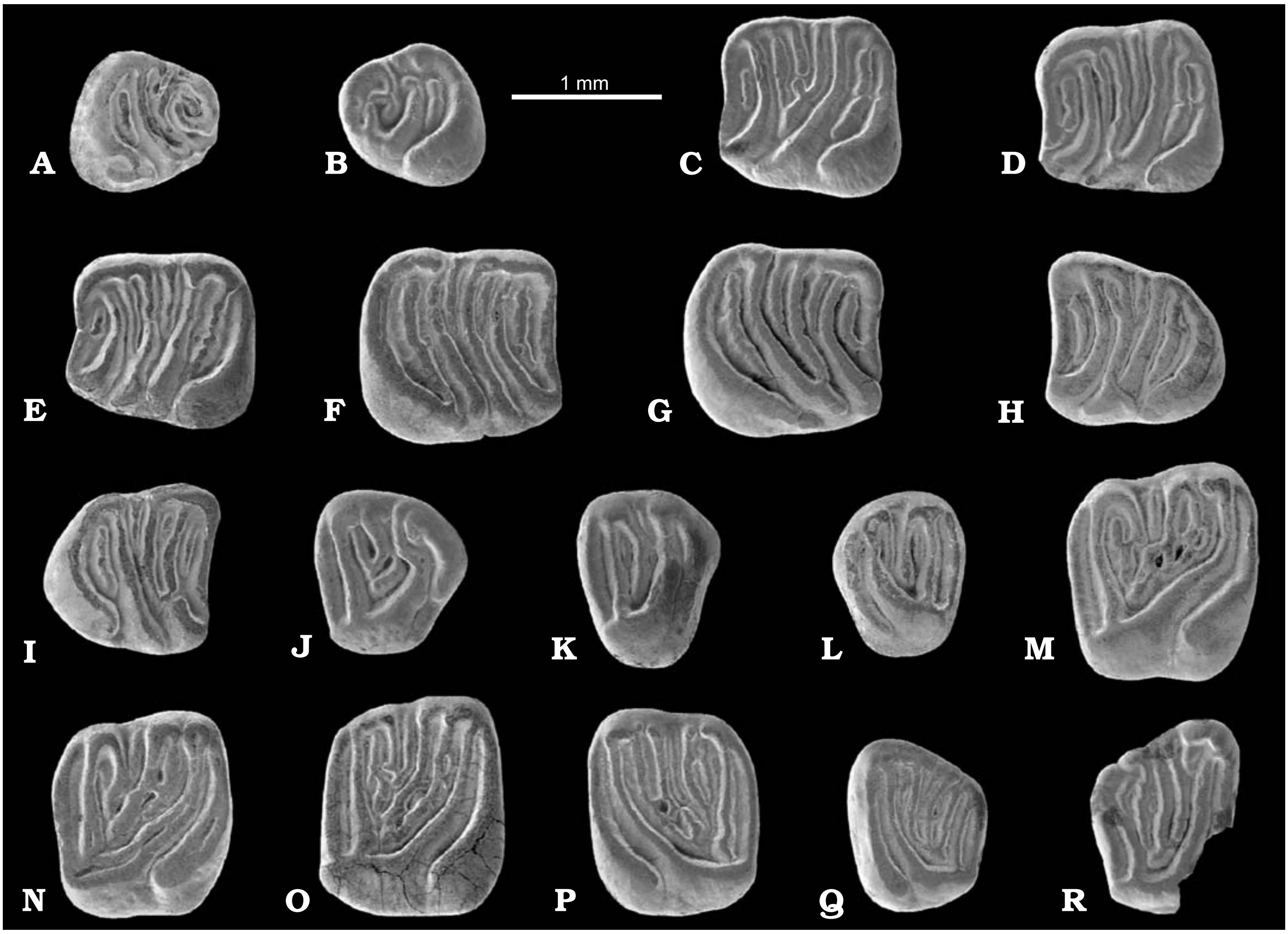

Fig. 4. Upper and lower dentition of the glirid *Vasseuromys cristinae* sp. nov. from PF2, Ebro Basin, Spain, in occlusal view. **A**. PF2-103, right p4. **B**. PF2-104, left p4. **C**. PF2-81 (holotype), left m1. **D**. PF2-84, left m1. **E**. PF2-85, left m1. **F**. PF2-90, right m2. **G**. PF2-92, right m2. **H**. PF2-98, left m3. **I**. PF2-100, right m3. **J**. PF2-80, right D4. **K**. PF2-78, right P4. **L**. PF2-79, left P4. **M**. PF2-63, right M1. **N**. PF2-72, right M1. **O**. PF2-62, right M2. **P**. PF2-71, left M2. **Q**. PF2-76, left M3. **R**. PF2-77, right M3.

metalophid and the centrolophid, a second centrolophid, and a posterotropid.

m1.—The anterolophid is either connected to the protoconid at a high level, or a tiny and shallow furrow is present between them (Fig. 4D). The metalophid is connected to the metaconid at either a high or a low level. In two of the specimens the centrolophid is double, with both ridges having at least one connection; in another specimen, the centrolophid is connected to the labial part of the metalophid, whereas it fuses at the labial border with the anterior prolongation of the mesoconid in five others (Fig. 4D). The mesolophid is connected to the entoconid. The labial part of the posterolophid is elongated longitudinally and separated from the mesoconid. The posterotropid is long and usually connected to the anterolingual part of the posterolophid (n = 7), with only one specimen lacking this connection. There are generally four extra ridges: an anterotropid (not present in one of the seven specimens), a ridge between the metalophid and the centrolophid, a second centrolophid, and a posterotropid. The posterior centrolophid either ends free, or is connected to the entoconid and/or lingual part of the centrolophid. The posterior centrolophid is of medium size (Fig. 4E) or long. It is generally isolated (n = 5), but can also be connected to the anterior centrolophid (n = 2) or labially fused to the elongated part of the mesoconid (n = 1).

m2.—In unworn specimens, the anterolophid is connected to the protoconid at either a high (n = 4) or a low level (n = 1). The metalophid is connected to the metaconid in four specimens, but unconnected in another two. The centrolophid is long, and either fused to the anterior prolongation of the mesoconid (n = 4) (Fig. 4G), or connected to the latter at a low level (Fig. 4F). The mesolophid is connected to the entoconid. The posterolophid curves and becomes lower along the labial border, either closely approaching the mesoconid (n = 4), or being connected to it (n = 2). In two specimens, the labial end of the posterolophid is attached to the mesoconid at a low level (Fig. 4G). Four extra ridges are present, including an anterotropid, a ridge between metalophid and centrolophid, a second

Table 1. Measurements (in tenths of millimetres) of the lower and upper teeth of *Vasseuromys cristinae* sp. nov. from PF2. Abbreviations: n, number of specimens; min., minimum; max., maximum.

