A new species of *Vasseuromys* (Gliridae, Mammalia) from the Upper Oligocene of the Ebro Basin (Spain)

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Abstract In this paper, a new species of *Vasseuromys*, *V. bergasensis* sp. nov., from the locality of Bergasa (Ebro Basin, Spain), is described. Bergasa contains a fauna belonging to the Late Oligocene (zone MP30), composed—among other species—of *Issiodoromys pseudanaema* and *Rhodanomys transiens*. The main diagnostic features of *V. bergasensis* sp. nov. are the presence of a long centrolophid (fused or not to the mesoconid) in the lower molars, a large reduction in the number and length of extra ridges in the upper and lower molars, the absence of extra ridges between metalophid and centrolophid and between centrolophid and mesolophid, and the absence of the metatrope in more than half the specimens of the upper teeth M1 and M2. *V. bergasensis* sp. nov. is similar in size to *V. elegans* and smaller than the other members of the genus. The age and simple dental pattern of the new species of *Vasseuromys* allow us to hypothesize about relationships within the genus.

Keywords *Vasseuromys* · Gliridae · Rodentia · MP30 · Phylogeny · New species

Kurzfassung In dieser Arbeit wird eine neue Art von *Vasseuromys*, *V. bergasensis* sp. nov., aus der Lokalität Bergasa (Ebro Becken, Spanien) beschrieben. Bergasa enthält eine Fauna des späten Oligozän (Zone MP30) mit, unter anderen Arten *Issiodoromys pseudanaema* und *Rhodanomys transiens*. Die wichtigste diagnostische Merkmale von *V. bergasensis* sp. nov. sind: ein langes Centrolophid, verbunden oder nicht mit dem Mesoconid, in den unteren Backenzähnen, die starke Reduzierung der Anzahl und der Länge der zusätzlichen Rippen in den oberen und unteren Molaren, die Abwesenheit von zusätzlichen Graten zwischen metalophid und centrolophid und zwischen Centrolophid und Mesolophid und die Abwesenheit des Metatropes in mehr als die Hälfte der M1,2. Die Größe des *V. bergasensis* sp. nov. ist *V. elegans* ähnlich, und kleiner als die anderen Arten der Gattung. Das Alter und das einfache Zahnmuster der neuen Art erlauben Hypothesen auf die Beziehungen innerhalb der Gattung.

Schlüsselwörter *Vasseuromys* · Gliridae · Rodentia · MP30 · Phylogenie · Neue Spezies

Introduction

Baudelot and de Bonis (1966) created the genus *Vasseuromys* on the basis of Gliridae material of medium size

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from Laugnac and Moissac I (France, Lower Miocene), which exhibited concave occlusal surfaces and a tendency for the molar cusps to form longitudinal walls.

Subsequently, other species were described, and its geographical range now extends throughout Europe and Turkey. The main European area with localities containing remains of the genus *Vasseuromys* is the Ebro Basin. Four species of this genus have been described from the Ebro Basin so far: *V. autolensis*, *V. bacchius*, *V. rambliensis*, and *V. cristinae* (Cuenca 1985; Martínez-Salanova 1987; Ruiz-Sánchez et al. 2012a, b), and there are also records of two other species from this area (*V. priscus* and *V. rugosus*). The temporal range of the genus is the Miocene (MN1 to MN11) (Table 1) (Daams 1999; Ruiz-Sánchez et al. 2012b).

However, the Oligocene locality of Bergasa has yielded a glirid assemblage with concave occlusal surfaces and a tendency for the cusps to form longitudinal walls. This was named *Ebromys bergasensis* by Lacomba (1988) in his thesis. However, this new species was never formally published.

In this paper, we describe the assemblage of *Vasseuromys* from the locality of Bergasa (Ebro Basin, Spain) (Fig. 1) as *Vasseuromys bergasensis*.

The Late Oligocene age of Bergasa is supported by the presence of a fossil assemblage (aside from *Vasseuromys*) containing *Issiodoromys pseudanaema* (Gervais, 1848), *Eucricetodon collatus* Schaub 1925, *Peridyromys murinus* Pomel 1853, *Microdyromys* sp., *Rhodanomys transiens* Hugueney 1969, *Pseudotheridomys schaubi* Lavocat 1951, *Plesiosminthus* sp. and Sciurinae indet. (Álvarez-Sierra 1987; Álvarez-Sierra et al. 1987; Cuenca et al. 1992). The inferred age of this locality implies that the *Vasseuromys* record from Bergasa is the oldest known so far.

Table 1 Age, geographic distribution, and bibliography of species of the genus *Vasseuromys*

Species	Age	Geography	Bibliography
V. pannonicus	MN11	Central Europe	Kretzoi (1978)
V. aff. *multicrestatus*	MN5	Spain	Agustí et al. (2011)
V. cristinae	MN4/5	Spain	Ruiz-Sánchez et al. (2012a)
V. elegans	MN3	Central Europe	Wu (1993)
V. rambliensis	MN3	Spain	Ruiz-Sánchez et al. (2012b)
V. duplex	MN2	Anatolia	Ünay (1994)
V. bacchius	MN2	Spain	Martínez-Salanova (1987)
V. rugosus	MN1/2	SW Europe	Baudelot and de Bonis (1966)
V. autolensis	MN1	Spain	Cuenca (1985)
V. priscus	MN1	SW Europe	de Bonis (1973)
V. bergasensis sp. nov.	MP30	Spain	This paper and Lacomba (1988)

Material, methods and abbreviations

The fossils are kept in the Department of Paleontology of the Universidad Complutense of Madrid (UCM) with the field label BER-. The nomenclature used in the descriptions of the teeth and the measurement method are those of Freudenthal (2004).

The lower teeth are denoted d4, p4, m1, m2 and m3, and the upper teeth D4, P4, M1, M2 and M3. Measurements are given in tenths of millimetres and were obtained with a Leica MZ7$_5$ binocular microscope.

Abbreviations: PF1, Pico del Fraile 1; PF2, Pico del Fraile 2; SCSIE(UV), Servei Central de Suport a la Investigació Experimental de la Universitat de València, Burjassot, Spain; UCM, Universidad Complutense de Madrid, Spain.

Systematic palaeontology

Order: Rodentia Bowdich, 1821
Family: Gliridae Muirhead, 1819
Genus: *Vasseuromys* Baudelot and de Bonis 1966

Synonymy: *Szechenyia* Kretzoi 1978; *Ebromys* Cuenca 1985
Other species: see Table 1

Vasseuromys bergasensis sp. nov. (Fig. 2)

Synonymy: *Ebromys bergasensis* Lacomba 1988 (unpublished)

Derivatio nominis: from the village Bergasa, where the fossil bed is located.

Holotype: BER-150, isolated upper molar housed in the UCM.

