Palaeontology and biostratigraphy (micro-mammals) of the continental Oligocene-Miocene deposits of the North-Central Ebro Basin (Huesca, Spain)

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In this paper the micromammals from three localities in the Oligocene/Miocene boundary interval and the Lower Miocene of the Ebro Basin in the Province of Huesca (northern Spain) are described. Twenty-five species are recognized, two of which are new (*Quercomys daamsi* de Visser and *Peridyromys turbatus* Alvarez Sierra et al.; Gliridae). One new subspecies belonging to the Ochotonidae (*Prolagus vasconiensis fortis* López Martínez & Sesé) is described. The biostratigraphy, palaeoecological implications and palaeobiogeography are discussed.

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Introduction

The Ebro Basin is one of the largest continental Tertiary basins of Europe. It is situated in the northeastern part of the Iberian Peninsula, extending over nearly 45 000 km^2 and has a triangular outline. The northern border has been tectonically active since the Cretaceous (Pyrenean and Cantabrian ranges); the southwestern (Iberian range) and southeastern (Catalonian range) borders are younger and have been less active; the major tectonic activity took place in Late Eocene-Oligocene times. The infilling of the basin is asymmetrical: in the northern part the thickness of the sediments may reach 5 km, and they are overthrusted by marine Mesozoic and Palaeogene nappes; in the southern part the sediments uncomformably overlap the margins of the basin.

The Ebro Basin has been studied intensively by French, Swiss, German, Dutch, and Spanish geologists since the end of the nineteenth century. The interest of its general geological and geodynamical setting increased because of the exploration of gas, oil and ore fields. Many tectonical and sedimentary processes have been modelled in this basin. A general and updated geological study was published by Riba et al. (1983).

The palaeontological data of the continental sediments of the Ebro Basin have traditionally been scarce. Ages are frequently attributed to the sediments on the basis of lithological correlations (even when lithological boundaries are evidently
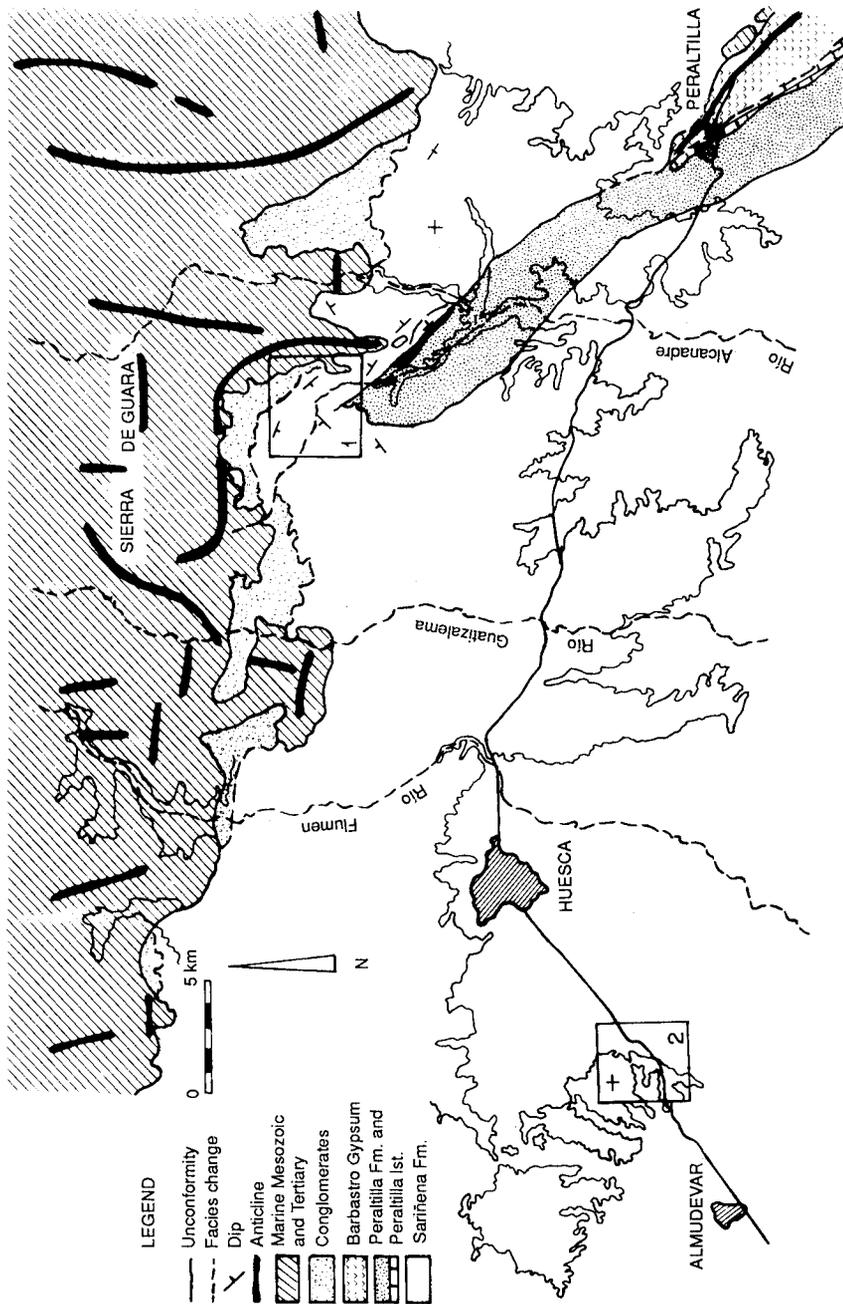
Fig. 1. Simplified geological map of the north-central part of the Ebro Basin. The squares 1 and 2 are enlarged in Figs. 2 and 3 to indicate the situation of the fossiliferous localities. The asterisk indicates the locality of Peraltilla.
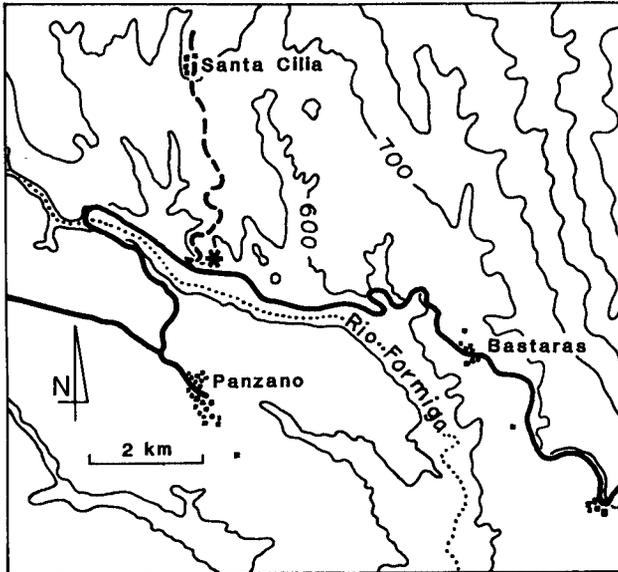
Fig. 2. Situation of the locality of Santa Cilia (asterisk). Detail of map 1:50 000, Alquézar, no. 249 (Almela & Ríos, 1950).

diachronous) or tectonic criteria. The main palaeontological data nowadays used for biostratigraphy in this basin are more than twenty years old (Crusafont et al., 1966). The chronostratigraphy has not yet been reviewed applying the modern criteria for continental deposits (Daams & Freudenthal, 1981; López Martínez, 1982). Recently, several studies on micromammal and charophyte biostratigraphy were made in the northwestern, central and eastern areas (Anadón & Feist, 1981; Cuenca Bescós, 1985; Anadón et al., 1983, 1987; Agustí et al., 1985, 1987; Martínez-Salanova, 1987). The aim of this paper is to contribute to the palaeontological and biostrati-graphical knowledge of the north-central part of the Ebro Basin on the basis of micromammals, in their geological context. This paper contributes to the recon-struction of the environment and the interpretation of the ecological conditions that prevailed in this area.

A palaeomagnetic study on the sections of San Juan, La Galocha and Santa Cilia is at present being carried out by S. Sen (Paris).

GEOLOGICAL FRAMEWORK

The studied area (Fig.1) forms part of the north central margin of the Ebro Basin, and it is limited by the thrust fold of the Sierras Exteriores or Marginales (Sierra de Guara). The allochtonous sediments consist mainly of marine Cretaceous and Palaeogene limestones in which a N-S and an E-W oriented fold-system are present. The autochtonous sediments of the Ebro Basin are Palaeogene and Early Miocene 'molasses', in which tectonic deformation decreases upwards and towards the centre of the basin (Almela & Rios, 1959; Riba et al., 1983; Nichols, 1987). The lower beds are in vertical position or overturned; the upper ones are subhorizontal in the
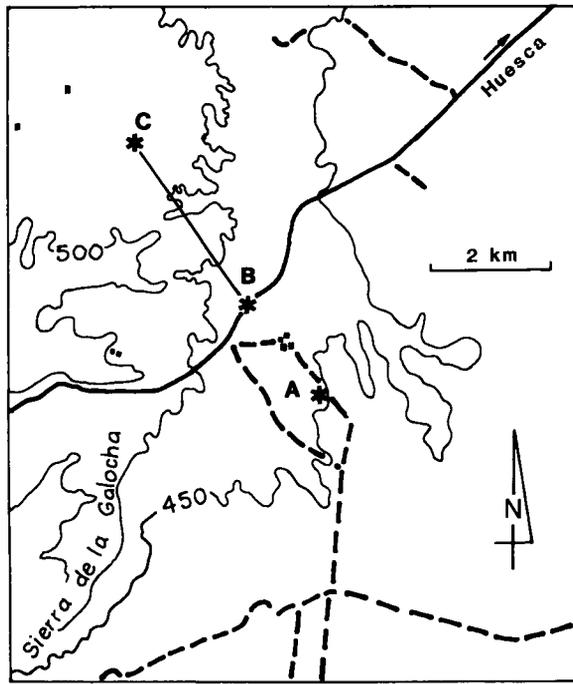
Fig. 3. Situation of the locality of San Juan (A) and thesection of La Galocha (B-C). Detail of map 1:50 000, Huesca, no. 286 (Larragán & Castell, 1952).

southwestern part of the studied area. The deposition was thus synchronous with the tectonic activity.

The southeastern part of the studied area shows the periclinal closure of the NW-SE directed Barbastro Anticline. The core of this anticline consists of an extensive massive evaporitic formation (the Barbastro Gypsum, Crusafont et al., 1966). Its thickness is unknown, as its lower limit is not exposed, but drillings have shown that it measures at least 2 km (Riba et al., 1983). The Barbastro Formation is considered to be of Late Eocene age, as in eastern Catalunya the underlying Igualada marls are of Bartonian/Priabonian age (Barnolas et al., 1981; Busquets et al., 1985).

The Barbastro Gypsum is overlain by a wide-spread, 15 m thick carbonate succession (here named the Peraltilla limestone). The transition from the gypsum to the limestones seems to be a paraconformity, but in some areas a clastic polygenic bed is present below the limestones (Garrido Megias, 1972). The age of this unit is considered to be Late Eocene/Early Oligocene by Reille (1967, 1971) on the basis of Charophyta. A micromammal faunule from the marls of the Peraltilla limestones, sampled by us near the village of Peraltilla in 1982 (Fig. 1) yielded some specimens of *Theridomys major* Depéret (see Alvarez Sierra et al., 1987). The presence of this species allows us to assign an Early Oligocene (Montalbán zone, MP 23 or R local zone) age to this level. The MP 23 zone has been correlated with the Nannoplankton Zone NN 23 or 24 (Rupelian) in the Rhein Graben by Tobien (1987). The species *Theridomys major* has originally been described from the Tarrega limestones in the eastern Ebro Basin (Depéret, 1906), which is also the type locality of the *Therido-*

LEGEND

Not exposed

Marls
Sandy marls

Clays
Silts

Sand(stone)s

Conglomerates

Channels

20 m

10 m

0 m
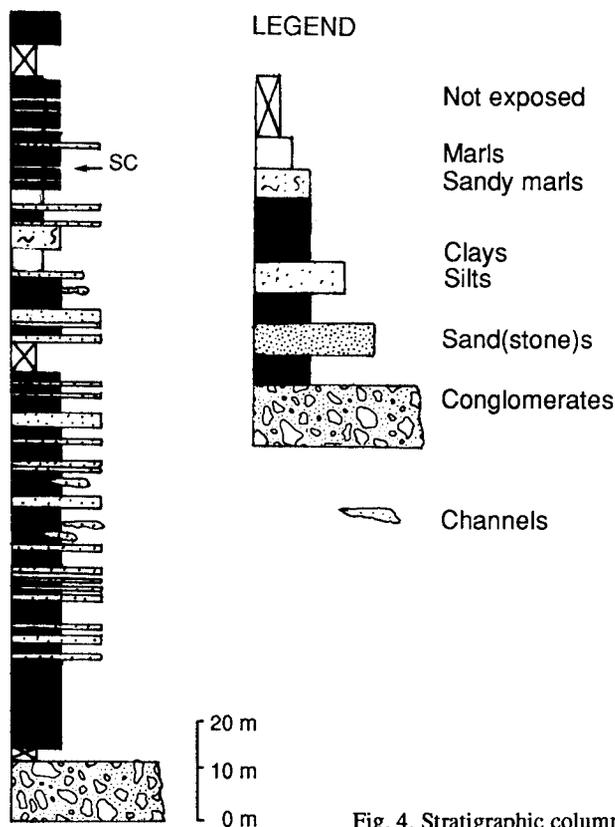
Fig. 4. Stratigraphic column of the Santa Cilia locality.

mys major Zone (Agustí et al., 1987).