Element	Parameter	n	Min.	Mean	Max.
p4	L	2	9.18	9.63	10.07
	W	2	7.73	8.30	8.86
m1	L	8	11.28	11.77	12.40
	W	7	9.81	11.11	11.80
m2	L	7	12.13	12.73	13.25
	W	8	12.07	12.57	13.00
m3	L	5	10.85	11.53	12.50
	W	4	10.63	11.21	11.52
D4	L	1	–	10.17	–
	W	1	–	10.77	–
P4	L	2	8.55	9.05	9.54
	W	2	10.66	11.14	11.61
M1	L	10	11.18	12.04	12.90
	W	7	12.67	13.48	14.21
M2	*L*	4	11.53	12.14	12.51
	W	3	13.83	14.20	14.59
M3	*L*	2	9.20	9.58	9.95
	W	2	11.61	12.14	12.66

centrolophid, and a posterotropid. The connection (at a high or a low level) of the lingual part of the posterior centrolophid to these ridges forms a nearly continuous endolophid (Fig. 4G). At the lingual border of the tooth, the posterior centrolophid is connected to the anterior centrolophid at a high level, whereas it is connected to the mesolophid at either a high or a low level, thus closing the central valley in several specimens. The posterotropid is long and reaches the labial portion of the posterolophid without being connected (n = 4) (Fig. 4G), or being connected to the latter at a low level (n = 2) (Fig. 4F). The posterotropid is connected to the anterolingual portion of the posterolophid at a low level (n = 5), or a tiny and shallow furrow separates both ridges.

m3.—The anterolophid is connected to the protoconid at either a high (n = 4) or a low (n = 1) level. The metalophid is connected to the metaconid. The centrolophid is long and fused to the anterior prolongation of the mesoconid (n = 3), not connected to the mesoconid (n = 1), or connected to the posterior part of the metalophid (n = 1). In one specimen, there is a longitudinal ridge connecting the centrolophid and mesolophid. The mesolophid is connected to the entoconid. In one specimen, the posterolophid is labially connected to the mesoconid. There are four extra ridges, including an anterotropid, a ridge between the metalophid and centrolophid, a second centrolophid, and a posterotropid. The second centrolophid and the extra ridge between the metalophid and centrolophid are short, with the latter usually being connected to the anterior part of the centrolophid. As on m2, the endolophid is nearly continuous (Fig. 4H). The posterotropid is lingually connected to the posterolophid (Fig. 4H).

dP4.—The anteroloph is connected to the protocone at a low level, while making contact with the paracone at a higher level (Fig. 4J). Both the metaloph and the strongly curved protoloph are connected to the protocone. The postcentroloph is strongly curved and connected to the protocone. The metaloph is connected to the protocone. The postcentroloph is of medium size. Only the lingual part of the precentroloph, which is situated in the central valley, is developed. The prototrope is absent. There is a relatively long metatrope, connected to the lingual end of the postcentroloph. The posteroloph is connected to the metacone and protocone.

P4.—The anteroloph is connected to the protocone at a low level. The anteroloph is labially connected to the paracone. The protoloph and metaloph are connected to the protocone. The precentroloph is either relatively long (n = 1) (Fig. 4L) or short (n = 1) (Fig. 4K), whereas the postcentroloph is long. The extra ridges are reduced to a short metatrope. The posteroloph is long and connected to the protocone.

M1.—The anteroloph is long and extends to the protocone without forming an endoloph. In unworn specimens, the paracone is divided into two cusps. The anterior cusp of the paracone continues into the protoloph (Fig. 4M, N), while the posterior cusp fuses with the precentroloph–prototrope complex. The centrolophs are long, with the precentroloph usually being longer than the postcentroloph (Fig. 4N). Generally there are three extra ridges, including a prototrope, a ridge between the precentroloph and postcentroloph, and a metatrope. Some specimens possess additional low extra ridges running parallel to the main ones (Fig. 4M). In some specimens, the union between the centrolophs and the extra ridge complex forms an irregular pattern (Fig. 4M). The metaloph is oriented transversely and connected to the protocone. There are no extra ridges outside the trigone. In unworn specimens, the posteroloph is connected to the protocone and metacone. A shallow furrow separates the labial end of the posteroloph and the metacone in some specimens (Fig. 4N).

M2.—The anteroloph is long, connected to the paracone, and connected to the protocone at a low level without forming an endoloph. The paracone shows a slight division into two cusps (Fig. 4P). The centrolophs are long, with the precentroloph being the longer one. There are three extra ridges, including a prototrope, a ridge between the precentroloph and postcentroloph, and a metatrope. The prototrope is very long and runs parallel to the precentroloph until they become connected near the protocone (Fig. 4O). Other longitudinal connections between both ridges are present. No extra ridges are found outside the trigone. The metaloph is transversely oriented and connected to the protocone and paracone, whereas the posteroloph is connected to the protocone and metacone.

M3.—The anteroloph is connected to the paracone and not connected to the protocone in one complete specimen (Fig. 4Q), while being connected to the latter at a low level in another one (Fig. 4R). The centrolophs are long. As on M2, there are three extra ridges and, in addition, one of the three specimens has a very short anterotrope. The connections between the centrolophs and the extra ridges form an irregular ridge pattern (Fig. 4R). The metacone is divided into several cusps, giving rise to the posterior centroloph and the metaloph (Fig. 4R). The posteroloph is connected to the protocone.

Geographic and stratigraphic range.—Pico del Fraile 2 (PF2) (MN4/5), Ebro Basin (Spain).

Discussion

Biometry and concavity of occlusal surfaces.—In terms of molar length and width, *Vasseuromys cristinae* sp. nov. is intermediate between the large-sized *V. bacchius* and the remaining species of the genus, which are generally smaller (Figs. 5, 6). There is almost no overlap of *V. cristinae* sp. nov. with *V. bacchius*, with the sole exception of the maximum length and width measurements of dP4. However, the number of specimens available for study is very small, with the dP4 of *V. bacchius* being represented by just four specimens and that of *V. cristinae* sp. nov. being known from just a single tooth.

V. cristinae sp. nov. is generally larger than *V. autolensis* from Autol 1, *V. priscus* from Moissac 1 and Santa Cilia, *V. duplex* from Harami 1, and *V. elegans* from Stubersheim 3, as well as *Vasseuromys* from Erkertshofen 2, Petersbuch 2, and the three species from Blanquatère 1 (Figs. 5–8).

The material of *V. rugosus* from its type locality at Laugnac (Baudelot and de Bonis 1966; de Bonis 1973) is very scarce, making comparisons difficult. Nevertheless, the maximum length values of most elements, as well as the width measurements of p4, m1, and M1–3 seem to overlap with the minimum values recorded for *V. cristinae* sp. nov., whereas the widths of P4 and M2 of the latter clearly exceed those of *V. rugosus*. The locality of Santa Cilia has yielded a significant number of additional specimens of *V. rugosus* (Álvarez-Sierra et al. 1991), overlapping in length and width with those from Laugnac. Interestingly, the M3 of *V. rugosus* from Santa Cilia is clearly larger than that of *V. cristinae* sp. nov. Generally, the measurement interval for *V. rugosus* is larger than that for *V. cristinae* sp. nov.