Paratypes: **2 d4** (BER-2542; BER-2548), **9 p4** (BER-2541; BER-2543 to BER-2547; BER-2549; BER-2552 to BER-2553), **40 m1** (BER-150; BER-153; BER-155; BER-159; BER-161; BER-162; BER-165; BER-170; BER-171; BER-173; BER-174; BER-2407 to BER-2412; BER-2414 to BER-2417; BER-2419; BER-2421 to BER-2423; BER-2426; BER-2427; BER-2429 to BER-2441), **47 m2** (BER-151; BER-152; BER-154; BER-156; BER-158; BER-160; BER-163; BER-166 to BER-169; BER-172; BER-175; BER-177; BER-179; BER-217; BER-218; BER-2356; BER-2442 to BER-2447; BER-2451 to BER-2455; BER-2457; BER-2459;

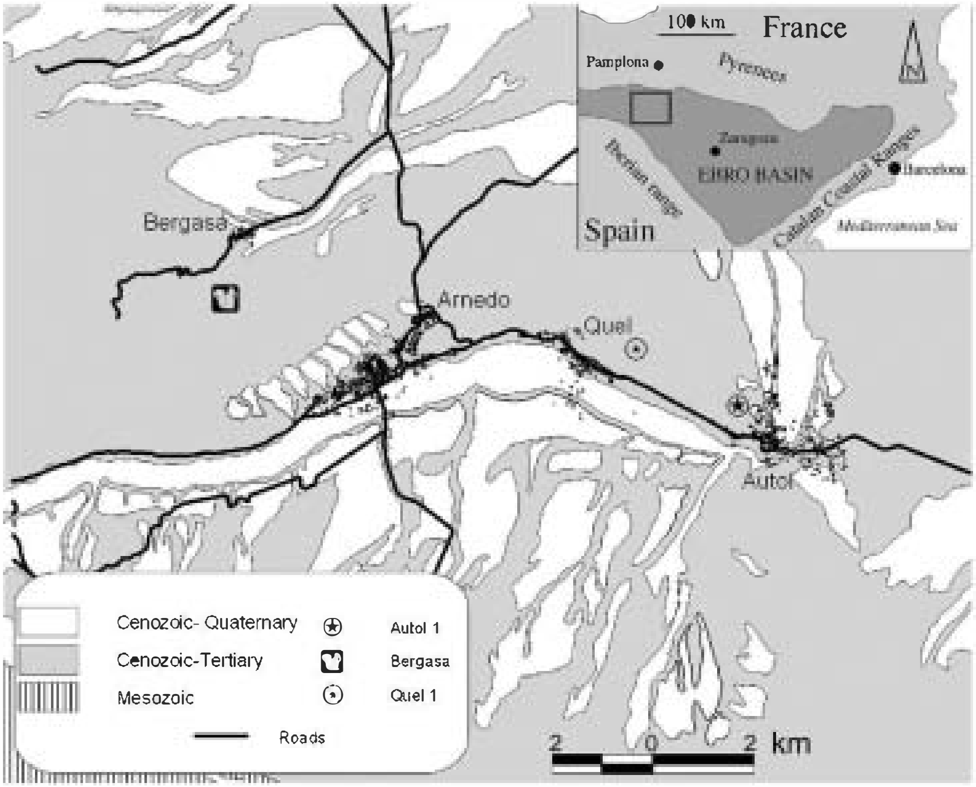

Fig. 1 Location of the Ebro Basin and geological map of the continental sediments in the Autol-Bergasa area, showing the locations of the Bergasa, Quel 1, and Autol localities (Álvarez-Sierra 1986)

BER-2462 to BER-2464; BER-2467 to BER-2470; BER-2472; BER-2474 to BER-2479; BER-2481; BER-2482), **17 m3** (BER-211 to BER-213; BER-215; BER-216; BER-2461; BER-2508 to BER-2511; BER-2513; BER-2514; BER-2518; BER-2520 to BER-2523), **3 D4** (BER-2529; BER-2534; BER-2539), **12 P4** (BER-191; BER-193; BER-194; BER-2525 to BER-2528; BER-2530 to BER-2533; BER-2535), **38 M1** (BER-185; BER-187; BER-189; BER-200; BER-219; BER-220; BER-2320 to BER-2328; BER-2330 to BER-2340; BER-2342 to BER-2344; BER-2347 to BER-2349; BER-2358 to BER-2362; BER-2373), **46 M2** (BER-181; BER-182; BER-184; BER-186; BER-188; BER-195; BER-196; BER-199; BER-201 to BER-204; BER-206; BER-207; BER-209; BER-221; BER-2366; BER-2370; BER-2372; BER-2375 to BER-2388; BER-2390 to BER-2394; BER-2396 to BER-2399; BER-2401 to BER-2404), **24 M3** (BER-223; BER-224; BER-226; BER-2483 to BER-2492; BER-2495 to BER-2497; BER-2499; BER-2501 to BER-2507).

Type locality: Bergasa (La Rioja), Upper Oligocene, Ebro Basin, Spain. Coordinates UTM 30TWM714771.

Original diagnosis from Lacomba (1988) (translated from the Spanish): medium-sized dormouse, characterized by strong concavity of the occlusal surface of the upper and lower molars. Endoloph absent in M1,2 and accesory ridges shorter than the main ridges.

Emended diagnosis: small-sized *Vasseuromys*. Lower molars with the anterotropid absent in 24 % of the m1 and 33 % of the m2 and the posterotropid always present; the extra ridge between metalophid and centrolophid and the second centrolophid are absent in m3; extra ridges shorter in m2 than in m1; up to 20 % of the lower molars have an endolophid; 100 % of the M1 and 95 % of the M2 without endoloph; M3 with endoloph; M1,2 with prototrope always present; about 60 % of the M1 and 50 % of the M2 have no metatrope.

Differential diagnosis: *Vasseuromys bergasensis* sp. nov. differs from *V. priscus*, *V. autolensis*, *V. rugosus* and *V. elegans* in: absence of anterotropid in some m1,2. Differs from *V. autolensis* in: presence of endoloph in some M2. Differs from *V. rugosus* in: posterotropid single in m1 and single or double in m2,3; extra ridge between metalophid and centrolophid, and second centrolophid absent in many m1,2,3; endoloph always present in M3; except for the prototrope, absence of extra ridge between centrolophs and of the metatrope in many M1,2. Differs from *V. duplex* in: single anterotropid; absence of the anterotrope and/or posterotrope in M1,2. Differs from *V. bacchius* in: centrolophid long; metalophid usually connected to the metaconid in m1,2,3; posterotropid single in m1; presence of some specimens with anterotrope and/or posterotrope in M1; posteroloph connected to the protocone. Differs from *V. rambliensis* and *V. cristinae* in: absence of the extra ridge between metalophid and centrolophid and second centrolophid in the m3; posterotropid sometimes double. Differs from *V. elegans* in: absence of extra ridges in D4;