A rapid transition exists between the lacustrine limestones of Peraltilla and the overlying detritic Peraltilla Formation (Crusafont et al., 1966). This formation consists of more than 700 m of red sand bodies, silts and clays.

An unconformity separates this unit from the ochreous clays and sand sheet beds of the Sariñena Formation (Quirantes, 1969) which contains the fossiliferous site of Santa Cilia at its base and the ones of San Juan and La Galocha near the top. Figures 2 and 3 show the situation of these sites, and Figs. 4 and 5 the stratigraphic sections.

MATERIAL AND METHODS

Nearly 1900 vertebrate fossils have been collected in the summers of 1982-1985 in the surroundings of Huesca and Barbastro (Fig.1) by screening more than 17.5 tons of sediment. We benefitted of the help of geologists working in the area (Drs P. Friend and P. Hirsch, Cambridge, England; Dr S.D. Nio and A. van Gelder, Utrecht, The Netherlands).

The material is stored in the collections of the Department of Palaeontology
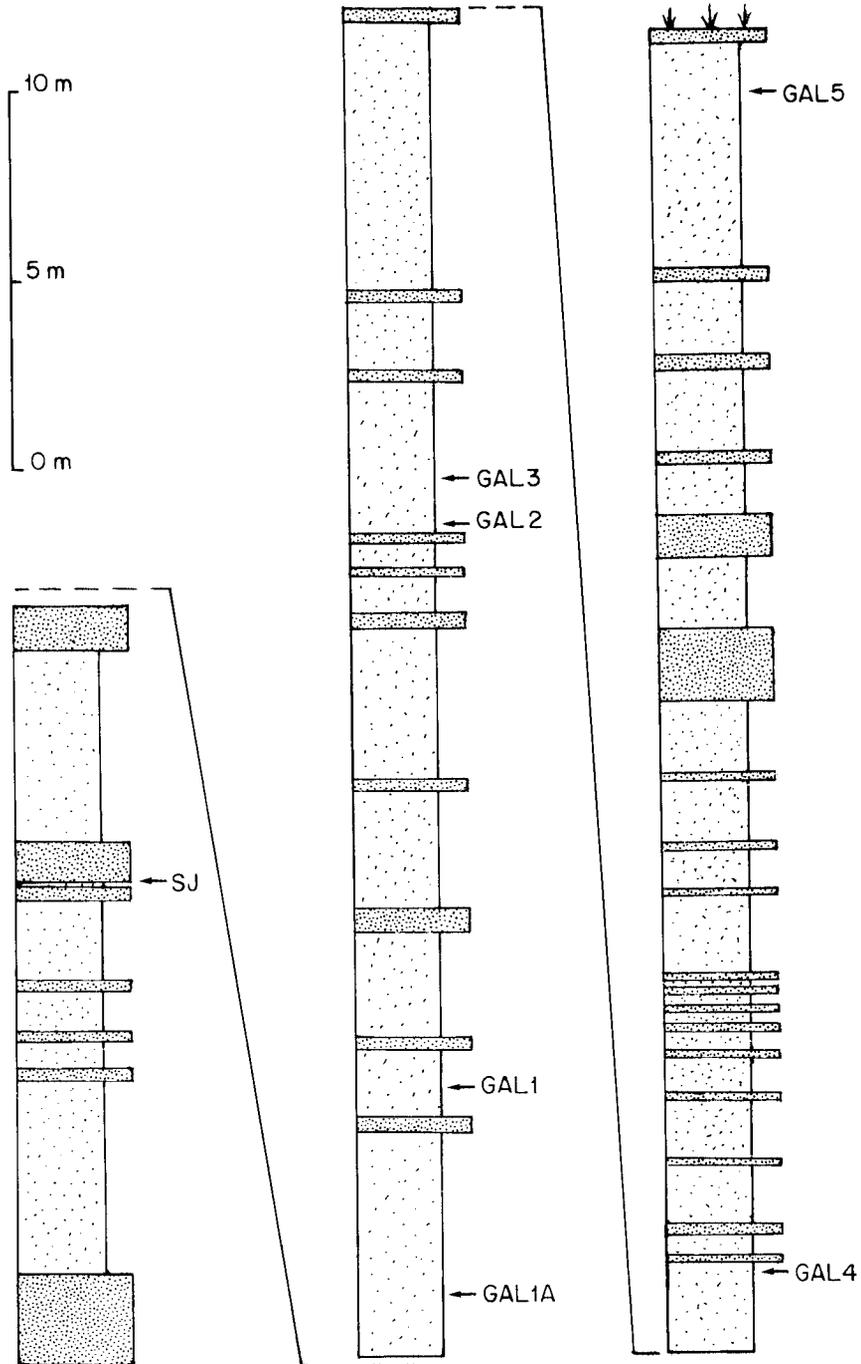
Fig. 5. Stratigraphic column of the the San Juan and La Galocha localities.
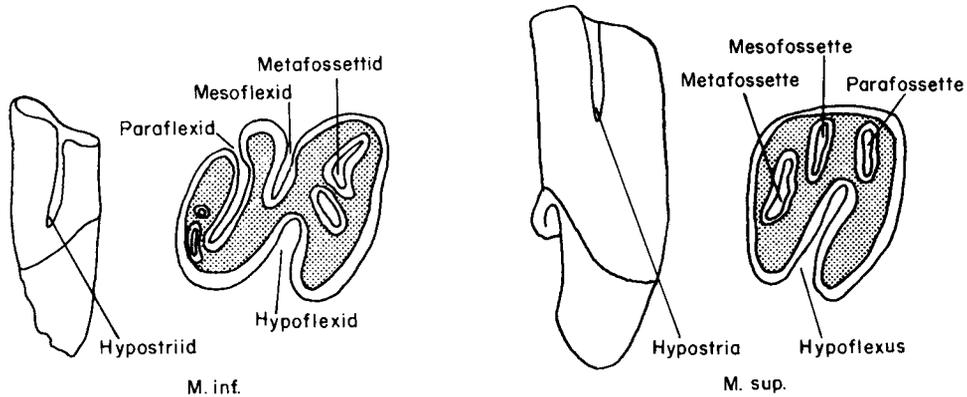
Fig. 6. Nomenclature of parts of the Castoridae cheek teeth (after Stirton, 1935).

of the Universidad Complutense, Madrid (U.C.M.). Some material from the collections of the Instituto de Paleontología de Sabadell (I.P.S.) is also studied in this paper. The catalogue numbers of the specimens from Santa Cilia and San Juan may be followed by C, G, or LO. The C stands for Cricetidae, the G for Gliridae and the LO for Lagomorpha.

For measurement procedures and nomenclature of parts of the cheek teeth of the small mammals, studied in this paper, the reader is referred to previous papers. De Bruijn (1967) for the Sciuridae, Stirton (1935) for the Castoridae (Fig. 6), Daams (1981) for the Gliridae, Alvarez Sierra (1987) for the Eomyidae, Mein & Freudenthal (1971) for the Cricetidae, and López Martínez (1986) for the Lagomorpha. Measurements are given in 0.1 mm units for all micromammals, with the exception of the Castoridae which are given in 1.0 mm units.

The biochronological framework of the European Palaeogene has been recently revised (Schmidt-Kittler, 1987); a regional scale for the Upper Oligocene/ Lower Neogene of Spain was proposed by Alvarez et al. (1987). The Neogene continental scale of MN units (Fahlbusch, 1976) is also used for comparison.

Acknowledgements

Systematic descriptions

LAGOMORPHA Brandt, 1855
OCHOTONIDAE Thomas, 1897

Titanomys visenoviensis von Meyer, 1843
Pl. 1, figs. 1-7.

Locality – Santa Cilia, Province of Huesca.

Material and measurements

	Length				Width			
	n	min	mean	max	n	min	mean	max
D^4	2	12.8	13.8	14.7	2	18.7	22.4	26.1
P^2	2	9.0	9.4	9.8	2	10.8	12.8	14.8
P^3	2	13.8	13.9	14.0	2	—	25.3	—
P^4	2	14.3	15.2	16.1	1	—	23.9	—
M^1	1	—	14.2	—	0	—	—	—
M^2	1	—	13.1	—	0	—	—	—
P_3	2	11.6	12.2	12.7	2	14.5	15.5	16.5
P_4	3	18.5	20.6	22.6	2	21.6	22.3	23.0
M_1	2	18.9	19.6	20.2	2	19.9	20.8	21.6
M_2	2	19.0	20.1	21.2	2	18.3	19.0	19.7

Description – The upper cheek teeth have one, two, or three roots. The lower ones possess one bilobated root.

D^4 – The two specimens have a protocone and hypocone of similar size, and a rather deep hypoflexus is present. The two labial cusps (paracone and metastyle) are separated by a metaloph reaching the external side. The paraflexus-fossette is J-shaped and the mesoflexus-fossette is short and rounded.

P^2 – The protocone and metacone are large, oval cusps. The protocone is somewhat larger than the metacone. The metastyle is reduced to a small labial wedge. The paraflexus is deep and oblique. The metaflexus is hardly developed and it is shorter than the paraflexus in the shaft of the crown.

P^3 – The hypoflexus is almost absent; only a shallow furrow marks the lingual face. The protoloph covers approximately half of the subrounded metacone. The labial part is formed by a metastyle, surrounded by some small, accessory cusps. The long and curved paraflexus is very deep in transverse direction, thus isolating the metacone from the posterior wall. A narrow isthmus connects the metacone to the metastyle labially. The shallow mesoflexus is postero-lingually oblique.

P^4-M^1 – Most of our specimens are longitudinally broken in the middle of the occlusal surface. The parafossette and the mesoflexus are present in the labial half of all specimens.

M^2 – In the little worn specimen the paraflexus and mesoflexus are open

posteriorly, thus isolating the very small and oblique metacone. The more worn specimen has lost the fossettes, and the hypoflexus penetrates approximately one fourth of the estimated crown width in between the two asymmetric lingual cusps.

P_3 – One specimen has two lobes joined by a central isthmus. These lobes are separated by two flexids; labially by the hypoflexid, and lingually by the mesoflexid. Both flexids are continuous along the major part of the crown height. The talonid is separated from the hypoconulid by a short metaflexid, which disappears at a short distance below the occlusal surface. The other specimen is more simple; it has no metaflexid, the mesoflexid is hardly developed, and the trigonid and talonid are connected on the lingual side by a wide isthmus. The metaconid is practically absent.

P_4-M_1-M_2 – These elements have a wide trigonid and a relatively narrow talonid, which are united by crown cement. Differentiation of the enamel is most evident in the trigonid, where it lacks in the anterior part, and it is thickened in the posterior wall. The talonid has a shallow metaflexid isolating the hypoconulid. This valley may be reduced to a metafossettid, and disappears with progressive wear.

Discussion – Our P_3 material was compared to the same elements of the *Titanomys-Amphilagus* group from other Upper Oligocene and Lower Miocene European localities (Fig. 7).

Pomel (1853) distinguished two species belonging to separate genera in the Lagomorph population from Langy (MN1, St Gérand Allier): *Lagodus picoides* without M_3 and *Amphilagus antiquus* with M_3. After the revision of the Allier faunas by Gervais (1848) and Filhol (1879), Major (1899) concluded that there are no criteria for subdividing the homogeneous Lagomorph population from Langy, and that it should be assigned to *Titanomys visenoviensis* von Meyer, 1843.

Viret (1929) and Tobien (1963, 1974) changed this conclusion, assigning the population from Coderet (MN 0, Allier, France) to *Amphilagus antiquus*, which would be different from *Titanomys visenoviensis* in the morphology of the P_3. According to their subdivision, *Titanomys* would be characterized by morphotype 2 (Fig. 7, hour-glass shaped P_3) and *Amphilagus* would feature morphotype 5 (Fig. 7, P_3 with a deep hypoflexus). The population of Santa Cilia shows both types of P_3, as is the case in other localities (see Fig. 7). On the other hand, Viret himself recognizes (1929, p. 87) that his *Amphilagus* morphology does not fit with the diagnosis of Pomel, since *Amphilagus* coincides with *Titanomys* (= *Lagodus*) in its P_3 having: 'un seul sillon sur les deux faces ... formée de deux cylindres comprimés réunis sur un seul point près du bord externe ..' (cf. morphotype 2). As Figure 7 shows, the claimed diagnostic character distinguishing *Amphilagus* from *Titanomys* appears to be individually variable in a single population. Either morphology may be observed in the majority of the populations attributed to the two taxa, although morphotype 2 is more frequent in little worn specimens, and in younger localities.