V. pannonicus from Eichkogel is very similar in size to *V. cristinae* sp. nov., with only the lengths of p4, dP4, and P4 and the widths of m3, D4, P4, and M3 of *V. pannonicus* being comparatively somewhat smaller. *V. pannonicus* from Kohfidisch (Daxner-Höck and Höck 2009) is generally somewhat larger than *V. pannonicus* from Eichkogel, and very similar in size to *V. cristinae* sp. nov.

While the presence of concave occlusal surfaces of the cheek teeth formed part of the original diagnosis of *Vasseuromys* (Baudelot and de Bonis 1966), this feature has so far never been quantified. The degree of concavity varies from species to species, with some taxa (e.g., *V. elegans*) showing a low degree of concavity (Wu 1993), whereas others (e.g., *V. duplex*) are marked by strongly concave occlusal surfaces (Ünay 1994).

In order to describe concavity, we used measurements derived from our concavity profiles of *V. cristinae* sp. nov to make comparisons with *V. autolensis* from the locality of Autol on the Iberian Peninsula and *V. duplex* from Harami 1, Turkey (Table 2). Specifically, we focused on values of h/r, where h is the maximum depth of the concavity and r the radius of the best-fitting circle (see Freudenthal and Martín-Suárez [2007b: fig. 2] for further details). Based on these data, it is clear that the occlusal surfaces of *V. cristinae* sp. nov. are slightly more concave than those of both *V. autolensis* and *V. duplex*, with the exception of the values for the posterior profile of m2.

Number and development of molar ridges.—Both the upper and the lower molars generally bear four main ridges, with the upper molars being characterised by an anteroloph, protoloph, metaloph, and posteroloph, as well as two smaller centrolophs, and the lower molars possessing an anterolophid, metalophid, mesolophid, and posterolophid, as well as a relatively less well developed centrolophid. Often, a highly variable number of additional ridges may also be developed, resulting in a substantial degree of both inter- and intraspecific variability. In order to explore this trait further, we compared the number of ridges occurring in an anterior (between the anteroloph and protoloph), central (within the trigone), and posterior (between the metaloph and posteroloph) position on the upper molars. Similarly, we also recorded the number of ridges occurring between the anterolophid and metalophid (anterior), between the metalophid and mesolophid (central), and between the mesolophid and posterolophid (posterior) on the lower molars.

The species with the smallest number of ridges on both the upper and lower molars include *Vasseuromys priscus*, *V. elegans*, and *V. cristinae* sp. nov. (Table 3). In addition to the four main ridges, the lower molars of *V. cristinae* sp. nov. show a well-developed centrolophid, a single anterotropid, two extra ridges located in the central valley and a single posterotropid. While a single posterotropid also occurs in other species (e.g., *V. priscus*, *V. duplex*, and *V. elegans*), it is generally variable in the latter (Wu 1993; Ünay 1994; Álvarez-Sierra et al. 1991), and constantly appears only in *V. cristinae* sp. nov. Furthermore, unlike in all other species of *Vasseuromys*, the posterotropid of the lower molars of *V. cristinae* sp. nov. is almost always connected to the lingual part of the posterolophid.

The upper molars of *Vasseuromys autolensis*, *V. rugosus*, *V. pannonicus*, and *V. elegans* bear anterotropes and/or posterotropes of variable length, whereas *V. duplex* always possesses long anterotropes and posterotropes (Ünay 1994). Out of the former, only *V. rugosus* from Laugnac and *V. duplex* always bear an anterotrope and a posterotrope on M1 and M2 (de Bonis 1973; Ünay 1994). Anterotropes and posterotropes are completely absent in *V. priscus* and *V. bacchius*. The same generally holds true for *V. cristinae* sp. nov., with the exception of a single M3 showing a very short anterotrope. By contrast, three well-developed extra ridges are present in the trigone.