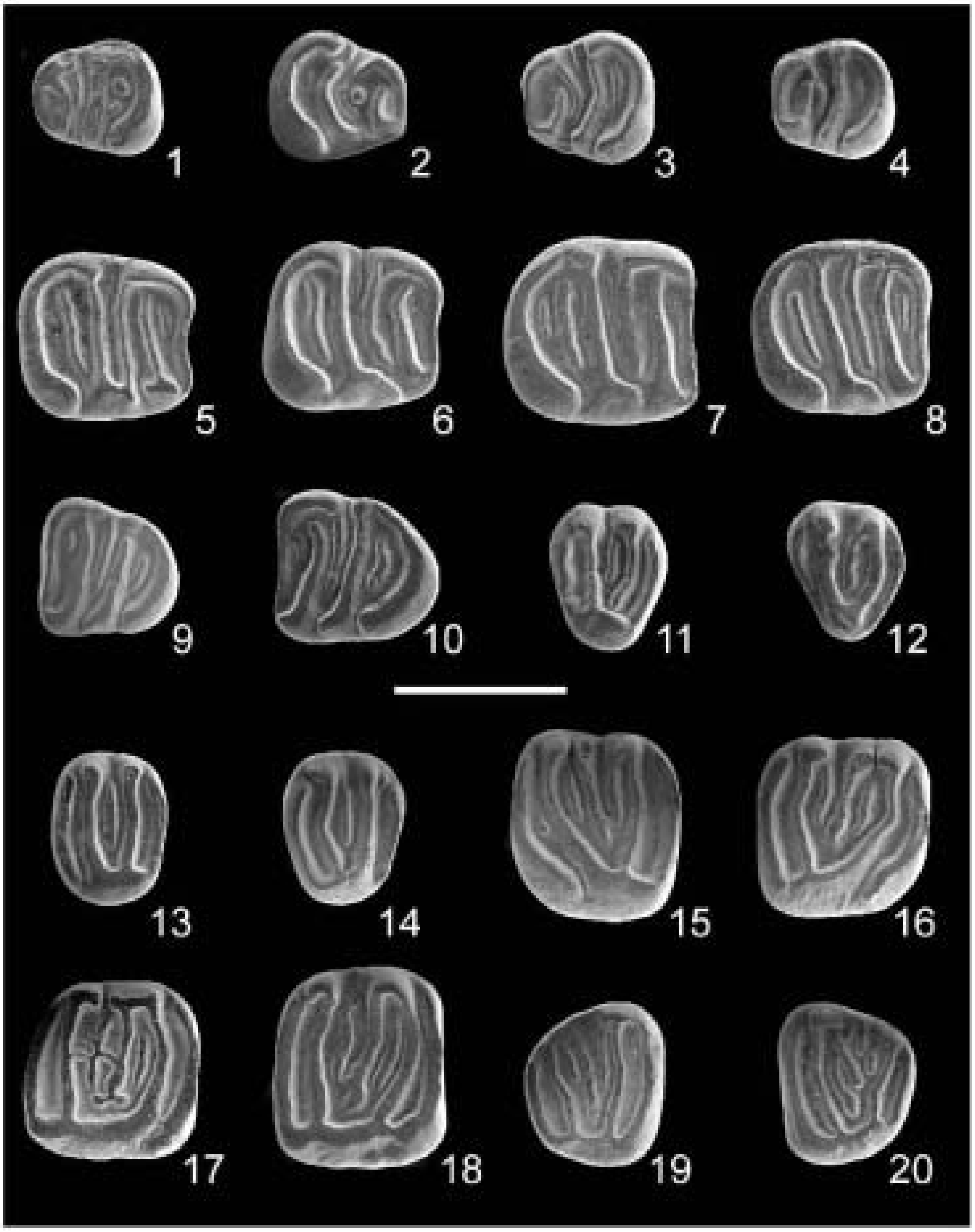

Fig. 2 *Vasseuromys bergasensis* sp. nov. from Bergasa, Ebro Basin. *1*, left d4, BER-2548; *2*, right p4, BER-2547; *3*, left p4, BER-2544; *4*, left p4, BER-2546; *5*, right m1, BER-150 (holotype); *6*, right m1, BER-170; *7*, right m2, BER-2470; *8*, right m2, BER-2474; *9*, left m3, BER-2521; *10*, left m3, BER-2522; *11*, left D4, BER-2529; *12*, left D4, BER-2539; *13*, left P4, BER-2525; *14*, right P4, BER-2526; *15*, left M1, BER-2339; *16*, right M1, BER-2342; *17*, right M2, BER-2385; *18*, right M2, BER-2394; *19*, right M3, BER-2489; *20*, left M3, BER-2504. *Scale* 1 mm

absence of endoloph in M1; less presence of the latter ridge in M2. Differs from *V. pannonicus* in: presence of divided paracone on some M1,2; presence of prototrope on M2 connected to the precentroloph. *V. bergasensis* sp. nov. is similar in size to *V. elegans* and smaller than the other members of the genus (Figs. 3, 4).

Measurements: see Table 2.

Description

d4: teeth of subrectangular shape. Anterolophid connected in two out of three specimens to protoconid and metalophid. The mesolophid is long and connected (2) or not (1) to the entoconid. Central valley opens lingually. Posterolophid long, connected to the entoconid and not connected to the mesoconid.