Another difference between *Amphilagus* and *Titanomys* according to Pomel (1853), Viret (1929) and Tobien (1974) would be the presence of M_3 in the former genus. However, this element is only present in part of the mandibles of a single population of *T. visenoviensis* (see for instance Major, 1899 and Tobien, 1974),

Localities	Lagomorph species	1	2	3	4	5	N
Santa Cilia	*Titanomys visenoviensis*		1			1	2
Poncenat			2				2
Chaveroche			2	2			2
Montaigu (St Gérand)			47			1	50
Weisenau			1	2			3
Saulcet		1	2	3		2	8
Kaubach I			2	3			5
Gans			1	1	1		3
Tomerdingen		1	1	8		2	12
Hochheim-Flörsheim	'Amphilagus antiquus' after Viret, 1929		1				1
Coderet		8	4	5	25		42

Morphotypes P_3

Mein, 1975: 1 (*Titanomys*), 0 (*Amphilagus*)

Fig. 7. Variation of the dental pattern of P_3 of *Amphilagus* and *Titanomys*.

whereas the P_3 only shows the hour-glass shaped type (Fig. 7, type 2). In Santa Cilia this element may also be present as one of the M_2 seems to have a wear facet on its posterior wall. Consequently there is no reason to consider two different genera and species in these populations, because each population shows variation in both claimed diagnostic characters (P_3 morphology and the presence of M_3). We agree with Major (1899) to recognize one single species in the Oligocene/Miocene boundary interval *(Titanomys visenoviensis* von Meyer). *Amphilagus antiquus* Pomel and *Lagodus picoides* Pomel are junior synonyms.

The population from the Upper Oligocene of Coderet (MN 0) appears to be more primitive than the ones from the Oligocene/Miocene boundary interval (MN zone 1/zone X) by the less hypsodont teeth, by the low frequency of morphotype 2 in its P_3 and by the more frequent M_3. It would be correct to consider it as a different species of the *Titanomys visenoviensis* lineage. *T. visenoviensis* is slightly younger, it has more hypsodont teeth and it has lost its M_3. It can, however, not be assigned to *A. antiquus* Pomel as this name was originally used for *T. visenoviensis* from younger levels.

Piezodus cf. *tomerdingensis* Tobien, 1975
Pl. 1, figs. 8-9.

Synonym: Titanomys visenoviensis pars in López Martínez, 1977, fig. 11.2.

Locality − Santa Cilia, Province of Huesca.

Material and measurements
P^2 (7.0 × 11.7, U.C.M).; P^3 (16.6 × −, IPS); 2 M^2 (1.18 × −, 13.5 × 20.8).

Description
    P^2 − It has three cusps of similar size, which are separated by two folds of equal depth. This tooth differs from the P^2 of *Titanomys* by the smaller metacone, the larger metastyle, a deeper and longitudinal mesoflexus, and by its larger crown height.
    P^3 − The broken specimen was provisionally included in *Titanomys* by López Martínez (1977, 1989). As mentioned in these papers, it differs from the P^3 of that genus by the shallower paraflexus and the larger protoloph. These distinctive features correspond better to the *Piezodus* morphology. New and better preserved material confirms the presence of this taxon in Santa Cilia.
    M^2 − These specimens are better preserved. One specimen has a J-shaped parafossette, the other one has lost all interior structures. In the first specimen the hypoflexus is deep, penetrating about 1/3 of the crown width. The curvature of the shaft is strong in both specimens; the radius of the circle measures 26 mm.

    Discussion − The size, the strong curvature of the shaft and the morphology of the P^2 and P^3 allow us to assign this material to the genus *Piezodus* Viret, 1929 (sensu Tobien, 1963). *P. tomerdingensis* Tobien, 1975 from the Upper Oligocene or

Lower Miocene of Tomerdingen fits best with the stage of hypsodonty and other dental features. However, the absence in Santa Cilia of the lower teeth prevents a definitive determination.

In Spain *Piezodus* has hitherto only been cited from Fuenmayor (La Rioja, zone Y1, Oligocene/Miocene boundary interval, Alvarez Sierra et al., 1987) by Martínez-Salanova (1988). This material was described as *P.* aff. *tomerdingensis*, differing from *P. tomerdingensis* Tobien, 1975 by its more hypsodont teeth.

Prolagus vasconiensis fortis López Martínez & Sesé, subsp. nov.
Pl. 2, figs. 1-10.

Type locality – San Juan, Province of Huesca.
Type horizon – Lower Miocene.
Holotype – P_3 dext., no. SJ.LO.33, Pl. 2, fig. 5.
Derivatio nominis – From *fortis*, Latin for strong, because of its large size.

Diagnosis and differential diagnosis – *Prolagus* with a similar dental pattern as that of *P. vasconiensis* Viret, 1930, but of significantly larger size.

Material and measurements

	Length				Width			
	n	min	mean	max	n	min	mean	max
D^2	8	11.0	12.6	14.6	8	16.3	17.0	23.1
$D^{3,4}$	2	12.7	13.0	13.3	3	25.9	26.5	27.4
P^2	7	9.3	9.5	11.5	6	16.8	17.8	20.4
P^3	10	15.0	17.5	19.0	8	24.5	29.1	32.2
P^4	7	13.3	14.6	15.1	5	24.7	28.5	31.8
M^1	23	12.0	14.7	15.2	13	26.3	30.5	32.9
M^2	10	12.2	12.5	14.3	8	21.6	25.4	29.6
D_3	10	20.5	21.6	22.0	9	16.0	18.5	21.0
D_4	3	14.4	16.0	17.3	2	14.3	14.5	14.9
P_3	6	17.1	18.1	18.9	8	16.3	18.8	19.7
P_4-M_1	2	16.4	17.0	17.5	1	——	19.5	——
M_2	1	——	19.6	—	1	——	18.7	—

Distribution – This new subspecies is only known from the Lower Miocene of San Juan. Material from La Galocha 5 (Ebro Basin) has been tentatively assigned to the new subspecies (see below).

Description – The population of San Juan has the dental features typical of *Prolagus*: rootless cheek teeth, the generally isolated anteroconid of P_3, the presence of a centroflexid, the protoconulid being connected to the protoconid, the three-lobed M_2, the absence of M_3, the strongly curved mesoflexus of P^3, and the presence of one or two fossettes in P^4-$M^{1,2}$.

D^2 – The hypoflexus is wide and it separates the protocone from the hypocone. These cusps are more or less of the same size and have a triangular shape. The protocone is connected to the protoloph by a narrow isthmus. The protoloph is the most anterior ridge of the tooth and it has generally a rounded or lengthened shape. Paraflexus, mesoflexus and metaflexus are deep valleys. Mesoflexus is smaller than paraflexus and metaflexus is smaller than mesoflexus. The metacone and the metastyle are more or less rounded or lengthened. The metaflexus delimits a little poststyle at the labial border of the tooth.

D^3-D^4 – In all specimens the paracone, metacone and metastyle are labially fused. Two fossettes are present. The labial border of the tooth has no enamel.

P^2 – The hypoflexus is absent, with the exception of one specimen in which this character is slightly distinct. The three main cusps (protocone, metacone and metastyle) are successively of smaller size. The deep flexuses are straight and parallel and run from the anterior to the posterior part.

P^3 – The relatively long metacone reaches the labial border of the tooth. The paraflexus is deeper than the mesoflexus, and they are both open. The metaflexus is absent.

P^4-M^1-M^2 – In the P^4 two fossettes of different size are present: the smaller mesofossette has a subquadrate shape and the larger parafossette a J-shape. The parafossette surrounds the metafossette. In M^1 and M^2 only a large, J-shaped parafossette is present. The hypoflexus in the three elements is relatively shallow and does generally not exceed one third of the tooth width.

D_3 – The dental pattern of this element consists of three lobes: the anterior one is always isolated, and the two posterior ones are generally connected to each other by an isthmus. The anteroconid has a labial anteroflexid. The centroflexid is absent or hardly developed. A hypoconulid is absent.

D_4 – This tooth does not show any features of systematic interest. The anterior widened lobe is separated from the posterior one by the mesoflexid and the hypoflexid.

P_3 – The anteroconid is generally rounded. This cusp is more or less of the same size as the metaconid, or slightly smaller. The anteroconid is generally isolated, but in three specimens an anterolophid connects this cusp to the the the trigonid. All specimens have a protolophid connecting the protoconid to the metaconid. The centroflexid is distinct or weak. The mesoflexid shows an obtuse angle. The protoflexid has a small protoconulid, which varies from distinct to weak, or nearly absent. The well-developed entoconid has a small ridge which is divided towards the metaconid. The thickness of the enamel is fairly regular around the entire tooth.

P_4-M_1 – The dental pattern consists of two lobes: the talonid and trigonid. Fossettes are absent.

M_2 – In this element the hypoconulid tends to be isolated. Several specimens have the hypoconulid connected to the talonid by an isthmus of narrow enamel. In other specimens the hypoconulid has the shape of an isolated cylindrical column, which is stuck to the talonid by means of cement.

Prolagus vasconiensis aff. *fortis* López Martínez & Sesé, subsp. nov.
Pl. 2, figs. 11-14.

Locality – La Galocha 5, Province of Huesca.

Material and measurements

	Length				Width			
	n	min	mean	max	n	min	mean	max
D^4	1	——	13.8	——	0	——	——	—
P^2	3	10.7	13.0	14.4	3	18.1	18.8	19.7
M^1	2	14.1	15.4	16.7	2	—	30.6	——
D$_3$	2	21.1	21.6	22.0	1	—	26.3	——
P$_3$	1	——	17.6	——	0	—	—	—

Description

D^2 – The only specimen has a damaged labial part, and therefore the metastyle is not present. The other dental features are similar to those of the ones from San Juan, in which the protoloph is lengthened.

D^4 – The dental pattern of this tooth, in which the lingual wall is missing, is similar to that of the D^4 from San Juan.

P^2 – The three specimens are relatively well preserved and they show two deep valleys (para- and mesoflexus) which are at right angles with the posterior side of the tooth (Pl. 2, figs. 13-14). The metastyl is of the same size as the protocone, giving a symmetrical aspect to the tooth. There is no hypoflexus.

M^1-M^2 – As these element are fragile, only two could be measured. In M^1 the hypoflexus penetrates until half the width of the tooth; in M^2 the hypoflexus is somewhat shorter. The J-shaped parafossette is present in the labial part of the tooth.

D$_3$ – The dental pattern of this element consists of three lobes. The two posterior ones are connected to one another by an isthmus. The centroflexid can hardly be distinguished, and a hypoconulid is absent. The well-developed anteroflexid divides the anterior lobe in two. In one specimen there is a small, additional flexid in the antero-lingual part, which delimits a small lobe.

P$_3$ – The only specimen available is poorly preserved. Its morphology is similar to that of the same element from San Juan, with a rounded anteroconid, a distinct centroflexid and the mesoflexid with obtuse angles.

M$_1$-M$_2$ – Both specimens are too poorly preserved to allow a detailed description, or measuring.

Discussion – The *Prolagus* assemblages from San Juan and La Galocha 5 have the following features in common with *P. vasconiensis*; these characters distinguish them at the same time from *P. tobieni*:
In P$_3$ the anteroconid is generally rounded; the centroflexid is weak to well-developed; the mesoflexid shows always an obtuse angle; frequently a protoflexid is

present, which gives way to a protoconulid; the thickness of the enamel is fairly regular around the entire tooth.

In P^2 there is generally no hypoflexus.

In P^3 the long metaloph reaches the labial border of the tooth. The hypoflexus is relatively shallow in the upper cheek teeth.

The presence of two fossettes in P^4.

The presence of a relatively large, J-shaped fossette in M^1 and M^2.

The Spanish assemblages of *Prolagus vasconiensis* from San Juan and Navarrete (see López Martínez, 1984) are more evolved than that of Laugnac in the tendency towards the isolation of the hypoconulid of M_2. In Laugnac this cusp has a wide connection to the talonid, like in *Piezodus*.

López Martínez (1984) showed that in the Ramblian (Lower Miocene) faunal succession of the Calamocha area *Prolagus tobieni* López Martínez, 1977 may be the direct descendant of *P. vasconiensis*. The stratigraphical range of the latter species is zone Z (Lower Ramblian) and that of the former one from zone A (Upper Ramblian) to the end of the Aragonian (zone G) (López Martínez, 1977, 1984). In France *P. vasconiensis* is known from MN zone 2b to MN zone 3. In Germany this species is known from Schnaitheim and Wintershof-West (MN zone 3) where it co-exists with *P. schnaitheimensis* Tobien, 1975. It thus appears that *P. tobieni* is hitherto exclusively a Spanish form and contemporaneous with *P. vasconiensis* from Germany. The evolutionary trends in the *P. vasconiensis - P. tobieni* lineage are as follows (see also López Martínez, 1984): towards the development of a hypoflexus in P^2; towards a shortening of the metaloph in P^3; in P_3 towards an antero-posterior compression of the anteroconid, towards smaller centroflexids and protoflexids, and towards a mesoflexid at right or sharp angles.