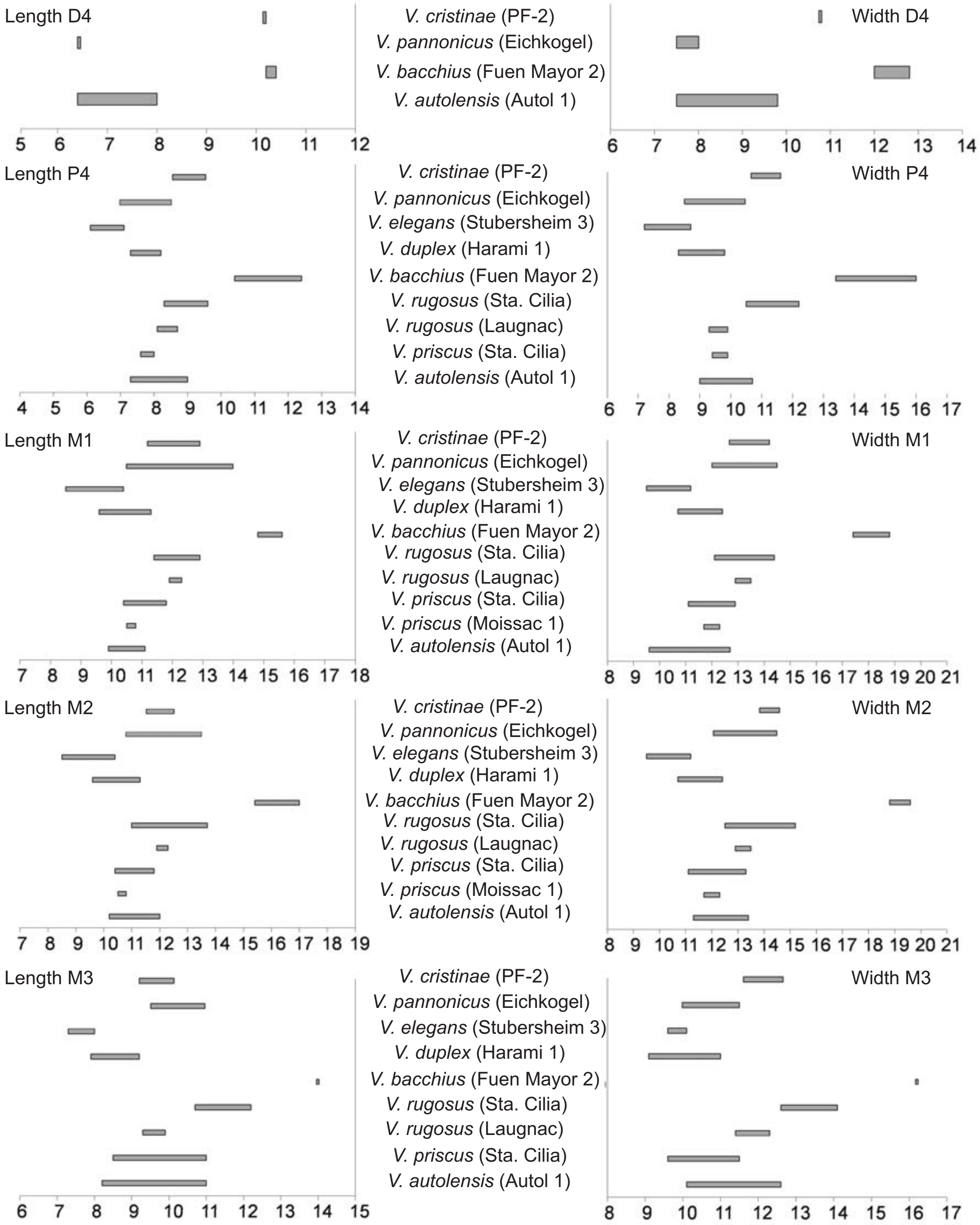

Fig. 5. Ranges of size variation (in tenths of millimetres) in the upper dentition of *Vasseuromys cristinae* sp. nov., *V. pannonicus*, *V. elegans*, *V. duplex*, *V. bacchius*, *V. rugosus*, *V. priscus*, and *V. autolensis*. Localities for each taxon are shown in parentheses.

Comparisons of other morphological features.—Other distinctive morphological features of *V. cristinae* sp. nov. include the connection of the metalophid and metaconid, the length, completeness and connections of the mesolophid and centrolophid on the lower molars, and the development of an endoloph on the upper molars.

In *V. cristinae* sp. nov., the metalophid is generally connected to the metaconid on m1 and m3, resembling the condition seen in *V. priscus*, *V. autolensis*, *V. rugosus*, and *V. elegans*. By contrast, this connection is absent in all of the lower molars of *V. bacchius*, the m1 of *V. pannonicus*, and in 52% of the lower molars of *V. duplex* (Ünay 1994).

The mesolophid on the lower molars of *V. cristinae* sp. nov. is continuous and reaches the mesoconid and entoconid. In other *Vasseuromys* species, this ridge may be interrupted and not connected to the entoconid, as frequently observed in

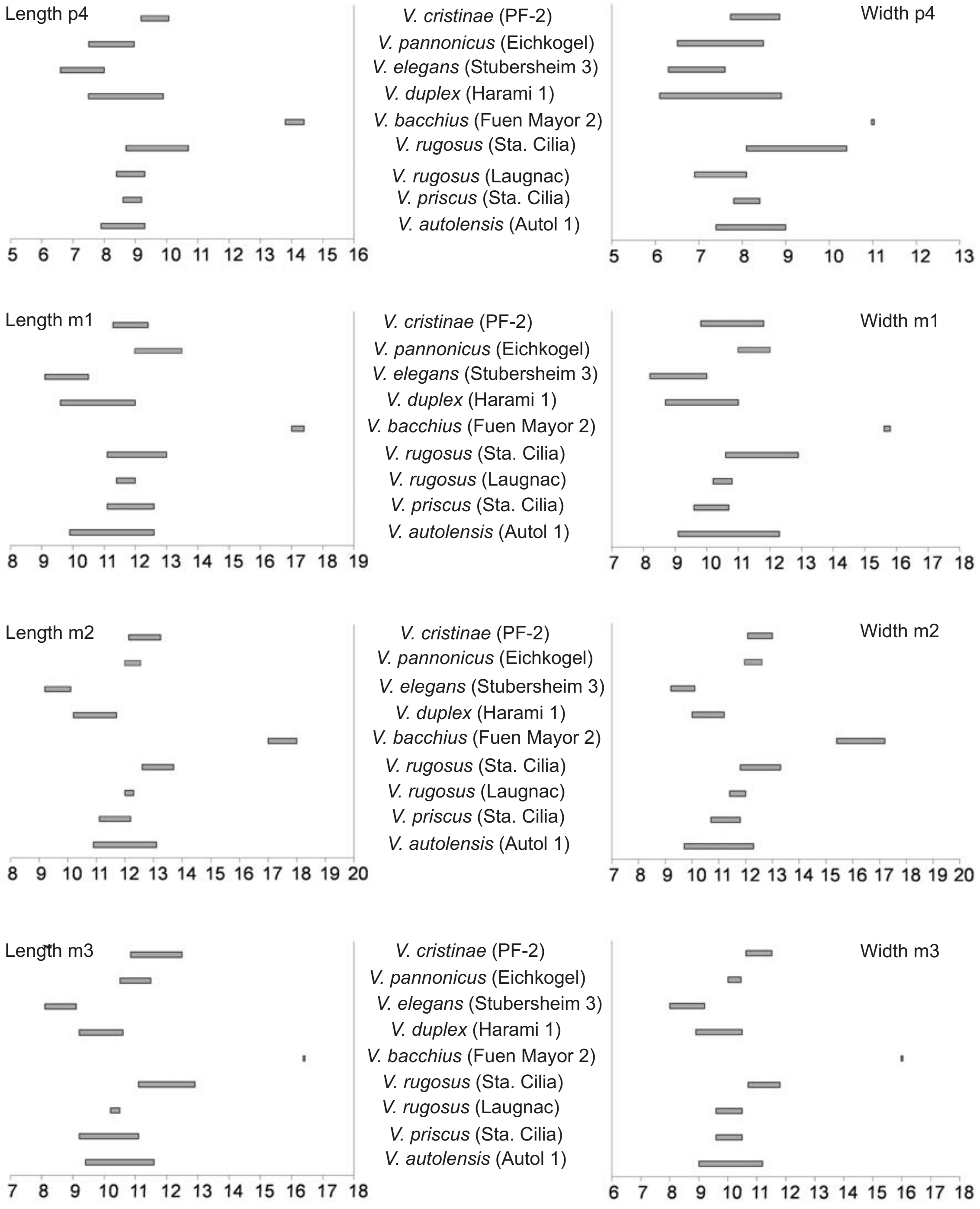

Fig. 6. Ranges of size variation (in tenths of millimetres) in the lower dentition of *Vasseuromys cristinae* sp. nov., *V. pannonicus*, *V. elegans*, *V. duplex*, *V. bacchius*, *V. rugosus*, *V. priscus*, and *V.autolensis*. Localities for each taxon are shown in parentheses.

V. priscus and *V. rugosus,* as well as, albeit somewhat less often, the remaining members of the genus (Álvarez-Sierra et al. 1991).

As is characteristic of the genus (Baudelot and de Bonis 1966), the lower molars of *V. cristinae* sp. nov. have a long centrolophid occasionally reaching the labial border of the tooth. In some specimens, the centrolophid connects with the second (posterior) centrolophid or with the mesolophid. The labial cusps of the lower molars show longitudinal prolongations, forming a nearly continuous external wall. In several specimens, the labial border of the valley between the mesoconid and hypoconid is closed, and in most specimens the mesoconid extends strongly towards the protoconid.