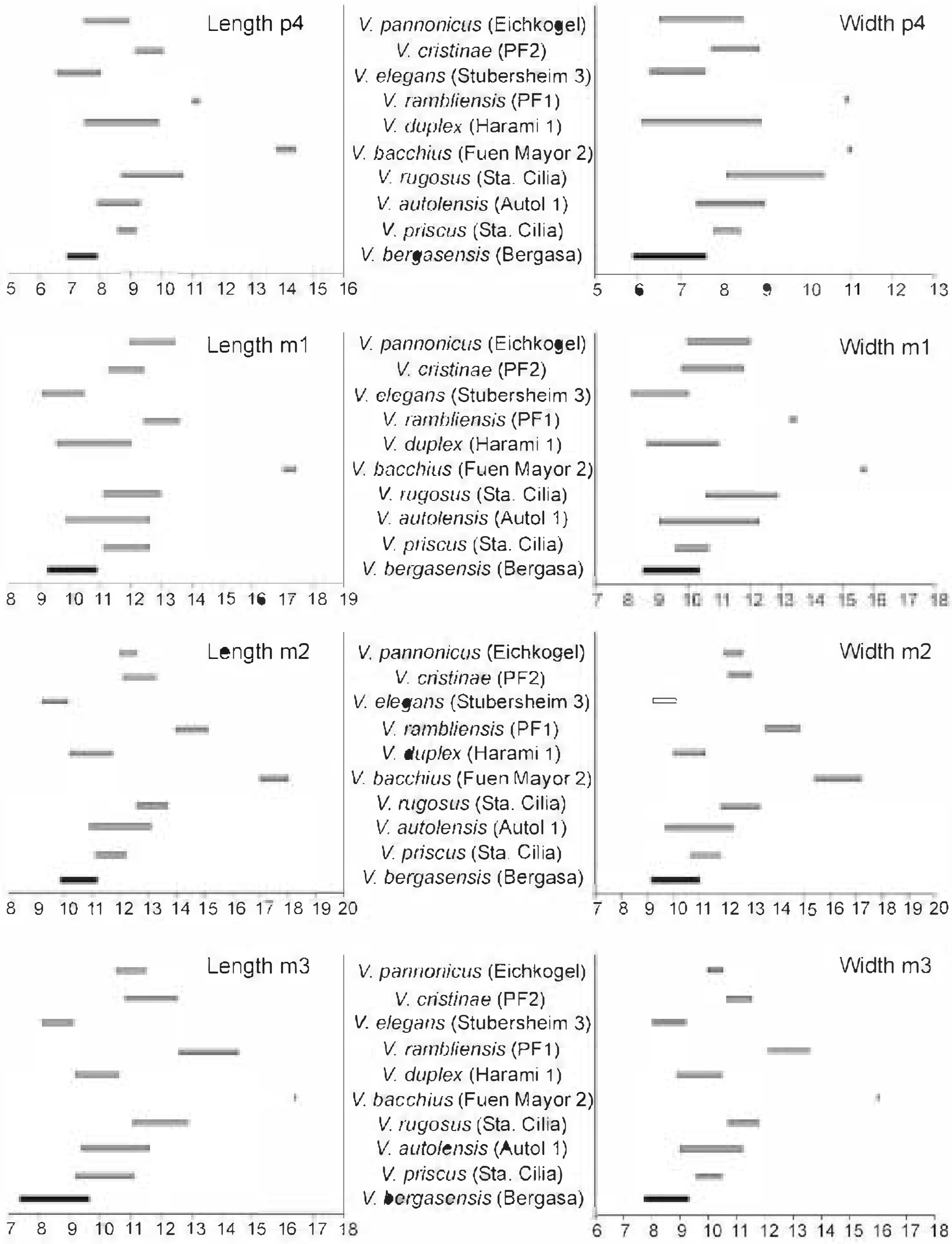

Fig. 3 Ranges of variation of several parameters of the lower molars of *V. autolensis* from Autol 1 (Cuenca 1985), *V. priscus* and *V. rugosus* from Santa Cilia (Álvarez-Sierra et al. 1991), *V. bacchius* from Fuenmayor 2 (Martínez-Salanova 1987), *V. duplex* from Harami 1 (Ünay 1994), *V. elegans* from Stubersheim 3 (Wu 1993), *V. pannonicus* from Eichkogel (Daxner-Höck and de Bruijn 1981), *V. rambliensis* from Pico del Fraile 1 (PF1) (Ruiz-Sánchez et al. 2012b), *V. cristinae* from Pico del Fraile 2 (PF2) (Ruiz-Sánchez et al. 2012a) and *V. bergasensis* sp. nov. from Bergasa

p4: teeth of subtrapezoidal shape, with the anterior side narrower than the posterior one. The anterolophid is connected to the protoconid. Anterotropid absent (7) or very reduced (1) (Fig. 2.3). Metalophid connected to the metaconid (7) or not (1). The centrolophid is of medium-long size (7) or very reduced (1), connecting to the posterior side of the metalophid (6) or reaching the labial border (2). The central valley is open lingually. Mesolophid and hypoconid connected to the entoconid. Posterotropid single, very reduced (1), of medium size (5) or long (1), connected to the entoconid (1) or not (7).

m1: teeth of subrectangular shape. The anterior side is a bit narrower than the posterior one. The labial cusps are elongated. The anterolophid is connected to the protoconid and entoconid. The metalophid is connected to the metaconid. The centrolophid is long. The centrolophid ends free, it is connected to the metalophid or even to the protoconid. The mesolophid and the posterolophid are connected to the entoconid. The hypoconid is not connected to the mesoconid. This molar generally displays four extra ridges: an anterotropid (not present in 9 out of 38 specimens; Fig. 2.6), a ridge between the metalophid and the centrolophid (not present in 19 out of 38 specimens), short or very short (14), of medium size (4) or perpendicular to the metalophid (1), a second centrolophid (23; Fig. 2.6) and a posterotropid (single in 35 specimens, double in 1;