In our present study we found another character, which can be used to distinguish between both species: the milk teeth of *P. vasconiensis* are relatively larger than those of *P. tobieni*. The mean value of the ratio LD_3/LP_3 of *Prolagus* from San Juan is 1.17, and in *P. vasconiensis* from Navarrete and Bouzigues it is 1.12 and 1.09 respectively (López Martínez, 1977). This ratio is 0.94 and 0.95 in *P. tobieni* from Villafeliche 2A and Escobosa respectively. Thus, in *P. vasconiensis* the D_3 is larger than P_3, and in *P. tobieni* it is the reverse.

All these features allow to refer the *Prolagus* populations from San Juan and La Galocha 5 to the species *P. vasconiensis*. Nevertheless, the *Prolagus* assemblages from San Juan and La Galocha 5 have larger teeth than all other hitherto described assemblages of *P. vasconiensis* from Spain and France. The minimum values for the length of P_3 and P^4-M^1 from San Juan and La Galocha 5 hardly show any overlap with the maximum values of *P. vasconiensis* from Spain and France (see Measurements). The teeth of *P. v. fortis* are also higher, proportionally to the general size increase.

Other distinctive features of the *Prolagus* from San Juan and La Galocha 5 with respect to all other *P. vasconiensis* assemblages, are the occasional presence of a hypoflexus in P^2, the absence of the metaflexus and the generally open mesoflexus of P^3. These features are however not sufficient for specific distinction. Therefore, the *Prolagus* from Huesca is assigned to *P. vasconiensis* on the basis of the dental

pattern, although it is of larger size. Because of the size difference and its separate geographic distribution, we consider these asssemblages as a distinct geographic subspecies.

It is possible that in the *Prolagus* assemblages from Navarrete and Ramblar 1 some large specimens may belong to our new subspecies. If both taxa would coexist in the same area, *P. v. fortis* should be considered as a separate species. But the scarcity of *Prolagus* teeth of large size in these assemblages from the Ramblian of Teruel does not permit any further confirmation.

The *Prolagus* assemblage from La Galocha 5 is only tentatively assigned to the subspecies from San Juan, as its size is even larger (see Measurements). This size difference is clear in the majority of the elements, but exceedingly so in P^2. This tooth is morphologically also different. In La Galocha 5 the metacone is considerably smaller than in San Juan, and the metastyle is larger, reaching the size of the protocone. This derived feature is not a common character of *Prolagus* species, and is only present in *P. major* López Martínez, 1977 from the Middle Miocene of the Calatayud-Teruel Basin. *P. major* is the largest mainland *Prolagus* species, and it is even of larger size than the teeth of the *Prolagus* assemblages from San Juan and La Galocha 5. The morphological and biometrical resemblances between *P. vasconiensis* aff. *fortis* and *P. major* suggest that the latter species may be a descendant of the former subspecies.

CASTORIDAE Gray, 1825

Palaeomys castoroides Kaup, 1832
Pl. 3, figs. 8-19.

Synonymy
Steneofiber castorinus Pomel, 1847, pl. 4.
Chalicomys eseri von Meyer, in Schlosser, 1884, pl. X, figs. 2, 3, 7, 8.
Steneofiber eseri (von Meyer), in Viret, 1929, pl. II, figs. 2, 4-8, non fig. 3.
'*Monosaulax*' *eseri* (von Meyer), in Stirton, 1935, figs. 82a-b.

Locality – San Juan.

Material and measurements

	Length				Width			
	n	min	mean	max	n	min	mean	max
D^4	2	4.2	4.3	4.4	2	4.2	4.25	4.3
$M^{1,2}$	2	4.5	4.55	4.6	2	4.4	4.7	5.0
M^3	1	——	3.7	——	1	——	4.0	——
P_4	1	——	6.1	——	1	——	5.2	——
$M_{1,2}$	4	4.0	4.5	5.0	4	4.2	4.5	5.8

Antero-posterior length of upper incisor: 5.5; transverse width of upper incisor: 4.6.

Description – The cheek teeth are fairly hypsodont, and crown cement is absent. In the upper cheek teeth the hypoflexus is situated in front of the paraflexus-parafossette. Three roots are present: two small labial ones and a big lingual root.

I^1 – It has a subtriangular section. The anterior enamel band is slightly convex. The bevel is sharp, with differential wear, and it consists of enamel exclusively in its most anterior part.

D^4 – The occlusal surface has a subquadrate profile. In some specimens the mesoflexus is open and J-shaped. The parafossette points forward. The composite mesoflexus-mesofossette generally surrounds the metafossette. The metafossette may be simple, or divided into two fossettes. An accessory small fossette may be present behind the parafossette. The hypoflexus penetrates about one third of the crown width into the molar. The hypostria is relatively long, and it nearly reaches the crown base.

$M^{1,2}$ – The occlusal surface has a subquadrate to circular outline. The flexuses are open in one unworn specimen. The arrangement and morphology of the flexuses and fossettes are more or less the same as in D^4. The hypoflexus is also as deep as in D^4. The hypostria is long, but it does not end as low as in D^4.

M^3 – The occlusal surface has a subtriangular outline. The mesoflexus and metaflexus are open. The flexus and the parafossette have an irregular outline. The hypostria is long, but it is shorter than in $M^{1,2}$. The mesostria is the longest labial stria.

I_1 – Its anterior face is slightly convex in tranverse direction. The bevel is very sharp and it forms a regular and slightly concave lingual surface.

P_4 – The occlusal outline is 8-shaped. The mesoflexid is the only open lingual flexid. The parafossettid, the mesoflexid and the metafossettid are parallel, and point toward the anto-labial side. The hypoflexid penetrates about one-third of the crown width into the molar, and it ends between the mesoflexid and the metafossettid. The mesostriid is short. The hypostriid is long and it ends near the crown base. Two roots are present.

$M_{1,2}$ – The occlusal surface has a subquadrate or an 8-shaped outline. The parafossettid is closed in all specimens, and it may be single or preceded by a smaller, parallel running anterofossettid. The mesostriid is longer than the metastriid, and both disappear with moderate wear. Lingual fossettids are generally parallel and point toward the antero-labial side. Occasionally a small accessory fossettid may be present in front of the metafossettid. The hypoflexid penetrates about two-fifth of the crown width into the molar, and it ends generally between the mesoflexid and metaflexid. The hypostriid is as long as in P_4. Three roots are present: two small anterior ones and a large posterior one.

Discussion – The Castoridae from San Juan correspond to a middle-sized beaver, well represented by isolated teeth and some postcranial elements.

Size has traditionally been the principal character to distinguish different castorid taxa. The majority of the Oligocene-Miocene European Castoridae was traditionally considered to belong to one evolutionary lineage, consisting of four successive taxa: a small-sized species (*'Steneofiber' dehmi* Freudenberg, 1941) from the

Oligocene-Early Miocene; a medium-sized species (*Steneofiber castorinus* Pomel, 1847) from the Early Miocene; a larger form (*Steneofiber depereti* Mayet, 1908) from the Early-Middle Miocene and a huge species (*Chalicomys jaegeri* Kaup, 1832) from the Middle-Late Miocene.

The Late Oligocene and Early Miocene European castorids were generally assigned to the genus *Steneofiber* Geoffroi, 1833, which was originally described from Langy (Allier, France), but a specific name was not given. *Steneofiber castorinus* Pomel, 1847 from St Gérand (Allier, France) is considered to be the type species of the genus. The material from St Gérand was described and figured by Gervais (1859) as *Steneofiber viciacensis*. This name is consequently a junior synonym of *S. castorinus*, but various authors (Filhol, 1879; Stehlin, 1914; Schreuder, 1929; Stehlin & Schaub, 1951; Bergounioux et al., 1964) have preferred to use *S. viciacensis*, as *S. castorinus* was only figured, and neither described nor diagnosed.

Some other authors (e.g. Schlosser, 1884; Viret, 1929; Hugueney, 1975) assigned the medium-sized Early Miocene castorid to *S. eseri* (von Meyer, 1846). The species *Chalicomys eseri* from the Middle Miocene Oeningen Marls near the Oerlingen Thal, Ulm, was named by von Meyer in 1846 (p. 474). Unfortunately von Meyer neither figured nor described this new species. In the same year 1846 the holotype of *C. eseri* was figured by Eser (Kuss, 1960, fide Hugueney, 1975), but the original material from Oeningen appeared to be lost and Stirton (1935) designated the mandible from the Early Miocene of Haslach figured by Schlosser (1884, pl. X, figs. 2, 3) to be the lectotype. The fauna of Haslach is of the same Early Miocene age as that of some localities from the region of St Gérand. The type locality of *Chalicomys eseri* von Meyer, 1846 is not of Early Miocene age as was generally supposed, but Middle Miocene (MN 6).

Stirton (1935) separated a French species (*Steneofiber castorinus*) from a German one (*Monosaulax eseri*) using the flattened or convex face of the lower and upper incisors as the main distinctive criterion. In spite of this, most authors agree that these middle-sized German and French castorids belong to a single species, and name it *S. eseri* (= *S. castorinus* = *S. viciacensis*).

According to Lavocat (1951) and our own observations, the German form appears to be slightly larger than the French one, but other distinctive features are not observed. The differences in the face of the incisors are weak and linked to the individual size. We do not consider these slight differences to be of taxonomic importance. As a matter of fact, our population from San Juan may be attributed to this species.

The correct name of this medium-sized species of San Juan, St Gérand and Haslach deserves further discussion, however. Kaup (1832) figured and described *Palaeomys castoroides* from the Early Miocene of Weisenau (Rhein Graben, Germany). Some castorids from this locality were also figured by Schlosser (1884, pl. X, figs. 7, 8) together with the Haslach material, and both assemblages were assigned to *Steneofiber* (*Chalicomys*) *eseri* von Meyer, 1846. The name *Palaeomys castoroides* Kaup would have priority according to the rules of zoological nomenclature, but these rules were not in use at that moment. Stirton (1935) assigned these two assemblages to two different genera, *Monosaulax eseri* from Haslach and

Palaeomys castoroides from Weisenau, because of the flattened or convex face of the incisor (see Stirton, 1935, figs. 82, 85). We do not consider this feature a valid criterion for taxonomic separation as stated above. Following Schlosser (1884), and according to the size, hypsodonty and mandibular characters, we consider the assemblages of Haslach and Weisenau to belong to one species. The name *Palaeomys castoroides* Kaup, 1832 has priority, and the type material from Weisenau was correctly described, figured and stored. In the hypothetical case that the Middle Miocene castorid from Oeningen, *Chalicomys eseri* von Meyer, 1846, would belong to the same species, it would be a junior synonym of *Palaeomys castoroides* Kaup, 1832.

Some authors (e.g. Stirton, 1935; Hünermann, 1966) following von Meyer (1838) considered *Palaeomys castoroides* Kaup, 1832 from the Lower Miocene of Weisenau to be a synonym of *Chalicomys jaegeri* Kaup, 1832 from the Upper Miocene of Eppelsheim. This was based on the erroneous supposition of a similar stratigraphic age for both samples, and also caused by the much worn type specimen of *P. castoroides* from Weisenau. However, both taxa may be easily distinguished from one another on the basis of size, stoutness, height of the mandible, hypsodonty, length of the striids, and the depth of the hypoflexus (compare e.g. Stirton, 1935, figs. 85 and 89). Crusafont et al. (1947) indicate the presence of an accessory fossette behind the parafossette as a difference between *Palaeomys* and *Chalicomys jaegeri*. We may add the P_4/M_1 length ratio as another diagnostic feature; in *P. castoroides* it is smaller than in *Chalicomys jaegeri* (Table 1). Moreover, there is an age difference of some 10 million years.

The generic name *Steneofiber* has been incorrectly used for *Chalicomys jaegeri* by many authors who followed Viret (1929). *Chalicomys jaegeri* is the type species of the genus *Chalicomys* Kaup, 1832 and it has consequently priority over *Steneofiber* Geoffroi, 1833.

Since a single lineage was already admitted by the majority of the authors cited above, it may be discussed if two generic names are justified. Unfortunately, very few characters were used in the systematic differentiation of this group. The distinguishing features are summarized in Table 1. Both genera (*Palaeomys* Kaup and *Chalicomys* Kaup) have been retained because of a major discontinuity in the character distribution.

Palaeomys dehmi (Freudenberg, 1941)
Pl. 3, figs. 1-5.

Synonym: Steneofiber eseri (von Meyer) in Viret, 1929

Locality — Santa Cilia, Province of Huesca.

Table 1. Diagnostic features of the Castoridae species of the Late Oligocene to Late Miocene of Europe (*Euroxenomys* and *Dipoides* excluded); measurements in mm.