Unlike the lingual end of the posteroloph, the anteroloph is not connected to the protocone on M1 and M2 of *V.*

Table 2. Concavity parameters of *Vasseuromys cristinae* sp. nov. from PF2, compared to *V. autolensis* from Autol 1 and *V. duplex* from Harami 1 (both represented by one specimen each). Data for *V. autolensis* and *V. duplex* were taken from Freudenthal and Martín-Suárez (2007b). Drawings were rescaled to w = 10, following Freudenthal and Martín-Suarez (2007b). Abbreviations: b, distance between the limits of the occlusal concavity; h, maximum depth of the concavity; r, radius of the best-fitting circle; S, surface of the area enclosed by b and the occlusal profile; w, maximum width of the molar as seen in profile. For further details, see Freudenthal and Martín-Suárez (2007b: fig. 2).

	S	w	b	h	S/b	h/b	r	h/r	b/2r	w/2r	skewness	mean dev
Anterior profiles of m1												
V. cristinae PF2-81	1.10	10.00	6.89	0.38	0.16	0.06	5.16	0.07	0.67	0.97	42.2	0.45
V. cristinae PF2-84	1.24	10.00	7.01	0.40	0.18	0.06	4.81	0.08	0.73	1.04	58.3	0.42
V. cristinae PF2-85	1.38	9.99	6.94	0.37	0.20	0.05	5.94	0.06	0.58	0.84	52.2	0.16
V. duplex	1.98	10.00	7.01	0.52	0.28	0.07	10.61	0.05	0.33	0.47	61.4	0.05
Posterior profiles of m1												
V. cristinae PF2-81	2.50	10.00	6.63	0.81	0.38	0.12	4.38	0.18	0.76	1.14	53.3	0.15
V. cristinae PF2-84	2.50	10.00	6.42	0.79	0.39	0.12	4.41	0.18	0.73	1.13	57.8	0.13
V. cristinae PF2-85	2.37	10.00	6.18	0.70	0.38	0.11	3.61	0.19	0.86	1.38	38.1	0.15
V. duplex	2.96	10.00	7.53	0.71	0.39	0.09	8.84	0.08	0.43	0.57	54.3	0.06
Anterior profiles of m2												
V. cristinae PF2-90	3.19	10.00	7.52	0.88	0.42	0.12	5.22	0.17	0.72	0.96	71.4	0.21
V. cristinae PF2-92	1.75	10.00	6.40	0.56	0.27	0.09	4.75	0.12	0.67	1.05	60.8	0.19
V. cristinae PF2-93	2.41	10.00	6.19	0.68	0.39	0.11	4.47	0.15	0.69	1.12	71.7	0.20
V. cristinae PF2-95	1.72	10.00	6.35	0.51	0.27	0.08	4.74	0.11	0.67	1.06	65.2	0.16
V. autolensis	2.92	10.00	7.09	0.77	0.41	0.11	7.44	0.10	0.48	0.67	65.8	0.09
Posterior profiles of m2												
V. cristinae PF2-90	2.86	10.00	7.28	0.66	0.39	0.09	5.05	0.13	0.72	0.99	66.7	0.26
V. cristinae PF2-92	2.19	10.00	5.98	0.65	0.37	0.11	3.64	0.18	0.82	1.37	60.2	0.17
V. cristinae PF2-93	3.11	10.00	6.22	0.91	0.50	0.15	4.12	0.22	0.75	1.21	70.8	0.16
V. cristinae PF2-95	1.15	10.00	6.08	0.36	0.19	0.06	4.53	0.08	0.67	1.10	81.2	0.21
V. autolensis	4.42	10.00	7.25	1.07	0.61	0.15	5.70	0.19	0.64	0.88	57.0	0.10
Anterior profiles of M1												
V. cristinae PF2-61	2.83	10.00	5.81	0.92	0.49	0.16	3.60	0.26	0.81	1.39	53.6	0.09
V. cristinae PF2-63	2.83	10.00	5.62	0.92	0.50	0.16	3.70	0.25	0.76	1.35	53.5	0.07
V. cristinae PF2-72	2.89	10.00	6.74	0.72	0.43	0.11	4.44	0.16	0.76	1.13	49.4	0.15
V. autolensis	4.44	10.00	7.42	1.04	0.60	0.14	7.09	0.15	0.52	0.71	61.7	0.07
V. duplex	4.30	10.00	7.60	0.95	0.57	0.13	7.80	0.12	0.49	0.64	47.7	0.04
Posterior profiles of M1												
V. cristinae PF2-61	2.88	10.00	6.94	0.76	0.42	0.11	4.99	0.15	0.70	1.00	56.8	0.17
V. cristinae PF2-63	4.30	10.00	7.12	1.06	0.60	0.15	4.41	0.24	0.81	1.13	53.4	0.13
V. cristinae PF2-72	3.74	10.00	7.37	0.92	0.51	0.12	4.32	0.21	0.85	1.16	56.1	0.17
V. autolensis	4.18	10.00	7.48	1.07	0.56	0.14	6.05	0.18	0.62	0.83	53.7	0.09
V. duplex	3.75	10.00	7.55	0.91	0.50	0.12	7.93	0.11	0.48	0.63	53.7	0.07
Anterior profiles of M2												
V. cristinae PF2-62	4.77	10.00	6.76	1.19	0.71	0.18	3.76	0.32	0.90	1.33	60.6	0.11
V. cristinae PF2-71	3.96	10.00	6.84	1.08	0.58	0.16	3.92	0.28	0.87	1.27	64.5	0.13
V. autolensis	4.97	10.00	6.54	1.21	0.76	0.19	4.71	0.26	0.69	1.06	48.6	0.04
V. duplex	5.86	10.00	7.61	1.31	0.77	0.17	5.74	0.23	0.66	0.87	56.6	0.07
Posterior profiles of M2												
V. cristinae PF2-62	3.56	10.00	7.68	0.88	0.46	0.11	5.00	0.18	0.77	1.00	63.9	0.18
V. cristinae PF2-71	3.21	10.00	7.54	0.78	0.43	0.10	5.63	0.14	0.67	0.89	55.9	0.17
V. autolensis	4.01	10.00	7.84	0.95	0.51	0.12	8.08	0.12	0.49	0.62	56.7	0.11
V. duplex	4.77	10.00	8.13	1.05	0.59	0.13	7.76	0.14	0.52	0.64	56.9	0.08

cristinae sp. nov., resulting in the absence of a complete endoloph on these teeth. By contrast, a complete endoloph is developed on M3. The presence of an endoloph on the single upper molar of *Vasseuromys* from Laugnac was used to emend (de Bonis 1973) the original diagnosis of the genus (Baudelot and de Bonis 1966). However, examination of

Table 3. Number of ridges (main and extra) in several species of *Vasseuromys*. Abbreviations: av, anterior valley; cv, central valley; pv, posterior valley; TR, total number of ridges (main and extra ridges).