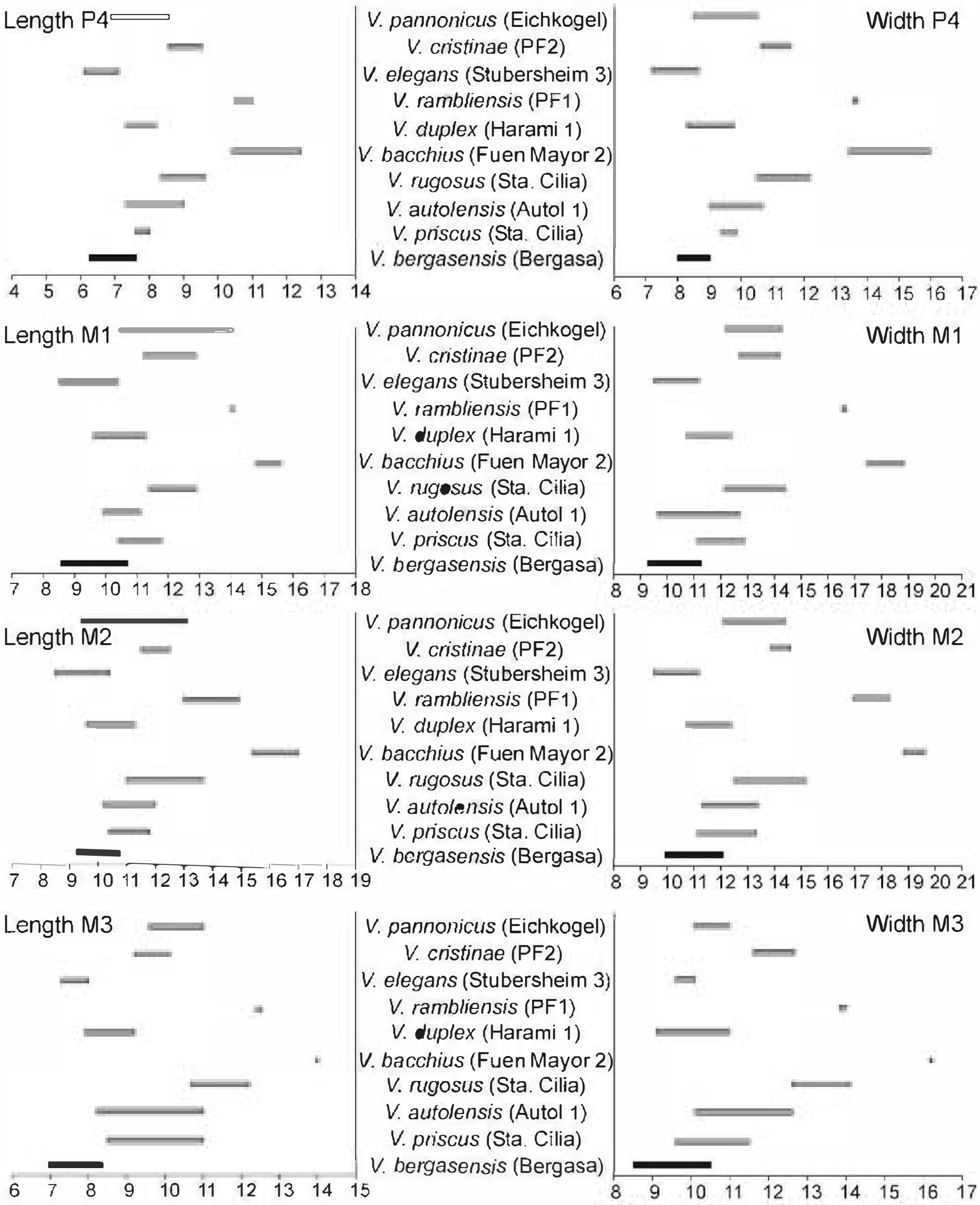

Fig. 4 Ranges of variation of several parameters of the upper molars of *V. autolensis* from Autol 1 (Cuenca 1985), *V. priscus* and *V. rugosus* from Santa Cilia (Álvarez-Sierra et al. 1991), *V. bacchius* from Fuenmayor 2 (Martínez-Salanova 1987), *V. duplex* from Harami 1 (Ünay 1994), *V. elegans* from Stubersheim 3 (Wu 1993), *V. pannonicus* from Eichkogel (Daxner-Höck and de Bruijn 1981), *V. rambliensis* from Pico del Fraile 1 (PF1) (Ruiz-Sánchez et al. 2012b), *V. cristinae* from Pico del Fraile 2 (PF2) (Ruiz-Sánchez et al. 2012a) and *V. bergasensis* sp. nov. from Bergasa

Fig. 2.5, and triple in 2). The posterior centrolophid either ends free or is connected to the entoconid and/or lingual part of the centrolophid, sometimes closing the lingual border of the central valley. The posterotropid is frequently connected to the lingual part of the posterolophid, reaching the labial border in nearly 50 % of the specimens.

m2: the anterolophid is connected to the protoconid (33) or not (9). The metalophid is connected to the metaconid (30) or not (12). The centrolophid is long. It fuses at the labial border, at an angle of 90°, with the anterior prolongation of the mesoconid (4) or it connects to the posterior side of the metalophid or even to the protoconid (6). The mesolophid is connected to the entoconid. The hypoconid is connected to the mesoconid (1) or not (43). In 9 out of 47 specimens, the connection, at a high or low level, of metaconid, entoconid and the lingual part of the posterior centrolophid forms a continuous endolophid (Fig. 2.8). There are between 1 and 4 extra ridges, including an anterotropid, a ridge between metalophid and centrolophid, a second centrolophid, and a single or double posterotropid. Thirty out of 45 teeth have an anterotropid. In 19 specimens, the anterotropid is short or very short (Fig. 2.7), in 9 it is of medium size and in 2 it is long. Five out of 45 teeth have a very short extra ridge between metalophid and centrolophid. The second centrolophid is present in 24 out of 45 specimens, being very short in 4, short in 10 and of medium size in 10. The posterotropid is long, without being connected to the posterolophid. In 2 out of 45 specimens the posterotropid is double (Fig. 2.7).

Table 2 Measurements (in tenths of a millimeter) of the lower and upper teeth of *V. bergasensis* sp. nov. from Bergasa

Element	Parameter	*n*	Minimum	Mean	Maximum
dp4	L	2	7.2	7.4	7.5
	W	2		6.5	
p4	L	11	6.9	7.4	7.9
	W	12	5.9	7.1	7.7
m1	L	41	9.3	10.1	11.0
	W	41	8.6	9.5	10.4
m2	L	53	9.9	10.3	11.2
	W	53	9.1	10.0	11.0
m3	L	18	7.3	8.7	9.7
	W	18	7.7	8.5	9.3
dP4	L	3	6.5	6.8	7.0
	W	3	7.9	8.2	8.7
P4	L	14	6.2	6.6	7.7
	W	15	8.0	8.3	9.0
M1	L	41	8.6	9.8	10.8
	W	39	9.3	10.5	11.3
M2	L	54	9.3	10.1	10.8
	W	56	9.9	10.9	12.1
M3	L	26	6.9	7.7	8.4
	W	27	8.4	9.7	10.6

m3: the anterolophid is connected to the protoconid. The metalophid is connected to the metaconid (8) or not (9). The centrolophid is long and fused to the mesoconid (3) or not (14). Except in one specimen, the mesolophid is connected to the entoconid. Three out of 17 teeth have a partially interrupted mesolophid. In three specimens, the hypoconid is connected to the mesoconid. There are between 1 and 3 extra ridges, including an anterotropid and a posterotropid. The specimen with three extra ridges has two posterotropids. The anterotropid is short (7) or very short (3) (Fig. 2.9) and the posterotropid is of medium size. In just one specimen the posterotropid connects to the posterolophid. Two out of 17 teeth develop a nearly continuous endolophid (Fig. 2.9).

D4: the anteroloph is connected to the protocone, and in contact with the paracone at a high level (1) or not connected (2). The protoloph is transverse, curved and is connected to the protocone. The metaloph is curved and connected to the protocone (2) or to the posterior side to the protoloph (1), forming a composite Y-shaped ridge in the latter. Precentroloph absent (Fig. 2.11). Postcentroloph long (2) or short (1). Extra ridges absent. The posteroloph is connected to the protocone and not connected to the metacone.

P4: the anteroloph is connected to the protocone at a low level and not connected to the paracone. The protoloph and metaloph are connected to the protocone. The precentroloph is short (4) or absent (8), whereas the postcentroloph is relatively long. The extra ridges are absent, except in one out of 12 specimens where a short metatrope is present. The posteroloph is long and connected to the protocone, whereas it is connected to the metacone (3) or not (9).

M1: the anteroloph is directed backward, towards the protocone, without forming an endoloph. In 4 out of 34 specimens, the paracone is divided into two cusps (Fig. 2.15). The anterior cusp continues into the protoloph, and the posterior one continues into the precentroloph. The trigone is V-shaped. The centrolophs are long and the precentroloph is longer than postcentroloph. There are between 1 and 3 extra ridges, including an anterotrope in 5 out of 35 specimens (Fig. 2.15), an ever-present prototrope, a ridge between the centrolophs in 5 out of 35, and a metatrope in 8 out of 35 specimens. A posterotrope is invariably absent. Except for the prototrope, the extra ridges are short or very short. Only one specimen has a double prototrope. The metaloph is oriented transversely and connected to the protocone. The posteroloph is connected to the protocone. A shallow or deep furrow usually separates the labial end of the posteroloph and the metacone (Fig. 2.16).