Age	L. Oligocene, Oligocene/ Miocene boundary interval	E. Miocene	M. Miocene	L. Miocene
Species	*Palaeomys dehmi*	*P. castoroides*	*Chalicomys depereti*	*Ch. jaegeri*
Localities	Gaimersheim, Cournon, Chauffours, Sta Cilia, St Gérand	Weisenau, Haslach, Poncenat, San Juan, St Gérand	Artenay, Pontlevoy St Quirze, St. Gérand	Eppelsheim, Los Valles de Fuentidueña
Occlusal length: upper	—	17-19	—	28-32
lower	14.2-16.6	17-20	23-28	27-34
Length $P_4/M_{1,2}$	1.30	1.35-1.38	1.66	1.60
Depth of hypoflexid	1/3 width	1/3-2/5	2/5	2/5
Height of mandible under P_4	11	15-18	17-20	24
accessory fossettes: upper	many	one behind parafossette	rarely	none
lower	many	double parafossettid	in front of parafossettid	rarely in M_3 in front of parafossettid
Hypsod. min. L/H	0.65	0.50	—	0.30
Incisors ant. side	mainly convex	slightly convex	flattened	flattened

Material and measurements

	Length				Width			
	n	min	mean	max	n	min	mean	max
P4	1	—	4.5	—	1	—	5.0	—
M1,2	2	3.5	3.6	3.7	2	4.3	4.7	5.0
M3	1	—	3.6	—	1	—	3.9	—
M1,2	1	—	4.2	—	1	—	4.5	—

Description – In the upper cheek teeth the paraflexus is situated in front of the hypoflexus. All the flexuses point to the postero-lingual side. Three roots are present; two small labial ones, and one large lingual root.

P4 – The only available specimen lacks the posterior part. The parafossette surrounds a small posteriorly situated, accessory fossette. The mesofossette is J-shaped and it curves obliquely backwards.

M1,2 – The labial flexus is not preserved. The mesofossette curves to the postero-lingual side and encloses a small metafossette.

M3 – The occlusal surface has a subtriangular outline. The parafossette is subdivided into three small fossettes. A large accessory fossette is present behind these small fossettes. The mesoflexus curves to the postero-lingual side and it encloses the metafossette. The posterior end of the mesoflexus is isolated by an isthmus (metalophule I, according to Hugueney, 1975), and it is connected to the metafossette.

$M_{1,2}$ – The occlusal surface has a subquadrate circumference. The hypoflexid ends between the mesofossettid and the metafossettid. The lingual fossettids point slightly to the antero-labial side. The mesoflexid forms a right angle with the longitudinal axis of the tooth. Two small anterior roots and a large posterior one are present.

Discussion – The small-sized castorid from Santa Cilia agrees in size, hypsodonty and morphology with the castorids from Cournon and Chauffours, which were described as *Steneofiber antiquus* by Lavocat (1951). Hugueney (1975) attributed this material to the German species *Steneofiber dehmi* Freudenberg, 1941 from the Late Oligocene of Gaimersheim. Some adult specimens from the mixed assemblages of St Gérand (the ancient collections of this 'locality' consist of fossils from levels of different age and from different quarries) figured by Viret (1929, pl. II, fig. 3) under the name *Steneofiber eseri* are rather small, and may be attributed to that species too. It differs clearly from the juvenile forms described as *Steneofiber julieni* from the same region by Viret (1925) that may be considered as a junior synonym of the medium-sized castorid species of the Early Miocene, *Palaeomys castoroides* (= *Steneofiber eseri*), as Viret (1929) recognized.

Castoridae gen. et sp. indet.
Pl. 3, figs. 6-7.

Locality — Santa Cilia, Province of Huesca.

Material and measurements — 1 $M^{1,2}$ (L = 3; W = 3.6; H = 6.5; L/H = 0.46).

Description — The only available specimen differs from the other beaver of Santa Cilia by its smaller size and its stronger hypsodonty. The parafossette is situated in front of the hypoflexus. An accessory fossette is present behind the parafossette. The mesofossette curves towards the metafossette, which in turn is subdivided into two fossettes.The hypostria is long, and it ends near the crown basis. Two small labial roots and a large lingual one are present.

Discussion — The smallest castorid from Santa Cilia, represented by one tooth only, cannot be assigned to any known taxon, and one single specimen does not serve as a basis for the creation of a new genus and species. Its hypsodonty is too large (L/H = 0.45) in order to fit in *Palaeomys*, and there are no sufficient criteria for a generic assignment. This tooth is the first indication of a second castorid lineage in the Late Oligocene - Early Miocene of Europe.

SCIURIDAE Gray, 1821

Palaeosciurus feignouxi Pomel, 1853
Pl. 4, fig. 1.

Locality — Santa Cilia, Province of Huesca.

Material and measurements — 1 M^2 (20.2 × 24.0).

Description — The large and straight anteroloph reaches the base of the paracone. The protoloph curves slightly backwards. The mesostyl is connected to the paracone, thus forming an ectoloph-like ridge. Anteroconule and protoconule are absent. The metacone is more robust than the metaconule. This latter cusp meets the protocone. The posteroloph is low and short.

Discussion — The size and morphology of this single specimen agree well with *P. feignouxi* from La Paillade and Caunelles (Aguilar, 1974), and from Navarrete del Rio (Cuenca Bescós, 1988).

Heteroxerus paulhiacensis Black, 1965
Pl. 4, figs. 2-15.

Locality — Santa Cilia, Province of Huesca.

Material and measurements

| | Length | | | | Width | | | |
	n	min	mean	max	n	min	mean	max
D⁴	0	—	—	—	1	—	14.8	—
M¹	2	12.9	14.0	15.2	2	15.9	17.2	18.5
M²	10	14.1	15.0	16.3	9	17.0	18.5	19.2
M³	4	16.3	16.6	17.0	4	15.9	16.5	17.8
D₄	1	—	11.5	—	1	—	9.6	—
P₄	2	12.2	12.4	12.6	2	10.7	10.9	11.1
M₁	5	14.4	14.7	15.5	5	12.2	14.1	15.2
M₂	2	14.4	14.8	15.2	1	—	15.9	—
M₃	3	17.0	17.7	18.1	3	14.4	15.0	15.5

Description

D^4 – Two poorly preserved specimens are present. A low anteroloph is present, and the metacone and metaconule are of the same size. The metaconule is connected to both protocone and hypoconule. The posteroloph is very low.

P^4 – The anteroloph is very low. One specimen has an anteroconule. The metacone and metaconule are of similar size. In one specimen a very low connection is present between the metaconule and the protocone. The low posteroloph ascends to contact the metacone.

$M^{1,2}$ – The low anteroloph shows a small anteroconule. A small protoconule is also present. The metaconule is slightly larger than the metacone. A very thin and low connection is present between the metaconule and the protocone.

M^3 – The anteroloph is low. The connection between the protocone and protoconule is weakly developed. A mesostyl is present. The posterior part is bordered by a continuous wall in which the hypoconule is discernable.

P_4 – The low and small anteroconid is connected to the protoconid. The exolophid is straight or slightly curved. The posterior part of the tooth is bordered by a continuous wall in which hypoconulid, entoconid and mesostylid are poorly individualized.

M_1 – The low anteroconid is connected to the protoconid. The metalophid is complete. The sinusid is narrow and deep. The curved exolophid shows a small mesoconid in 2 out of 5 specimens. A mesostylid is present. The low entolophid is interrupted in 2 specimens. The hypoconulid and entoconid are connected by the posterolophid.

M_2 – Basically its pattern is similar to that of M_1, but the anteroconid is somewhat smaller. The entolophid is complete in 2 out of 5 specimens.

M_3 – The anteroconid is absent. The metalophid is reduced. The exolophid is strongly curved. In the posterior wall the entoconid is present.

Discussion – The size of the teeth of *H. paulhiacensis* from Santa Cilia is slightly larger than that of the same species from Autol (Cuenca Bescós, 1985). It coincides more or less with that of the same species from Coderet (Hugueney, 1969), but the

third molars are considerably larger in Santa Cilia.

Heteroxerus cf. *rubricati* Crusafont, de Villalta & Truyols,1955

Locality – San Juan.

Material and measurements – 2 D⁴ (13.7 × 14.4, 13.8 × 14.9).

Description – One specimen has a protoconule. The metaconule is connected to the protocone by a thin ridge in one specimen, and in the other one this connection is absent.

Locality – La Galocha 5.

Material and measurements – 1 M² (16.8 × 19.7).

Description – The anteroloph is separated from the paracone. The metaloph points towards the protocone and it meets this cusp by means of a narrow ridge. The metaconule is connected to the posteroloph. A very small metastyl is present.

CRICETIDAE Rochebrune, 1883
EUCRICETODONTINAE Mein & Freudenthal, 1971

Eucricetodon aff. *aquitanicus* Baudelot & de Boni, 1968
Pl. 5, figs. 1-5.

Locality – San Juan.

Material and measurements
2 M² (18.9 × 16.6, 18.5 × 16.3); 1 M³ (— × 13.3);
2 M₁ (22.6 × 15.9, 21.8 × 15.5); 2M₂(19.6 × 16.6).

Description
      M² – The lingual anteroloph is very small, whereas the well-developed labial anteroloph is connected to the base of the paracone. A short, obliquely backwards pointing mesoloph is present. The paracone has a small posterior spur. The deep and narrow sinus points obliquely forward. One specimen lacks the posterosinus, the other one has a small one.
      M³ – The lingual anteroloph is absent. The labial one is well developed and it is connected to the base of the paracone. The long, oblique and backwards pointing mesoloph reaches the labial border of the tooth.
      M₁ – From the small anteroconid two cingulum ridges descend backwards. The labial one is longer than the lingual one, and it closes the wide protosinusid. The anterolophulid and metalophulid point obliquely forward. A mesolophid is

absent. The posterolophid is connected to the base of the entoconid, thus closing the posterosinusid.

M_2 – A small lingual anterolophid is present. The labial anterolophid descends to reach the anterior part of the protoconid, thus closing the protosinusid. The protolophulid and metalophulid point obliquely forward. A very short mesolophid is present. The sinusid is transverse. The posterolophid widens at the place of the hypoconulid, and it is connected halfway to the entoconid, thus enclosing the deep posterosinusid.

Discussion – See below.

Eucricetodon sp.
Pl. 5, fig. 6.

Locality – San Juan.

Material and measurements: 1 M^1 (20.0 × —).

Description – The specimen is damaged at the postero-labial part. The anterocone is divided into two cusps by a deep furrow. The anterolophule is connected to the base of the lingual cusp of the anterocone. The anterosinus is enclosed by a low cingulum ridge. The entoloph is wide and short, and it is interrupted behind the protocone. A mesoloph is absent.

Discussion of the Cricetidae – The size and dental pattern of *E.* aff. *aquitanicus* from San Juan agree with those of the same species from Navarrete and Ramblar 1 from the Ramblian of the Calamocha area in the Calatayud-Teruel Basin (Sesé, 1987).

The dental pattern of the M^1 of *Eucricetodon* sp. from San Juan would agree with an advanced evolutionary stage of the supposed *E. aquitanicus* - *E. infralactorensis* lineage: the perfectly subdivided anterocone, the backward pointing ridges and the absence of a mesoloph. On the other hand, the size of this specimen is definitely smaller than that found in the species of this lineage.

The existence of representatives of two different *Eucricetodon* lineages in a single locality was observed by Daams (1976) in Cetina de Aragon. The smaller one of the two is *E. gerandianus*, the larger one *E. cetinensis*. *E.* aff. *aquitanicus* from San Juan would fit in the hitherto hypothetical *E. gerandianus* - *E. infralactorensis* lineage, but *E.* sp. would represent a third lineage because of its small size.

EOMYIDAE Depéret & Douxami, 1902

Rhodanomys oscensis Alvarez Sierra, 1987

Locality —Santa Cilia, Province of Huesca.

Material and measurements

	Length				Width			
	n	min	mean	max	n	min	mean	max
D^4	98	8.7	9.8	11.4	99	8.8	10.0	11.2
P^4	72	8.3	10.1	11.8	72	9.5	10.7	11.8
M^1	101	9.3	10.9	11.7	90	10.4	12.2	13.6
M^2	98	8.0	9.0	10.1	95	10.1	11.3	12.6
M^3	50	7.0	7.6	8.5	50	8.2	9.1	10.3
D_4	57	9.8	11.2	12.8	63	7.2	8.3	9.3
P_4	49	7.8	8.8	10.0	46	7.7	8.9	10.1
M_{1-2}	194	8.6	10.5	12.2	195	8.8	10.8	12.7
M_3	75	7.5	9.0	10.0	73	7.8	8.7	10.1

Discussion – *Rhodanomys oscensis* Alvarez Sierra, 1987 from Santa Cilia (its type locality) was described in a detailed study on the Upper Oligocene and Lower Miocene Eomyidae from Spain. Therefore, only some important morphological features are mentioned here.

This species is characterized by a mixture of specimens with reduced meso-loph(id)s and others in which these ridges are well developed. 40 % of the M^1, none of the M^2 and 8 % of the M^3 have a long mesoloph reaching the labial border of the molar. 55 % of the $M_{1,2}$ have a mesolophid, but in the majority of these specimens this ridge is reduced.