Zone (Mein 1990)	Locality	Species	Extra ridges (m1, 2)				Extra ridges (M1, 2)			
			av	cv	pv	TR (m1, 2)	av	cv	pv	TR (M1, 2)
MN11	Eichkogel	*Vasseuromys pannonicus*	1	0–2	2–3	8–11	0–1	1–6	0–1	7–14
MN4–MN5	Pico del Fraile 2 (PF2)	*Vasseuromys cristinae*	1	2	1	9	0	3	0	9
MN4–MN5	Blanquatère 1	*Vasseuromys* sp.	1	2	1	9	0	2–3	0	8–9
MN4–MN5	Blanquatère 1	*Vasseuromys* aff. *elegans*	–	–	–	–	1	3	0	10
MN4–MN5	Blanquatère 1	*Vasseuromys* aff. *priscus*	–	–	–	–	0	2	0	8
MN4	Petersbuch 2	*Vasseuromys* aff. *elegans*	1	1–3	1	8–10	0–1	2–3	0	8–10
MN4	Erkertshofen 2	*Vasseuromys* aff. *elegans*	1	0–2	1	7–9	0	2–3	0	8–9
MN3	Stubersheim 3	*Vasseuromys elegans*	1	1–3	1	8–10	0–1	2–3	0	8–10
MN2	Harami 1	*Vasseuromys duplex*	1–2	0–2	1–3	7–12	1	1–3	1	9–11
MN2B	Fuenmayor 2	*Vasseuromys bacchius*	1–2	1–2	1–3	8–12	0	2–3	0	8–9
MN2B	Santa Cilia	*Vasseuromys rugosus*	1	2	3	11	0–1	3	0–1	9–11
MN2B	Laugnac	*Vasseuromys rugosus*	1	2	3	11	1	3	1	11
MN1	Autol	*Vasseuromys autolensis*	1	1–2	1–3	8–11	0–1	3	0–1	9–11
MN1	Santa Cilia	*Vasseuromys priscus*	1	0	1	7	0	1–2	0	7–8
MN1	Moissac 1	*Vasseuromys priscus*	1	2	1	9	0	2–3	0	8–9

other species has shown that this character has a high degree of variability, occurring in just a few specimens of a minority of the members of the genus (de Bonis 1973; Kretzoi 1978; Daxner-Höck and de Bruijn 1981; Cuenca 1985; Martínez-Salanova 1987; Álvarez-Sierra et al. 1991; Wu 1993; Ünay 1994).

Comparisons with other *Vasseuromys* assemblages of Aragonian age.—European localities of Aragonian age which have yielded remains of *Vasseuromys* include Blanquatère 1, Petersbuch 2, Erkertshofen 2 (Wu 1993), and Pico del Fraile 2. The karstic locality of Blanquatère 1 has yielded a small number of specimens representing *V.* aff. *elegans* (1 M2), *V.* aff. *priscus* (1 M2) and *Vasseuromys* sp. (2 m1, 1 M1, and 1 M2) (Aguilar and Lazzari 2006). However, the excessive number of rodent species (34) identified in this locality casts doubt on its homogeneity, and we thus refrain from making further comparisons.

Vasseuromys aff. *elegans* from Petersbuch 2 differs from *V. elegans* from Stubersheim 3 mainly in its broader tooth crowns, a rectangular field between the anterolophid and metalophid, the presence of an endolophid on several teeth, and a trend of the labial cusps to connect, thus forming an ectolophid. *V. cristinae* sp. nov. is larger than *Vasseuromys* aff. *elegans* from Petersbuch 2 (Figs. 7, 8) and does not show any of the features listed above, with the exception of a rectangular field between the anterolophid and metalophid, which is present in several, but not all specimens.

Biostratigraphy

So far, the oldest records of *Vasseuromys* are *V. priscus* and *V. autolensis* from the Early Miocene (zone MN1) of Europe (de Bonis 1973; Álvarez-Sierra et al. 1991; Cuenca 1985). Lacomba (1988) named *Ebromys bergasensis* from the locality of Bergasa, which is placed in zone MP30 based on the presence of *Issiodoromys pseudanoema* (see also Álvarez-Sierra et al. 1987). However, although this material was later mentioned by Daams (1989), who compared it with his new species *Peridyromys columbarii*, *E. bergasensis* was never formally described, and should be considered a nomen nudum. We are currently revising the specimens described by Lacomba (1988), and it is possible that they might eventually be assigned to *Vasseuromys*. If so, they would represent the oldest record of the genus.

Most of the other members of the genus have also been recorded from Early Miocene strata, including *V. rugosus* (zones MN1 and MN2), *V. duplex* (zone MN2, Ünay 1994), *V. bacchius* (upper part of zone MN2) and *V. elegans* (zone MN3). By contrast, the youngest record of the genus is *V. pannonicus* from the Late Vallesian or Early Turolian (zone MN11) of Central Europe (Daxner-Höck and de Bruijn 1981; Daams 1999; Daxner-Höck and Höck 2009).

Until 1990 (Sümengen et al. 1990) there were no records of *Vasseuromys* from deposits of Aragonian (Middle Miocene) age, but the genus has now also been documented from the karstic MN4 localities of Petersbuch 2 and Ekertshofen 2 (Wu 1993), as well as the somewhat younger (MN4–MN5) locality of Blanquatère 1 (Aguilar and Lazzari 2006). The preliminary faunal list of PF2 (and particularly *M. primitivus*) places this locality, and thus *V. cristinae* sp. nov., in Aragonian zone C or the lower part of zone D, straddling zones MN4/MN5 (Middle Miocene, 15.8 Ma). Thus, the range of localities now comprises the Lower Aragonian (MN4) (Wu 1993), the Lower–Middle Aragonian boundary (MN4–MN5) (Aguilar and Lazzari 2006; this work) and the Upper Aragonian (MN8) (Sümengen et al. 1990).