M2: the anteroloph is long and not connected to the paracone. Only two specimens have a continuous endoloph (Fig. 2.18). Four out of 43 specimens have a paracone, slightly or deeply divided into 2 cusps. The trigone is U-shaped. The centrolophs are long, the precentroloph being larger than the postcentroloph. There are between 1 and 4 extra ridges, including an anterotrope in 1 out of 43 specimens, a prototrope in 43 out of 44, a ridge between the precentroloph and postcentroloph in 6 out of 43, a metatrope in 17 out of 44, and a posterotrope in 1 out of 44. The prototrope is very long and connects to the precentroloph near the protocone in 23 out of 44 specimens. Other longitudinal connections in the trigone are present in several specimens (Fig. 2.17). Except in one specimen, no extra ridges are found outside the trigone. The metaloph is transversely oriented and connected to protocone and paracone, whereas the posteroloph is connected to the protocone and in 12 out of 47 specimens to the metacone.

M3: the anteroloph is connected to the paracone, and connected (13) or not connected (4) to the protocone. Usually, the precentroloph is long, while the postcentroloph is not connected to the metacone. There are 3 extra ridges, a very short anterotrope (2 out of 20), a prototrope (4 out of 20), a ridge between the centrolophs (8 out of 19) and a short metatrope (14 out of 20). Except for two specimens with a short anterotrope (Fig. 2.19), there are no extra ridges outside the trigone. Several specimens show a continuous labial wall (Fig. 2.20). The posteroloph is connected to the protocone, while it is connected to the metacone (6) or not (14).

Discussion

Cuenca (1985) created the genus *Ebromys* for the glirids of medium size from the locality of Autol. That author based the differences from the genus *Vasseuromys* mainly on the absence in *Ebromys* of an endoloph in the M1,2. Lacomba (1988) defined a new species of *Ebromys*, which he named *E. bergasensis*, for the small-sized glirids from Bergasa. Based on the presence of *Eucricetodon collatus*, *Issiodoromys pseudanaema* and *Rhodanomys transiens*, Bergasa is placed in Unit MP30 (local zone W) (Álvarez-Sierra 1987; Álvarez-Sierra et al. 1987; Cuenca et al. 1992). However, although this species was later mentioned by other authors (Daams 1989; Cuenca et al. 1992), *E. bergasensis* was never formally described, and should be considered a nomen nudum.

The scarce material of *Vasseuromys* from Laugnac and Moissac I (Baudelot and de Bonis 1966) does not permit study of its morphologic variability. The presence of M1,2 without endoloph in *V. rugosus* from Laugnac (collections of the University of Utrecht) and the small differences between the material of Autol and Laugnac are the factors that led Álvarez-Sierra et al. (1991) to consider the genus *Ebromys* a junior synonym of *Vasseuromys*.

Ebromys (*Vasseuromys*) aff. *bergasensis* was mentioned from the locality of Ventas 4 (Cuenca et al. 1992). The presence of *Issiodoromys pseudanaema* and *Rhodanomys transiens* in Bergasa, and *Rhodanomys transiens* in Ventas 4, allow these localities to be dated as Late Oligocene (zone MP30) (Schmidt-Kittler 1987).

Biometry

Vasseuromys bergasensis sp. nov. is a small-sized representative of the genus *Vasseuromys*. In general, together with *V. duplex* Ünay 1994 and *V. elegans* Wu 1993, *V. bergasensis* sp. nov. is the smallest species of the genus (Figs. 3, 4). In comparison with the other species of the genus, *V. bergasensis* sp. nov. is clearly smaller than *V. rugosus* from Laugnac (MN2) and Santa Cilia (MN1) (Baudelot and de Bonis 1966; Álvarez-Sierra et al. 1991), *V. bacchius* from Fuenmayor 2 (MN2) (Martínez-Salanova 1987), *V. rambliensis* from Pico del Fraile 1 (MN3) (Ruiz-Sánchez et al. 2012b) and *V. cristinae* from Pico del Fraile 2 (MN4/MN5) (Ruiz-Sánchez et al. 2012a), and, in general, smaller than *V. priscus* from Santa Cilia (Álvarez-Sierra et al. 1991), *V. autolensis* from Autol (MN1) (Cuenca 1985), *V. duplex* from Harami 1 (MN2) (Ünay 1994) and *V. pannonicus* from Eichkogel (MN11) (Daxner-Höck and de Bruijn 1981). The minimum length and width values of most elements of *V. priscus* and *V. autolensis* and some of *V. pannonicus* seem to overlap with the maximum values recorded for *V. bergasensis* sp. nov. (Figs. 3, 4).

Vasseuromys bergasensis sp. nov. is similar in size to *V. elegans* from Stubersheim 3 (MN3) (Wu 1993). The minimum length values of the p4, m1, m2, P4 and M2 and the width values of the m1, P4 and M2 of *V. elegans* from Stubersheim 3 are lower than those of *V. bergasensis* sp. nov.

Morphology

Lower molars

The number of ridges in *Vasseuromys* shows great variability (Ruiz-Sánchez et al. 2012a; Table 3; Ruiz-Sánchez et al. 2012b). Whereas *V. autolensis*, *V. rugosus*, *V. bacchius*, *V. duplex* and *V. pannonicus* generally have between 9 and 11 ridges, *V. priscus* and *V. elegans* have between 8 and 9, *V. cristinae* and *V.* aff. *multicrestatus* (Agustí et al. 2011) always have 9 ridges in the lower molars, and *V. bergasensis* sp. nov. has between 7 and 9 ridges. While the m1 and m2 of *V. bergasensis* sp. nov. have 4 main ridges, the centrolophid and 4 extra ridges, the m3 has 4 main ridges, the centrolophid and 2 extra ridges (anterotropid and posterotropid).

The number and length of the extra ridges are, in general, less in *V. bergasensis* sp. nov. than in other species of the genus. Only in *V. priscus*, the development of extra ridges is similar to that described in *V. bergasensis* sp. nov. (Ruiz-Sánchez et al. 2012a, b). The development of extra ridges is much more pronounced in the forms of a similar size (*V. elegans* from Stubersheim 3 and *V.* aff. *elegans* from Petersbuch 2 and Erkertshofen 2) than in *V. bergasensis* sp. nov. (Wu 1993). In *V. bergasensis* sp. nov., 9 out of 38 m1, 15 out of 45 m2 and 7 out of 17 m3 do not have an anterotropid. This situation is more pronounced for the extra ridge between metalophid and centrolophid: this extra ridge is absent in 19 out of 38 m1, 40 out of 45 m2 and all m3. The same occurs in the development of the second centrolophid in the m1, m2 and m3. While about 50 % of the specimens have a second centrolophid in the m1 and m2, this ridge is absent in the m3. Only the posterotropid is always present.