In the upper cheek teeth the mesoloph is reduced in 4 % of the D^4, in 27 % of the M^1 and in 42 % of M^2. This ridge is absent in 40 % of the D^4, in 33 % of the M^1 and in 54 % of the M^2.

Crusafont et al. (1966) cited *Ritteneria manca* Stehlin & Schaub, 1951 from Santa Cilia, and Agustí et al. (1985) assigned the assemblage to *Rhodanomys schlosseri* Depéret & Douxami 1902, on the basis of small collections stored at the Sabadell Museum. The new and large collections of the *Rhodanomys-Ritteneria* group (Alvarez Sierra, 1987) shed new light on its variation, which made her re-define these genera and distinguish two additional new species. Several authors (Stehlin & Schaub, 1951; Hugueney, 1969, 1974; Fahlbusch, 1970, 1973, 1979; Aguilar, 1974; Daams, 1976; Alvarez Sierra, 1987) propose a phylogenetic relation between *Rhodanomys* and *Ritteneria*, characterized by evolutionary trends such as size decrease, simplification of the dental pattern and increase of hypsodonty. *Rh. oscensis* is considered as the step between *Rh. schlosseri* and *Ritteneria molinae* Alvarez Sierra (1987), the latter one being the ancestor of *R. manca*.

Hitherto, no other assemblages comparable to the one from Santa Cilia are known. Hugueney (1974) mentions *Rh. schlosseri* from La Carrière Cluzel, and notes that the longitudinal ridge of the lower molars is generally reduced and that the mesoloph of the upper molars is long. This assemblage would be more evolved than other ones of *Rh. schlosseri* but the well-developed mesolophs of $M^{1,2}$ do not coincide with the more simple dental pattern of those of *Rh. oscensis*.

Eomyidae gen. et sp. indet.
Pl. 5, fig. 14.

Locality – San Juan.

Material and measurements – 1 P_4 (8.2 × 8.0).

Description – The anterolophid and the posterolophid are absent. The longitudinal ridge is complete and it is situated in the labial half of the tooth.

Discussion – Unfortunately the only element found of Eomyidae gen. indet. is a P_4. It falls within the range of variation of both *Rhodanomys* and *Ritteneria*, thus hampering us to give a more precise determination. It belongs however to one of these genera.

Pseudotheridomys sp.
Pl. 5, figs. 7-13.

Locality – San Juan.

Material and measurements

	Length				Width			
	n	min	mean	max	n	min	mean	max
D⁴	1	——	11.3	——	1	——	12.1	——
M¹	1	——	11.9	——	1	——	13.3	——
M³	2	8.2	8.3	8.4	3	10.8	11.1	11.4
D₄	1	——	13.1	——	1	——	9.5	——
M₁,₂	2	11.1	11.4	11.7	3	10.8	11.1	11.5

Description
    D⁴ – The anteroloph and the protoloph are labially separated. The longitudinal ridge is complete, the mesoloph is long and the sinus points strongly forwards.
    M¹ – Antero- and protoloph are labially separated. The mesoloph is long. The meta- and posteroloph form a composite ellipse. The sinus points strongly forwards.
    M³ – The antero- and posteroloph are both labially and lingually connected. In one specimen there is a postero-lingual ridge in the central part of the tooth. In the other specimen there are two more or less transverse ridges, which join each other in the middle of the tooth through a small longitudinal ridge.
    D₄ – The anterolophid is lingually and labially connected to the metalophid. The longitudinal ridge is complete. Lingually the hypolophid is separated from the posterolophid. The sinusid points backwards.
    M₁,₂ – The anterolophid is long or short; lingually it is connected to the

metalophid and labially as well, with one exception. The longitudinal ridge is always present, and the mesolophid and the hypolophid are more or less parallel ridges. The sinusid points slightly backwards.

Discussion of the Eomyidae from San Juan — *Pseudotheridomys* sp. is intermediate in size between *P. parvulus* (Schlosser, 1884) from the Lower Miocene of France and Germany and *P. fejfari* Alvarez Sierra & Daams, 1987 from the Lower Miocene of Spain (Alvarez Sierra & Daams, 1987). Morphologically it resembles both *P. parvulus* and *P. fejfari* because of the similar number of ridges in both upper and lower molars, and because of the lophodont pattern in which the cusps are not or hardly distinct. Only the two M^3 present have a somewhat deviating pattern with three or four transverse ridges respectively in stead of the usual five in *Pseudotheridomys*. We do however consider *Pseudotheridomys* sp. from San Juan as a descendant of *P. parvulus* from the Lower Miocene of France and as an ancestor of *P. fejfari* from the Lower Miocene of Moratilla, Rubielos de Mora and Bañon 11. A specific determination is not given because of the scarcity of the material.

<div align="center">

Ligerimys cf. *fahlbuschi* Alvarez Sierra, 1987
Pl. 5, figs. 15-17.

</div>

Locality — La Galocha 5.

Material and measurements — 2 P_4 (12.1 × 10.6, 12.2 × 11.0); 1 $M_{1,2}$ (12.0 × 11.8).

Description

$M^{1,2}$ — The only specimen has a damaged labial border. In the longitudinal ridge, between the proto- and metaloph, there is a little cusp.

P_4 — The anterolophid is long, and it is lingually and labially connected to the metalophid. The mesolophid reaches the lingual border, and the sinusid points slightly backwards.

$M_{1,2}$ — The anterolophid is connected to the metalophid at both ends. The mesolophid is long, and its height decreases towards the lingual border. The sinusid points backwards.

Discussion — The small *Ligerimys* assemblage from La Galocha 5 shows conservative features such as the complete mesolophids and well-developed anterolophids. Two Spanish species represent these characteristics: *L. antiquus* Fahlbusch, 1970 and *L. fahlbuschi* Alvarez Sierra, 1987. These two Ramblian species differ in size, the latter one being larger, and in the direction of the mesosinusid and sinusid of the lower molars. In *L. antiquus*, these two valleys form an almost straight line, whereas in *L. fahlbuschi* the mesosinusid is at right angles to the longitudinal axis of the tooth, and the sinusid makes a relatively sharp angle with the same axis. Our small assemblage from La Galocha 5 resembles most, both morphologically and metrically, *L. fahlbuschi* from the Ramblian of the Calatayud-Teruel Basin, but the scar-

city of the material does not permit a more exact specific identification.

GLIRIDAE Thomas, 1897
MYOMIMINAE Daams, 1981

Peridyromys murinus (Pomel, 1853)

Material and measurements

	Length				Width			
	n	min	mean	max	n	min	mean	max
Santa Cilia								
P⁴	4	7.1	7.3	7.8	4	7.9	8.5	8.9
M¹	20	8.8	9.6	11.1	18	10.0	10.7	11.5
M²	16	8.4	9.1	10.4	15	9.6	10.6	11.1
P₄	2	7.1	7.1	7.1	2	6.8	6.9	7.1
M₁	14	9.0	9.6	10.0	14	8.9	9.6	10.3
M₂	17	9.0	9.7	10.6	16	8.7	9.5	10.7
M₃	3	7.7	7.8	8.1	2	8.4	8.6	8.8
San Juan								
M¹˒²	18	8.9	9.5	10.2	17	9.1	11.0	12.5
M₁	6	9.5	9.8	10.5	5	8.5	9.5	10.3
M₂	11	9.2	10.1	10.4	11	8.7	9.8	10.6
M₃	2	9.0	9.1	9.2	2	8.6	8.9	9.2
La Galocha 5								
D⁴	2	7.6	8.1	8.5	2	6.3	6.7	7.1
P⁴	2	7.4	7.5	7.6	2	8.6	9.0	9.4
M¹˒²	18	9.0	9.8	10.8	16	9.5	10.9	12.4
M³	2	7.1	7.4	7.7	2	8.7	9.2	9.7
P₄	4	6.8	7.2	7.7	4	5.5	6.6	7.4
M₁	5	9.5	10.3	11.0	5	9.1	9.5	9.9
M₂	9	9.9	10.4	10.8	8	9.1	10.0	10.8
M₃	4	9.4	9.9	10.1	3	8.2	8.4	8.6

Discussion – A detailed description of this well-known species is not given here, although a distribution of the morphotypes of M1,2 such as defined by Daams (1981) is shown (see Figs. 8 and 9). For comparison data from Cetina de Aragon, Bouzigues (see Daams, 1981) and the unpublished fauna of Agreda (Zone A, Upper Ramblian) are given. It appears that the majority of the M¹˒² belongs to type C (both centrolophs present), and that specimens with one extra ridge (type D) are well-represented in La Galocha 5. Specimens with the anterior centroloph only (type B) are common in all studied Spanish localities, but not in Bouzigues. In that respect *P. murinus* from La Galocha 5 resembles more the same species from France than its Spanish representatives. In Santa Cilia, San Juan and La Galocha 5 the anterior centroloph is longer than the posterior one in all M¹˒², whereas in Bouzigues this situation is the reverse in 19 % of the specimens (see Daams, 1981).

Morphotypes $M^{1,2}$ / Localities				N
Agreda	31	66	3	235
La Galocha 5	10	60	30	20
San Juan	26	74	-	19
Bouzigues	1	82	17	403
Cetina	21	71	8	42
Santa Cilia	24	76	-	37

Fig. 8. Distribution of morphotypes of $M^{1,2}$ of *Peridyromys murinus* in percentages.

As to the lower molars, specimens with a posterior extra ridge (type 2) are scarce in all Spanish assemblages, whereas specimens of this type are more frequent in Bouzigues.

Morphotypes $M_{1,2}$ / Localities			N
Agreda	99.5	0.5	209
La Galocha 5	95	5	19
San Juan	100	-	17
Bouzigues	70	30	316
Cetina	93	7	55
Santa Cilia	94	6	32

Fig. 9. Distribution of morphotypes of $M_{1,2}$ of *Peridyromys murinus* in percentages.

Peridyromys turbatus sp. nov.
Pl. 6, figs. 1-25.

Type locality – San Juan.
Holotype – M_2 dext.,no. SJ 113, Pl. 6, fig. 20.
Derivatio nominis – Latin *turbatus* (from *urbare*) chaotic, because of the chaotical dental pattern.

Diagnosis – A *Peridyromys* species with well-developed centrolophs and one or two extra ridges in the upper molars. M^2 has a more complex dental pattern than M^1 and M^3. The ridge pattern in the central valley of the upper molars may be chaotical. The lower molars have one or two extra ridges, which are chaotically arranged in many specimens. M_1, M_2 and M_3 have a comparable complex ridge pattern.

Differential diagnosis – P. *turbatus* sp. nov. differs from *P. jaegeri* Aguilar, 1974 from the Lower Miocene of Les Cévennes and La Paillade by: its slightly larger P^4 and M_3; its shorter centrolophid of the lower molars; the absence of accessory ridges between the anterior and posterior centroloph; its obliquely V-shaped trigone in M^1, M^2 and M^3; its chaotical ridge pattern.

P. *turbatus* differs from *P. murinus* (Pomel, 1853) from the Lower Miocene of Spain and France by its larger size and its more complicated and chaotical dental pattern.

P. *turbatus* differs from *P. aquatilis* de Bruijn & Moltzer, 1974 from the Lower Miocene of Rubielos de Mora by its larger size and by its more chaotical dental pattern.

P. *turbatus* differs from *Vasseuromys*? *priscus* de Bonis, 1973 from the Lower Miocene of Santa Cilia by: the shorter centrolophid in the lower molars; the absence of an endolophid in M_1 and M_3; the continuous U-shaped pattern formed by mesolophid and posterolophid; the V-shaped trigone of M^2; the absence of an endoloph; the shorter anterior centroloph of the upper molars; the more chaotical dental pattern.

Material and measurements

| | Length | | | | Width | | | |
	n	min	mean	max	n	min	mean	max
D^4	4	8.0	8.6	9.2	4	8.4	9.0	9.5
P^4	21	7.7	8.4	9.5	21	8.9	9.8	10.7
$M^{1,2}$	42	9.3	10.6	11.7	35	10.8	12.2	13.4
M^3	21	7.7	8.6	9.2	22	9.6	10.9	11.8
P_4	19	7.3	8.1	9.2	21	6.7	7.8	8.4
M_1	19	10.3	10.8	11.8	14	8.4	10.0	11.4
M_2	19	11.1	11.8	12.4	19	10.3	11.6	12.4
M_3	24	9.5	10.9	11.6	24	9.4	10.2	10.8

Description

D[4] — The long anteroloph is connected to the paracone, but it is isolated from the protocone. Two centrolophs are present, of which the posterior one is longer than the anterior one. The centrolophs are connected to the para- and metacone respectively. The well-developed posteroloph is connected to both proto- and metacone. One specimen has an extra ridge between the posterior centroloph and the metaloph.