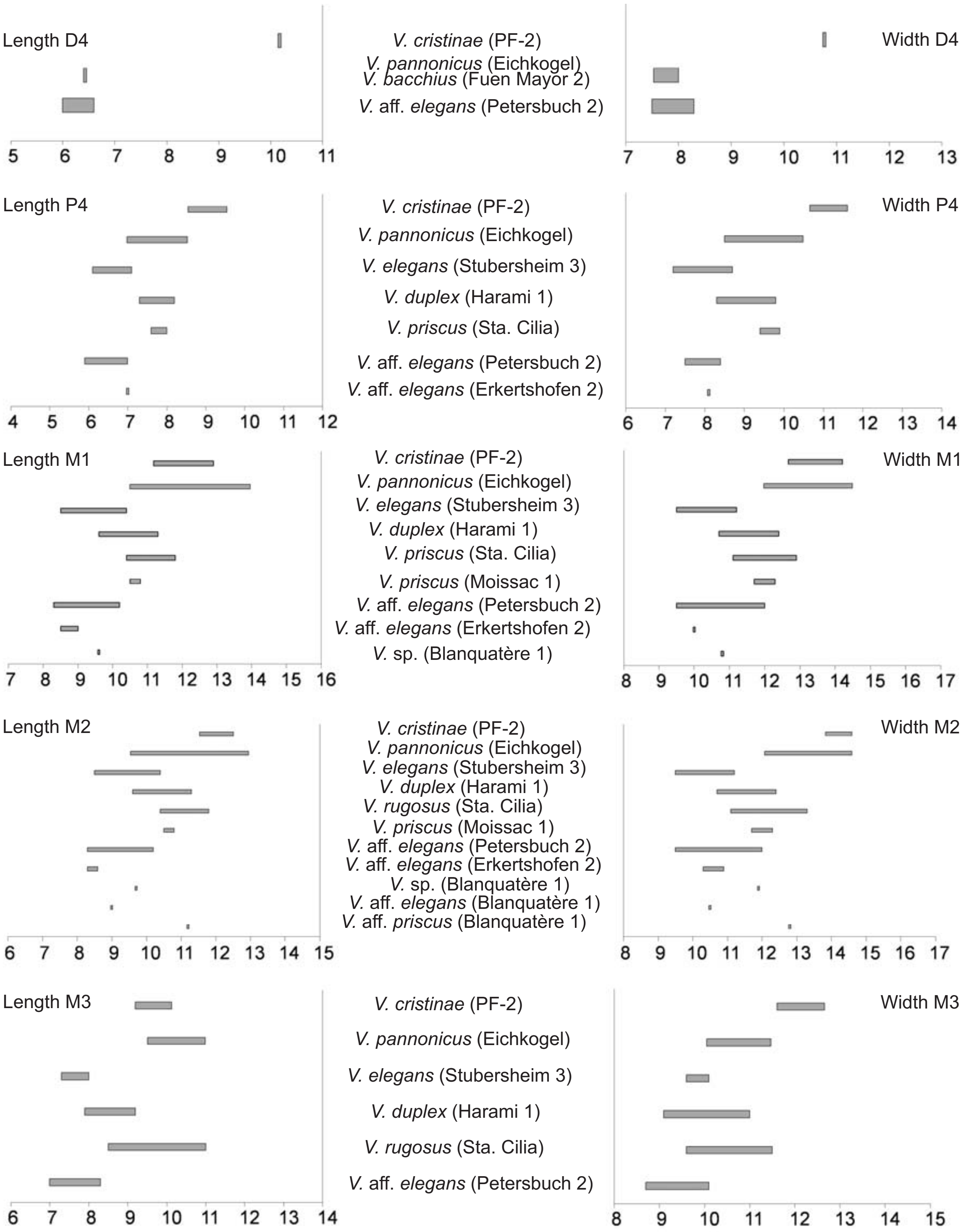

Fig. 7. Ranges of size variation (in tenths of millimetres) in the upper dentition of *Vasseuromys cristinae* sp. nov., *V. pannonicus*, *V. elegans*, *V. duplex*, *V. priscus*, *V.* aff. *elegans*, *V.* sp., and *V.* aff. *priscus*. Localities for each taxon are shown in parentheses.

Phylogeny

The presence of *V. cristinae* sp. nov. is the first Aragonian record of *Vasseuromys* from the Iberian Peninsula, making its ancestry very difficult to establish. We consider two possibilities: first, this species may have descended from a European ancestor; alternatively, in view of its age, it may have descended from an Anatolian population, which later migrated into Europe. Indeed, tectonic events and geographical changes during the European Late Oligocene and Neogene likely provided geographical barriers to dispersal, as well as concurrent land bridges allowing faunal inter-