Vasseuromys bergasensis sp. nov. has a long centrolophid that is sometimes fused to the mesoconid. In *V. priscus*, *V. bacchius* and *V. rambliensis*, the centrolophid is of medium size and generally has a free end (not connected to the mesoconid) (Martínez-Salanova 1987; Álvarez-Sierra et al. 1991; Ruiz-Sánchez et al. 2012a).

On the other hand, except for some specimens of *V. cristinae* from PF2 (Ruiz-Sánchez et al. 2012a), *V.* aff. *cristinae* from SA5 (Ruiz-Sánchez et al. 2013), *V. elegans* from Stubersheim 3, and *V.* aff. *elegans* from Petersbuch 2 and Erkertshofen 2, the lower molars of *Vasseuromys* do not have an endolophid. In *V. bergasensis* sp. nov., 9 out of

47 m2 develop an endolophid, and the same is seen for the m1 and m3. This morphology is also found in the material of the genus *Myolidus* Álvarez-Sierra 1986 in Álvarez-Sierra and García-Moreno (1986) from localities of the Duero Basin.

Upper molars

The upper molars of *V. autolensis*, *V. rugosus*, *V. duplex* and *V. pannonicus* generally have between 9 and 11 ridges, whereas *V. priscus, V. bacchius*, *V. rambliensis*, *V. elegans*, *V.* aff. *multicrestatus* and *V. cristinae* have a smaller number of ridges (8–9) (Ruiz-Sánchez et al. 2012a, b).

The upper molars of *V. bergasensis* sp. nov. display large reductions in the number and length of the extra ridges. While the D4 lacks extra ridges, the only extra ridge that is always present in M1,2 is the prototrope. About 60 % of the M1 and 50 % of the M2 of *V. bergasensis* sp. nov. from Bergasa only have the prototrope. The presence of extra ridges outside the trigone is therefore very limited. Only 1 M2 has 2 additional ridges.

In the M3 of *V. bergasensis* sp. nov., the number of extra ridges is also greatly reduced, and restricted to a short metatrope near the metaloph. The presence of anterotropes, prototropes and/or the extra ridge between the centrolophs is very low; 4 out of 20 in the case of the prototrope, and 8 out of 20 in the case of the extra ridge between the centrolophs. The anterotrope is still less frequent (2 out of 20) and the posterotrope is always absent.

The presence of an endoloph in the upper molars of *V. bergasensis* sp. nov. is generally very rare. While the endoloph is always absent from M1, only 2 out of 42 M2 have a complete endoloph. Twenty-one out of 22 M3 have an endoloph. Despite its scarce representation, the oldest assemblage of *Vasseuromys* shows the presence of specimens with and without an endoloph, as in other assemblages of the genus.

Biostratigraphy

The fossil record of the genus *Vasseuromys* currently extends throughout the Miocene (Daams 1999; Ruiz-Sánchez et al. 2012a, b), and is nearly all from Europe, with just 1 other species from the Turkish record. In the Agenian (MN1–MN2), the European record of *Vasseuromys* comprises *V. priscus*, *V. autolensis*, *V. rugosus* and *V. bacchius* (de Bonis 1973; Cuenca 1985; Martínez-Salanova 1987; Álvarez-Sierra et al. 1991) and *V.* aff. *duplex* and *V. duplex* in the Turkish record (Ünay 1994). In the Ramblian (MN3), 2 taxa have been recorded: *V. elegans* and *V. rambliensis* (Wu 1993; Ruiz-Sánchez et al. 2012b). In the Aragonian (MN4–MN7/8), there are 5 species, *V.* aff. *elegans*, *V.* aff. *priscus*, *Vasseuromys* sp., *V. cristinae* and *V.* aff. *multicrestatus* (Wu 1993; Aguilar and Lazzari 2006; Agustí et al. 2011; Ruiz-Sánchez et al. 2012a). Finally, in the Late Vallesian (MN10) and Early Turolian (MN11), only 1 species, *V. pannonicus*, has been documented (Daxner-Höck and de Bruijn 1981; de Bruijn 1989; Daxner-Höck and Höck 2009).

Vasseuromys bergasensis sp. nov. is restricted to the localities of the Ebro Basin, Bergasa and Ventas 4 (Lacomba 1988; Cuenca et al. 1992). The presence in Bergasa of *Issiodoromys pseudanaema*, *Rhodanomys transiens* and *Pseudotheridomys schaubi* (Álvarez-Sierra 1987; Álvarez-Sierra et al. 1987), and *Rhodanomys transiens* in Ventas 4 (Cuenca and Canudo 1990) is biostratigraphically significant. The presence in Bergasa of the theridomyid *Issiodoromys pseudanaema* is sufficient reason to date it as Oligocene (Schmidt-Kittler 1987). Moreover, the presence of *Rhodanomys transiens* in Bergasa and Ventas 4 allows these localities to be attributed to zone W (Álvarez-Sierra 1987; Álvarez-Sierra et al. 1987) (zone MP30) of the upper Oligocene.

Phylogeny

Ruiz-Sánchez et al. (2012b) hypothesized about the origin and phylogeny of *Vasseuromys*. Following Daams (1989), Ruiz-Sánchez et al. (2012b) supposed a phylogenetic relationship between *Peridyromys columbarii* Daams 1989 and *Vasseuromys*. The general morphology and the concave occlusal surface of M1,2 of *Peridyromys columbarii* from Sayatón 6 (Late Oligocene) support this hypothesis.

The strong concavity, development of the centrolophids and tendency for the molar cusps to form longitudinal walls in *V. bergasensis* sp. nov. from Bergasa are characteristic of most of the species of the genus. Except for *V. priscus*, *V. bacchius*, *V. rambliensis* and now *V. bergasensis* sp. nov., the number and length of extra ridges in the rest of the species of the genus are clearly larger.

Although the general dental pattern of *V. bergasensis* sp. nov. is clearly simple, it contains elements of two morphotypes. While the centrolophid is very well developed, similar to that of the complicated dental pattern group, the number and length of the extra ridges is, in general, very similar to the simple dental pattern group. The population from Bergasa (MP30) contains the two general morphotypes, which in MN1 characterize *V. priscus* (number and length of the extra ridges) and *V. autolensis* (centrolophid very well developed).

Because of the scarcity of type material of *V. priscus*, the status of this species as a representative of the genus *Vasseuromys* is questioned in Álvarez-Sierra et al. (1991). However, a comparison of the rich assemblage of Gliridae of medium size, with concave occlusal surfaces and a tendency for the molar cusps to form longitudinal walls from Santa Cilia (*Vasseuromys*? *priscus* in Álvarez-Sierra et al. 1991), with those of *V. bergasensis* sp. nov. from Bergasa shows that several morphological key features of *V. priscus* from Santa Cilia and those of *V. bergasensis* sp. nov. from Bergasa are coincident. Mainly, the V-shaped M1 and U-shaped M2 and the reduced number of extra ridges in the central valley of the lower and upper molars are distinctive morphological features of both species, and suggest a phylogenetic relationship among them.