P[4] — The well-developed anteroloph is generally connected to the paracone, or a narrow furrow may be present. The anteroloph is separated from the protocone. Four specimens have only one centroloph, the remaining 17 have two centrolophs of which the posterior one is generally the longest. In 11 specimens the centrolophs are fused in the central valley to form an oblique V-pattern. The centrolophs are connected to the paracone and metacone respectively. The posteroloph is well developed and it is separated from the protocone in nearly all specimens. Labially the posteroloph is connected to the metacone, or a tiny and shallow furrow may be present.

M[1,2] — An endoloph is absent, but in 3 out of 42 specimens the lingual end of the anteroloph is connected to the protocone below the occlusal surface. The protocone is situated near the postero-lingual border, thus causing an oblique V-shaped trigone. The anteroloph is labially connected to the paracone or a tiny and shallow furrow may be present. The two centrolophs are always present. The anterior one may be longer or shorter than the posterior one, they may fuse, or they may be interrupted. Eighteen specimens have two extra ridges and 23 have only one. When two extra ridges are present, the ridge pattern in the central valley tends to be chaotical. In specimens with a more regular ridge pattern the centrolophs are connected to the para- and metacone respectively, but in the more chaotical specimens extra ridges and/or centrolophs may end free at the labial border. The M[1] is on the average more simple than the M[2], although a strict distinction between these two elements is not always possible. Nineteen M[1] have one extra ridge, and only 3 have two accessory ridges. In M[2] this is the reverse; 4 specimens have only one extra ridge, and 15 teeth have two. The posteroloph is generally connected to the protocone, although a shallow and tiny furrow may be present. This is also true for the labial connection of the posteroloph.

M[3] — The dental pattern agrees basically with that of M[1,2], although it is somewhat more simple. Specimens with two extra ridges are absent, 20 specimens have one accessory ridge, and two specimens lack extra ridges.

P$_4$ — The anterior part exhibits a chaotical ridge pattern. The posterior part is more regular and presents the mesolophid and posterolophid forming a U-shaped ridge, enclosing an extra ridge in most specimens. This accessory ridge is generally connected to the entoconid.

M$_1$ — The anterolophid is labially connected to the protoconid or a tiny furrow may be present. The metalophid is straight and isolated from the metaconid. The centrolophid is relatively long, but it does not reach the labial border. It may join the metalophid at 25-30 % of the molar width from the labial border. The mesolophid and posterolophid meet at the entoconid, thus forming a U-shaped ridge

enclosing the posterior accessory ridge. In 12 out of 20 specimens this extra ridge is connected to the entoconid. Irregularly shaped extra ridges may be present in the anterior part of the tooth at either side of the centrolophid. Only 2 out of 20 specimens lack the anterior extra ridges. In 2 specimens an endolophid is present, interrupted by a tiny and shallow furrow between centrolophid and mesolophid. Two roots are present.

M_2 – The dental pattern of this element agrees basically with that of M_1. In 10 out of 20 specimens the posterior extra ridge is connected to the entoconid. The anterior part shows generally a chaotic ridge pattern. An endolophid is present in 2 specimens, although it is interrupted by a narrow and shallow furrow between the centrolophid and the mesolophid.

M_3 – This element is not as reduced as in other Gliridae species. The dental pattern corresponds basically to that of $M_{1,2}$. The posterior extra ridge is connected to the entoconid in 19 out of 26 specimens. The chaotical ridge pattern of the anterior part is also present, and the complexity is of the same order as that of M_1 and M_2.

Discussion – The only species showing a resemblance to *P. turbatus* is *P. jaegeri* as far as the general complexity is concerned. *P. jaegeri* is known from the Lower Miocene of France in older levels than those of *P. turbatus*. However, various features, such as the chaotical ridge pattern and the obliquely V-shaped trigone, make it possible to differentiate them.

P. turbatus differs from *P. murinus* by: a slightly larger size although there is an overlap; a more complex and chaotical ridge pattern; in *P. turbatus* the M^2 has the most complex ridge pattern of the three upper molars. In *P. murinus* M^1, M^2, and M^3 are of the same complexity; in *P. turbatus* the relative length of the centrolophs is variable. In *P. murinus* from Spain the anterior centroloph is nearly always longer than the posterior one, and if one centroloph is absent, it is always the posterior one; *P. turbatus* has longer centrolophids in the lower molars than *P. murinus*. Both species have the oblique V-shaped trigone in common. *P. murinus* is a common dormouse in the Lower Miocene of France and Spain, and it may be considered the ancestor of various other Myomiminae species such as *Peridyromys jaegeri, Peridyromys aquatilis* (de Bruijn & Moltzer, 1974) and *Armantomys bijmai* (Lacomba & Martínez-Salanova, 1988). Theoretically either *P. jaegeri* or *P. murinus* may be the ancestor of *P. turbatus*, but insufficient documentation hampers a more founded conclusion. A hitherto unpublished fauna from zone Y1 of the Loranca Basin contains a *Peridyromys* assemblage intermediate in morphology between *P. murinus* and *P. turbatus*. Therefore we are inclined to consider it more probable that *P. murinus* be the ancestor of *P. turbatus*. A descendant of *P. turbatus* may be *Peridyromys* aff. *jaegeri* from the Lower Aragonian of the Daroca-Villafeliche area (Daams, 1989). *P.* aff. *jaegeri* has also a relatively chaotical ridge pattern in various specimens, the trigone of the $M^{1,2}$ is obliquely V-shaped as in *P. turbatus*, M^2 is also the most complex element of the three molars, and the size of the teeth is only slightly larger.

'*Peridyromys' brailloni* (Thaler, 1966)
Pl. 7, figs. 1-17.

Locality – La Galocha 5.

Material and measurements

	Length				Width			
	n	min	mean	max	n	min	mean	max
D^4	3	8.1	8.4	8.7	3	8.4	9.3	10.1
P^4	4	9.3	9.6	10.4	4	10.4	10.9	11.8
M^1	3	13.5	13.9	14.3	3	14.0	14.7	15.2
M^2	6	12.8	13.8	14.9	6	13.2	14.9	15.9
M^3	5	10.6	11.3	12.7	5	12.4	13.1	13.9
D_4	3	8.5	8.8	9.3	3	5.7	6.0	6.5
P_4	1	—	9.9	—	2	8.5	9.0	9.4
M_1	3	13.9	14.5	14.9	4	12.5	13.0	13.7
M_2	5	14.4	15.1	15.5	5	12.8	13.4	13.7
M_3	2	13.1	13.2	13.2	2	9.6	10.8	12.0

Description

D^4 – A medium-sized to long, isolated anteroloph and one isolated, long centroloph are present. The posteroloph is long, connected to the protocone, and separated from the metacone by a shallow furrow.

P^4 – The anteroloph is long and forms an isolated ridge. The protoloph and metaloph join the protocone more or less separately, thus forming a narrow U-pattern. One isolated centroloph is present. The well-developed posteroloph is connected to the protocone, and it is separated from the metacone by a narrow furrow.

$M^{1,2}$ – The valleys are generally wide and shallow. The anteroloph forms an isolated ridge. Two centrolophs are present and they are connected to the paracone and metacone respectively. The anterior centroloph is longer than the posterior one. In 3 out of 9 specimens the centrolophs fuse to form a Y-pattern. Extra ridges are present between the protoloph and the anterior centroloph and between the metaloph and the posterior centroloph. Two specimens lack extra ridges, 4 have one accessory ridge, and 3 have two extra ones. One specimen has three extra ridges, the third one being situated between the centrolophs. The posteroloph is connected to the protocone, and it is separated from the metacone by a shallow furrow.

M^3 – The outline of this element is variable. It may be a robust trapezoidal form with diverging ridges (Pl. 7, fig. 6) or it may be a narrow trapezoid with parallel running ones (Pl. 7, fig. 10). The anteroloph is connected to the protocone below the occlusal surface. Labially it is either separated from or connected to the paracone. The posterior centroloph is longer than the anterior one. Three out of 5 specimens have an extra ridge between the posterior centroloph and the metaloph; the other 2 specimens lack extra ridges. The posteroloph joins the endoloph and it is

labially isolated from the metacone.

D_4 – Its dental morphology consists of a chaotical pattern of ridges and cusps (Pl. 7, fig. 5).

P_4 – The anterolophid, metalophid and centrolophid form a composite circular ridge. The mesolophid is connected to the posterolophid at the entoconid. An extra ridge is absent.

M_1 – The anterolophid is connected to the protoconid. The metalophid is separated from the metaconid in 3 out of 4 specimens. The centrolophid is long without reaching the labial border; in 1 specimen its labial end is connected to the metalophid. The mesolophid and posterolophid meet at the entoconid. A long posterior extra ridge is present in all 6 specimens, and it is connected to the entoconid in 3 cases. Three out of 5 specimens have an extra ridge between the anterolophid and the metalophid.

M_2 – The dental pattern is basically similar to that of M_1. The metalophid does not reach the metaconid in the 6 specimens in which this feature is visible. The anterolophid does not meet the protoconid. The long posterior extra ridge does not join the entoconid. The anterior extra ridge is present in all specimens.

M_3 – The anterolophid joins the protoconid below the occlusal surface. The metalophid is separated from the metaconid. The centrolophid is short to medium long. A posterior, isolated, extra ridge and the anterior extra ridge are present in all specimens.

Locality – San Juan.

Material and measurements

	Length				Width			
	n	min	mean	max	n	min	mean	max
D^4	1	—	8.0	—	1	—	8.9	—
M^2	1	—	14.6	—	1	—	15.9	—
M_1	3	12.8	13.4	13.9	3	11.9	12.5	12.9
M_3	1	—	12.4	—	1	—	11.0	—

Description – The few teeth agree rather well with those from La Galocha 5. The M^2 has fused centrolophs forming a Y-pattern, and it has only one tiny extra ridge behind the posterior centroloph. One out of 4 M_1 has the posterior extra ridge connected to the entoconid, and one out of 3 lacks the anterior extra ridge. In M_3 the mesolophid and posterolophid are separated at the entoconid by a deep furrow.

Discussion – The material from La Galocha 5 and San Juan agrees well with that from the type locality of Bouzigues, present in the collections of the University of Utrecht. It also agrees with '*P.*' *brailloni* described by Aguilar (1974) from Bouzigues. The well-developed, relatively wide anteroloph, the wide and shallow valleys, and the relatively low and wide ridges are characteristic for the species.

Thaler (1966) described this species as '*Dryomys*' *brailloni*, Aguilar (1974) assigned it to *Peridyromys* and Daams (1974) to *Pseudodryomys*. We think that none of these genus names should be applied to this species. *Dryomys* is of course excluded by the presence of an endoloph. We would prefer to use *Pseudodryomys* only for those species with wide and robust ridges and relatively deep valleys such as in *P. ibericus*. Whether or not *P. simplicidens* and *P. robustus* should also be included in *Pseudodryomys* is a question that will not be dealt with in this paper. We do not like to use *Peridyromys* for *brailloni* either. We would apply *Peridyromys* only to those species of relatively small size, with wide ridges and relatively hypsodont teeth. '*P. brailloni*' has relatively brachiodont molars. But before creating a new genus name for this species, it deserves recommendation to compare ridge shape, hypsodonty and other diagnostic features of genera such as *Pseudodryomys*, *Peridyromys*, *Miodyromys*, etc. A study on this subject is presently being carried out by one of us (R.D.).

Hitherto '*P.*' *brailloni* has not been cited from the Lower Miocene of Spain. It is surprising that this species is so well represented in La Galocha 5 (32 %), whereas in more or less contemporaneous faunas from the Calatayud-Teruel Basin this species is not mentioned. Recent, unpublished studies revealed the presence of this species in the above cited basin, however, but it is always present in low frequencies. In France it has been cited from its type locality Bouzigues (Thaler, 1966; Aguilar, 1974) and from Laugnac (de Bonis, 1973). In the latter locality this species has considerably smaller teeth than in Bouzigues, however. According to Aguilar (1974) there are morphological differences as well. Unfortunately these distinctive features were not specified. The stratigraphical range of this species seems to be restricted so far to the Ramblian and immediately preceding levels.

Quercomys bijmai Lacomba & Martínez-Salanova, 1988

Locality – Santa Cilia, Province of Huesca.

Material and measurements

	Length				Width			
	n	min	mean	max	n	min	mean	max
M^1	6	10.2	11.0	11.8	5	13.0	13.5	14.4
M^2	8	10.0	10.4	11.2	7	12.8	13.5	14.0
M$_1$	4	11.6	11.7	11.8	4	12.6	12.9	13.2
M$_2$	3	11.4	11.5	11.6	3	11.8	12.1	12.6
M$_3$	1	—	10.4	—	2	11.8	12.1	12.4

Description

M^{1,2} – The anteroloph is connected to the paracone in two specimens. The protoloph and metaloph fuse, thus forming a Y-shaped pattern. Two out of 14 speci-

mens lack the anterior centroloph, the other 12 all have this ridge. In the 2 specimens without centroloph a small isolated cusp is present next to the metaloph in the central valley.

$M_{1,2}$ – The metalophid is separated from the metaconid. The mesolophid is separated from the posterolophid at the entoconid. A short centrolophid is present in all specimens.