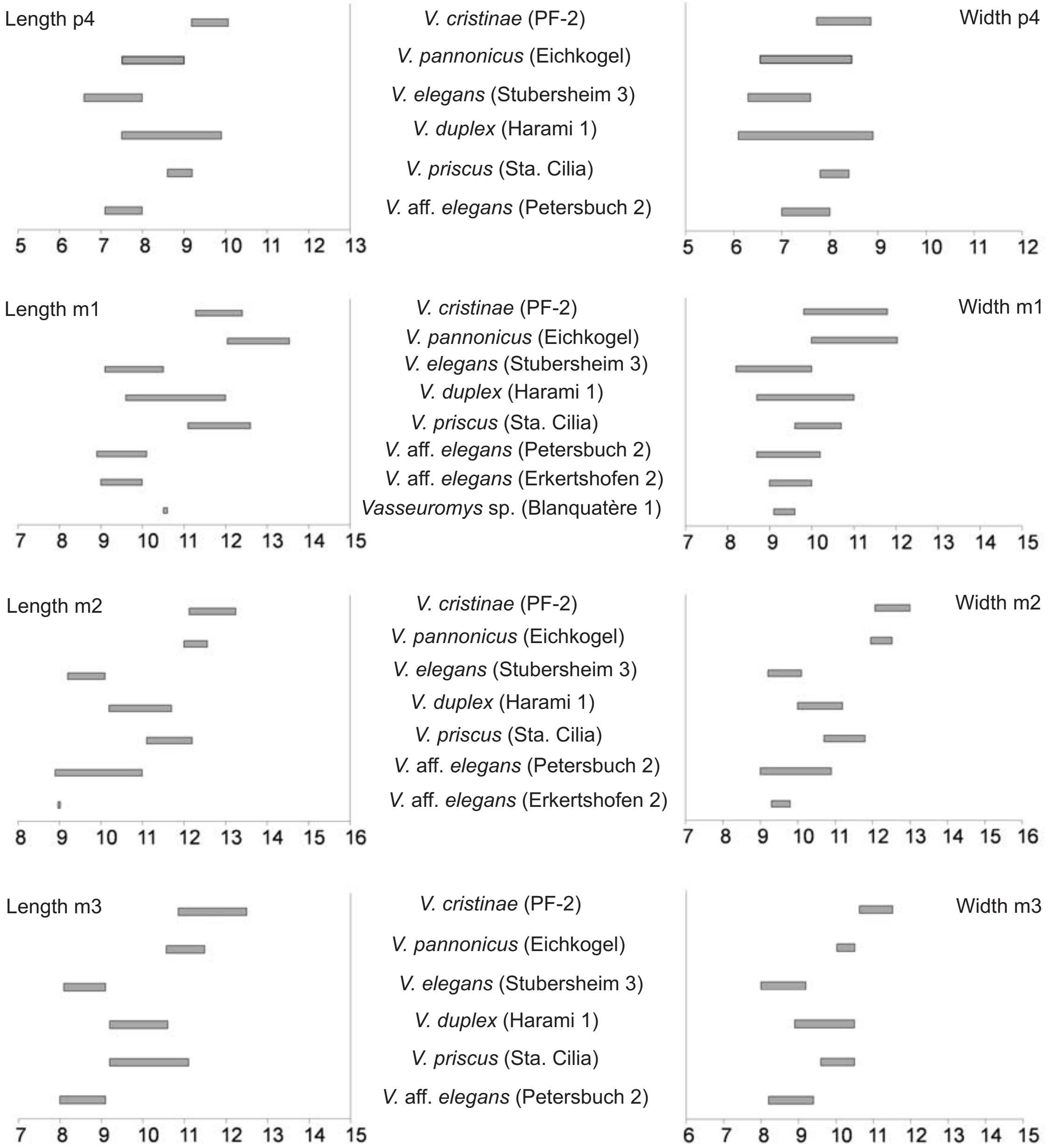

Fig. 8. Ranges of size variation (in tenths of millimetres) in the lower dentition of *Vasseuromys cristinae* sp. nov., *V. pannonicus*, *V. elegans*, *V. duplex*, *V. priscus*, *V.* aff. *elegans*, and *V.* sp. Localities for each taxon are shown in parentheses.

change (Rögl 1999; Meulenkamp and Sissingh 2003; Mein 2003).

In the Mediterranean region, Lower Miocene localities which have yielded remains of *Vasseuromys* generally fall into one of two clusters, the first one being located in the western and northern part of this area (Baudelot and de Bonis 1966; de Bonis 1973; Kretzoi 1978; Daxner-Höck and de Bruijn 1981; Cuenca 1985; Martínez-Salanova 1987; Álvarez-Sierra et al. 1991; Wu 1993; Aguilar and Lazzari 2006) and the second one in its eastern part, and in particular Anatolia (de Bruijn 1989; Sümengen et al. 1990; Ünay 1994; Ünay and Göktas 2000).

Two separate lineages have been suggested to occur in the western cluster (Álvarez-Sierra et al. 1991), comprising *V. autolensis* (MN1), *V. rugosus* (MN2), and *V. bacchius* (MN2) one the one hand, and *V. priscus* (MN1) on the other, with the former being characterised by a more complex dental pattern. By contrast, the eastern cluster has yielded only *Vasseuromys duplex* (MN2) and *V.* aff. *duplex* (MN1), considered by Ünay (1994) to form a lineage restricted to the eastern Mediterranean, and only distantly related to the taxa occurring further to the west. This hypothesis is based on the observation that the dominant m1–2 morphotype occurring in the eastern Mediterranean bears two extra ridges in the anterior valley and one extra ridge in the posterior valley, as well as a centrolophid always shorter than that observed in *V. rugosus* (Ünay 1994).

Compared to *V. cristinae* sp. nov., the upper molars of the Anatolian specimens generally have a more complex dental pattern in possessing both an anterotrope and posterotrope. Similarly, the lower molars of *V. duplex*, while resembling the dominant morphotype of the lower molars of *V. cristinae* sp. nov. in their posterior portion, show a more complex morphology anteriorly in possessing a second anterotropid. By contrast, the dental patterns of the taxa from the northern and western Mediterranean generally resemble *V. cristinae* sp. nov., and mainly differ from the latter in the complexity of the posterior valley of the lower molars.

V. rugosus differs from all other species in the presence of three posterotropids on m1–2 and two or three on m3 (Álvarez-Sierra et al. 1991). By contrast, 50% of the specimens interpreted as m1 and 25% of those interpreted as m2 of *V. bacchius* from Fuenmayor 2 (Martínez-Salanova 1987), as well as 50% of m1–2 of *V. autolensis* from Autol (Cuenca 1985) bear a single posterotropid. In *V. rugosus*, both anterotropes and posterotropes are absent on M1 and developed on just 23% of the specimens representing M2s (Álvarez-Sierra et al. 1991). Both structures are even more poorly developed in *V. autolensis*, with only 4 out of more than 60 M1–2 bearing an anterotrope and only 3 showing a posterotrope (Cuenca 1985), and they are completely absent in *V. bacchius*.

Based on the presence of just a single posterotropid, and the complete lack of both anteroropes and posterotropes in *V. cristinae* sp. nov., we suggest that the latter and *V. autolensis* are related, and that *V. rugosus*, another descendant of *V. autolensis*, belongs to a different branch.

Earlier work (Álvarez-Sierra et al. 1991) considered *V. autolensis* to have given rise to *V. bacchius* from the Lower Miocene (MN2) of Fuenmayor 2 (La Rioja, Spain), a locality situated in the same basin (Ebro Basin) as Autol, Santa Cilia and PF2, but located at a younger level than Santa Cilia (Álvarez-Sierra et al. 1991). Among other features, the teeth of *V. bacchius* are of much larger size and their dental pattern is slightly simpler than in *V. autolensis* (Martínez-Salanova 1987). Of the recently sampled localities in the Tudela Formation, Pico del Fraile 1 (Larrasoaña et al. 2006) has yielded some specimens which seem significantly larger than *V. cristinae* sp. nov. from PF2. The locality of Pico del Fraile 1 (PF1) is characterised by the absence of *Eucricetodon* and *Democricetodon*, the predominance of *Ligerimys* and the presence of *Peridyromys murinus* and *Pseudodryomys ibericus*, allowing its attribution to zone A of the Ramblian (MN3) (Larrasoaña et al. 2006). PF1 is therefore intermediate in age between PF2 (*V. cristinae* sp. nov.) and those localities of the Ebro Basin which have yielded remains of *V. autolensis* and *V. bacchius*. Although a detailed morphological study of the material from Pico del Fraile 1 has not yet been performed, the size of the *Vasseuromys* specimens from this locality, intermediate between that of *V. cristinae* sp. nov. and that of *V. bacchius*, may suggest a relationship between *V. autolensis* (MN1), *V. bacchius* (MN2), and the *Vasseuromys* assemblage from PF1 (MN3). Further sampling of new *Vasseuromys*-yielding localities in the Tudela Formation will enable us to test this hypothesis.

Conclusions

The *Vasseuromys* assemblage from Pico del Fraile 2 represents the first record of this genus from a locality on the Iberian Peninsula assignable to zones MN4 or MN5. *V. cristinae* sp. nov from PF2 is smaller than *V. bacchius*, larger than *V. elegans* and *V. duplex*, and matching or somewhat exceeding the size of the remaining members of the genus. The lower molars of this new species distinctly differ from those of all other *Vasseuromys* species in the constant presence of four extra ridges (including just one posterotropid), a metalophid generally connected to the metaconid, and a mesolophid connected to the entoconid. Furthermore, in the upper dentition, M1–2 are marked by an incomplete endoloph and the absence of extra ridges (anterotrope and posterotrope) outside the trigone. The dental pattern of *V. cristinae* sp. nov. is very similar to that of an Iberian lineage comprising *V. autolensis* and *V. bacchius*, which, combined with the stratigraphic position of PF2, may suggest a close phylogenetic relationship of these taxa.

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