We agree with Lacomba (1988) that *V. autolensis* should be considered an off-shoot of *V. bergasensis* sp. nov. While *V. autolensis* has a higher number of extra ridges in the central and posterior valleys of lower and upper molars (Ruiz-Sánchez et al. 2012a), the development of the centrolophid and the contacts of this ridge with the labial cusps of the lower molars are very similar in both species. Moreover, the V-shaped M1 and U-shaped M2 of *V. bergasensis* sp. nov. are also very similar, and coincident with *V. priscus*.

On the other hand, Martínez-Salanova (1987) considered *Vasseuromys bacchius* from the locality of Fuenmayor 2 (MN2) to be an off-shoot of *Vasseuromys autolensis* (MN1). According to that author, in the former species, the size increases and the labial cusps of the lower molars are not longitudinally elongated. The assignment to the genus *Ebromys* led Martínez-Salanova (1987) to exclude a comparison with the group of glirids with an endoloph in M1,2, and therefore with *V. priscus*. The synonymy of *Ebromys* and *Vasseuromys* (Álvarez-Sierra et al. 1991) allows us to take into account other possibilities, as described in preceding paragraphs. While the sizes of *V. bacchius* and *V. priscus* are clearly different, the reduced number and development of extra ridges and a centrolophid of medium size are coincident in both species. An ancestor–descendant relationship between *V. priscus* and *V. bacchius* is more probable than it is between *V. autolensis* and *V. bacchius*. In the former transition, only a size increase is necessary, while a simplification of the dental pattern and an increase in size is implicated in the second case. Another representative of this lineage would be *V. rambliensis* from the locality of Pico del Fraile 1 (MN3) (Ruiz-Sánchez et al. 2012b). This latter species is, in general, a bit smaller than *V. bacchius* and bigger than the other species of the genus *Vasseuromys*. Moreover, it presents fewer and less developed extra ridges and a centrolophid of similar size to those of *V. priscus* and *V. bacchius*.

In the locality of Santa Cilia, two *Vasseuromys* species were described: *V. priscus* and *V. rugosus* (Álvarez-Sierra et al. 1991). These authors showed that the only difference between *V. rugosus* from Santa Cilia and that from its type locality (Laugnac, MN2) is the slightly larger size of the former specimens. According to Álvarez-Sierra et al. (1991), *V. rugosus* from Santa Cilia has a slightly more complicated dental pattern and a somewhat larger size than *V. autolensis* from Autol. The general similarities of and differences between the two species led these authors to consider *V. autolensis* the probable ancestor of *V. rugosus*. In the same way, Álvarez-Sierra et al. (1991) considered that *V. priscus* represents a separate line, and is not the ancestor of *V. rugosus*, as suggested by de Bonis (1973).

Therefore, 3 *Vasseuromys* species, with identical M1,2 shapes, are present in MN1: 2 with a high number of extra ridges and a long centrolophid reaching the labial border of the teeth (*V. autolensis* and *V. rugosus*), and another 1 with a reduced number of extra ridges and a centrolophid of medium size (*V. priscus*). This situation is similar in MN2, where *V. bacchius* resembles the dental pattern of *V. priscus* from MN1, and *V. rugosus* that of *V. autolensis* from MN1. In MN3, Ruiz-Sánchez et al. (2012b) described *V. rambliensis*, a large-sized species with a morphology related to *V. bacchius* from MN2.

Based on the data provided in the present paper and in the literature, phylogenetic relationships among the species of the genus *Vasseuromys* can be proposed. Notice that the phylogenetic relationships in the branch containing the

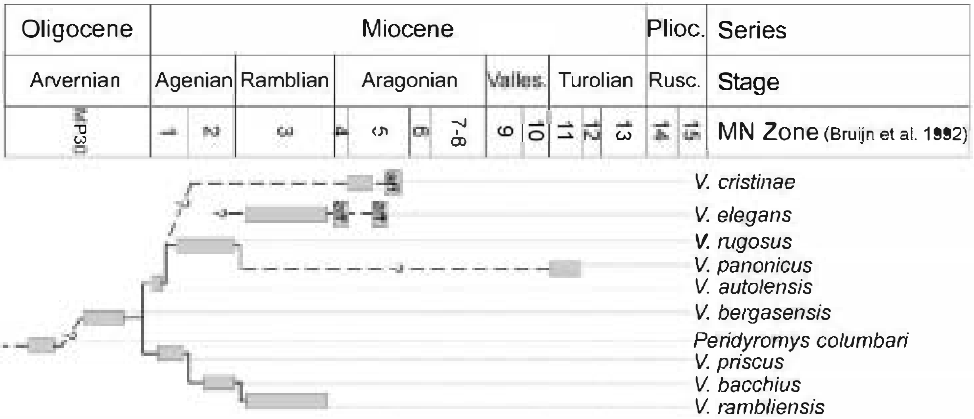

Fig. 5 Late Oligocene to Late Miocene stratigraphical distribution and proposed phylogenetic relationships in *Vasseuromys*

species *V. autolensis*, *V. rugosus*, *V. elegans*, *V. cristinae* and *V. pannonicus* are still uncertain (Fig. 5).

Conclusions

Vasseuromys bergasensis sp. nov. from Bergasa represents the first and, as yet, only record of the genus *Vasseuromys* in the Oligocene. This new glirid is characterized by its intermediate size between the smallest *V. elegans* and the other species of the genus.

Morphologically, the new species is characterized, apart from a well-developed centrolophid and strong concavity of the molars, by the presence of 5 main ridges and a variable number of extra ridges in the lower molars. In the lower molars, except for the posterotropid, the rest of the extra ridges are strongly reduced in number and in length. Some of these extra ridges are absent in a high percentage of the specimens. In the upper molars, one of the most striking features is the complete absence in M1 and a near-complete absence in M2 of an endoloph. The upper molars of *V. bergasensis* sp. nov. from Bergasa have 4 main ridges, 2 centrolophs and a variable number of extra ridges. Only the prototrope is always present in M1,2, whereas extra ridges in and outside the trigone are not very common. This set of morphological features distinguishes *V. bergasensis* sp. nov. from the other species of the genus, including those of a similar size (*V. elegans* and *V.* aff. *elegans*).

With respect to the phylogeny of the group, the presence of *V. bergasensis* sp. nov. in deposits of Late Oligocene age (MP30), along with a morphology characterized by a small number and poor development of extra ridges, long centrolophids in the lower molars, and a V-shaped trigone in M1 and a U-shaped trigone in M2, support the idea that *V. bergasensis* sp. nov. (MP30) is probably the ancestor of *V. priscus* (MN1) and *V. autolensis* (MN1). According to the dental patterns of these two species, this would mean that *V. priscus* is probably the ancestor of the lineage *V. bacchius* (MN2)–*V. rambliensis* (MN3) and *V. autolensis* the ancestor of *V. rugosus* (MN1–MN2) (Álvarez-Sierra et al. 1991).

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