M_3 – The metalophid meets the metaconid, and a short centrolophid is present. The mesolophid is separated from the posterolophid at the entoconid, and it meets the base of the hypoconid.

Discussion – See below under *Quercomys parsani*.

Quercomys daamsi de Visser, sp. nov.
Pl. 8, figs. 1-19.

Type locality – San Juan.
Holotype – M^1 dext., cat. no. SJ 193, Pl. 8, fig. 3.
Derivatio nominis – The species is named after Dr Remmert Daams, Madrid.

Diagnosis – A *Quercomys* species of medium size, of which the $M^{1,2}$ may have one or two short, centroloph-like ridges, and of which the $M_{1,2}$ may have a short centrolophid.

Differential diagnosis – *Quercomys daamsi* from San Juan differs from *Quercomys bijmai* from Santa Cilia and its type locality Quel 1 by its larger size, the scarcity of centrolophids, its more inclined ridges, and by the presence of M^1's with an isolated metaloph. On the other hand *Q. daamsi* shows the centroloph-like ridge in several M^1 and few M^2. Out of the 8 M_3 of *Q. daamsi* only one has the typical shape of *Quercomys* (Pl. 8, fig. 18), and the other specimens show the reduced posterior part, typical for *Armantomys*.

Quercomys parsani from La Galocha 5 is larger than *Q. daamsi* from San Juan and it lacks a centrolophid. Furthermore, centroloph-like ridges are present in M^1 and M^2. Only 2 M^1 and none M^2 have an isolated metaloph. *Q. daamsi* differs from *Armantomys aragonensis* de Bruijn, 1966 from the Lower Aragonian of Villafeliche 2A by its smaller size, by the presence of centroloph-like ridges and centrolophids in various specimens, and by the metaloph being connected to the protoloph in M^2.

Q. daamsi differs from *Praearmantomys crusafonti* de Bruijn, 1966 from the Upper Ramblian or Lower Aragonian of Ateca 1 by its smaller size, by its more hypsodont teeth, by its more inclined ridges of the lower molars, and by the presence of centroloph-like ridges in the $M^{1,2}$.

Material and measurements

	Length				Width			
	n	min	mean	max	n	min	mean	max
D^4	6	7.9	8.4	8.8	6	8.2	8.9	9.6
P^4	4	8.2	9.2	10.1	4	9.8	10.9	12.8
M^1	9	11.9	13.2	14.3	8	13.5	15.5	16.8
M^2	14	11.2	12.1	13.0	10	15.0	16.2	17.5
M^3	3	8.7	9.1	9.6	1	—	13.5	—
D_4	1	—	8.6	—	1	—	8.3	—
P_4	4	7.3	7.8	8.7	5	6.3	7.7	8.5
M_1	11	12.5	13.4	14.5	9	13.1	13.8	14.9
M_2	14	12.9	14.0	15.3	15	13.0	14.8	16.6
M_3	8	10.1	11.1	12.3	8	10.2	12.0	13.1

Description

D^4 — A medium-sized anteroloph is present. It is lower than the protoloph and it is connected to the base of the paracone. It does not reach the high protocone. The protoloph is not connected to the protocone in 1 specimen, and the metaloph is separated from this cusp in 2 cases. The posteroloph is separated from the metacone, but it is connected to the base of the protocone.

P^4 — The anteroloph is a short isolated ridge. The protoloph is continuous and the metaloph is separated from the protocone. The posteroloph is separated from the metacone, but it joins the base of the high protocone.

M^1 — The anteroloph is labially separated from the paracone by a shallow or deep furrow. The metaloph is not connected to the protocone in 4 out of 11 specimens. In 1 of these 4 specimens it is connected to the posteroloph, in the other 3 it ends free. The posteroloph is separated from the metacone by a deep furrow, but from the protocone by a shallow one. In 5 specimens a small centroloph-like ridge branches from the lingual side of the paracone into the central valley, thus forming a τ-pattern. This same phenomenon is seen in the metacone in 4 specimens. In 3 of these 4 specimens the anterior centroloph-like ridge is also present.

M^2 — The metaloph is always connected to the protoloph. The anterior centroloph-like ridge is present in 3 out of 14 specimens, the posterior one is absent.

M^3 — The anteroloph is connected to the protocone in one out of 2 specimens. Metaloph and protoloph form a Y-pattern.

D_4 and P_4 — These elements form an irregular cusp-like ridge pattern (Pl. 8, figs. 7-9).

M_1 — The relatively short to medium-sized anterolophid is separated from the protoconid and it is connected to the metaconid. A small centrolophid is present in 3 out of 11 specimens. The mesolophid and posterolophid are separated at the entoconid by a shallow furrow.

M_2 — The dental pattern is basically the same as in M_1, although the furrow at the entoconid is deeper. One out of 14 specimens has a short centrolophid.

M_3 — The anterior part is similar to that of M_1 and M_2. The mesolophid and

posterolophid form one composite ridge in 1 specimen (Pl. 8, fig. 17). In an other specimen the mesolophid is of medium length ending free labially (Pl. 8, fig. 19). In 5 specimens the mesolophid and posterolophid form a composite Y-shaped ridge (Pl. 8, fig. 16), and in 1 specimen the mesolophid is connected to the labial end of the curved posterolophid (Pl. 8, fig. 18).

Discussion — See below under *Quercomys parsani*.

Quercomys parsani Daams, 1991
Pl. 9, figs. 1-9.

Locality — La Galocha 5.

Material and measurements

	Length				Width			
	n	min	mean	max	n	min	mean	max
P⁴	2	10.6	11.5	12.4	2	12.1	13.5	14.8
M¹	2	—	15.5	—	2	17.7	18.3	18.8
M²	3	13.7	14.1	14.4	2	17.9	18.3	18.7
M³	3	9.0	10.0	11.4	2	14.0	14.2	14.4
M_1	1	—	15.7	—	1	—	15.2	—
M_2	3	16.1	16.8	17.7	4	15.1	16.1	16.7
M_3	3	11.4	13.4	15.3	3	13.2	13.8	14.8

Description

P⁴ — The anteroloph forms an isolated cusp. The metaloph is separated from the protocone and it is not connected to the posteroloph either. The posteroloph is a long and narrow ridge, labially isolated, and lingually joining the protocone.

M¹·² — The anteroloph is an isolated ridge. The metaloph is not connected to the protoloph in 2 out of 4 M¹. In all 4 M² the metaloph is connected to the protoloph, but in one of these specimens the labial end of the metaloph has an additional connection to the posteroloph. The posteroloph is connected to the protocone, or a tiny furrow may be present. 2 M¹ have a tiny centroloph-like ridge branching from the labial side of the metacone into the central valley. In two M² these centroloph-like ridges with a τ-shape are present, branching from both metaloph and protoloph into the central valley.

M³ — The anteroloph is an isolated ridge. The protoloph and metaloph form a Y-shaped pattern. The posteroloph ends free at the labial side, but lingually it is connected to the protocone.

M_1 — The anterolophid is separated from the protoconid. The mesolophid and posterolophid are separated at the entoconid.

M_2 — The medium to long anterolophid is connected to the protoconid in one out of 4 specimens. A furrow at the entoconid separates the mesolophid from the

posterolophid.

M_3 – The anterolophid is separated from the protoconid. One specimen has the posterior part consisting of two complete transverse ridges (Pl. 9, fig. 8), in the other 2 specimens the medium long mesolophid is connected to the middle part of the posterolophid (Pl. 9, fig. 9).

Discussion – Our *Quercomys* assemblages from San Juan and La Galocha 5 present the following characteristics: The M^1 is longer than M^2, but it is more or less of the same width. Centrolophids are present in various lower molars. Centroloph-like ridges are present in several $M^{1,2}$. Its molars are relatively hypsodont.

For further data and a discussion on *Quercomys, Armantomys* and *Prae-armantomys* the reader is referred to Daams (1991).

Pseudodryomys ibericus de Bruijn, 1966
Pl. 9, figs. 10-21.

Locality – Santa Cilia, Province of Huesca.

Material and measurements

	Length				Width			
	n	min	mean	max	n	min	mean	max
P^4	6	7.4	8.1	9.6	6	8.5	9.7	10.7
M^1	16	10.0	10.9	11.5	13	11.5	12.2	13.3
M^2	36	10.4	11.3	12.2	35	11.1	12.6	13.3
M^3	8	9.2	9.8	10.4	8	10.7	11.2	11.5
P_4	10	7.8	9.4	10.0	9	7.8	8.5	9.2
M_1	28	10.4	11.4	12.6	27	10.0	10.8	12.9
M_2	30	10.7	11.8	12.2	32	10.4	11.4	12.6
M_3	14	9.2	10.1	11.1	15	9.6	10.1	11.1

Description

P^4 – The four main ridges and one isolated centroloph are present.

M^1 – Two well-developed centrolophs are present. In 13 out of 24 specimens these two ridges meet in the central valley. Six specimens have a short extra ridge between the protoloph and the anterior centroloph, and in 5 other specimens an extra ridge is present between the posterior centroloph and the metaloph.

M^2 – In 8 out of 40 specimens the anterior and posterior centroloph meet in the central valley. Fifteen specimens have the anterior extra ridge only, and 4 show only the posterior extra ridge.

M^3 – The two centrolophs are always present. An endoloph is present in 5 out of 10 specimens. A short posterior extra ridge is present in 3 specimens.

P_4 – A short centrolophid is present in 5 out of 13 specimens. A short posterior extra ridge is observed in 4. The anterolophid is connected to the protoconid. In

3 specimens the protoconid meets the mesoconid.

M_1 – The centrolophid is of medium length to long, but it does not reach the labial border of the tooth. The anterolophid meets the protoconid in 14 out of 33 specimens. A short anterior extra ridge is present in 6 cases, and a well-developed posterior extra one in 27.

M_2 – The centrolophid is of medium length. A short anterior extra ridge is present in 2 out of 34 cases, and the posterior extra ridge in 29. The anterolophid meets the protoconid in 5 specimens.

M_3 – The centrolophid is somewhat shorter than in M_1 and M_2. A short posterior extra ridge is present in 5 out of 15 specimens, and in one of the former a short anterior extra ridge is present as well.

Discussion – Daams (1974) revised *Pseudodryomys* and emended the diagnosis of *P. ibericus*. He mentioned that this species has two centrolophs or only the anterior one, and that the number of extra ridges varies between zero and two. The lower molars always have the posterior extra ridge, and the anterior one may be present. The centrolophid is relatively long.

The size of the teeth of *P. ibericus* from Santa Cilia is smaller than that of the same species from the Lower Miocene of the Calatayud-Teruel Basin, and it agrees with *P.* aff. *ibericus* from the Lower Miocene of Rubielos de Mora (de Bruijn & Moltzer, 1974). On the other hand, the assemblage from Rubielos is characterized by a slightly more complicated dental pattern, and by the M_3 being more complicated than the M_1. Lacomba Andueza (in press) shows in his thesis on the Upper Oligocene and Lower Miocene faunas from the Loranca Basin that *P. ibericus* is of variable size and that the degree of complexity of the dental pattern shows ample variation as well, and he assigns all the assemblages, that of Rubielos included, to *P. ibericus*.

Vasseuromys rugosus Baudelot & de Bonis, 1966
Pl. 10, figs. 1-22.

Locality – Santa Cilia, Province of Huesca.

Material and measurements

	Length				Width			
	n	min	mean	max	n	min	mean	max
P⁴	11	8.3	9.2	9.6	12	10.5	11.3	12.2
M¹	7	11.4	11.9	12.9	7	12.1	13.1	14.4
M²	26	11.0	12.3	13.7	22	12.5	14.0	15.2
M³	10	10.7	11.7	12.2	9	12.6	13.5	14.1
P_4	11	8.7	9.8	10.7	10	8.1	9.1	10.4
M_1	16	11.1	12.4	13.0	16	10.6	11.9	12.9
M_2	13	12.6	13.1	13.7	11	11.8	12.7	13.3
M_3	16	11.1	12.2	12.9	15	10.7	11.2	11.8

Description – The occlusal surface is concave. The main ridges are generally wider than the accessory ones. The lower molars have generally six extra ridges, the upper ones three.

P[4] – The anteroloph is connected to the protocone in most specimens, but sometimes a tiny furrow is present. Labially the anteroloph is separated from the paracone by a narrow furrow, or it is connected to this cusp. The protoloph and metaloph join the endoloph separately. The centrolophs are long; the anterior one may be longer or shorter than the posterior one. Labially the anterior centroloph ends free in 2 out of 9 specimens, and the posterior centroloph ends always free. Extra ridges are narrower than the main ones. One relatively long extra ridge is present between the protoloph and the anterior centroloph. A short, labially situated one may be situated between the two centrolophs. Some specimens have a small extra ridge between the posterior centroloph and the metaloph.

M[1,2] – The anteroloph is long, and may descend to form an irregular wall nearly reaching the base of the protocone. In M[2], however, 6 out of 19 specimens have a continuous endoloph. Labially the anteroloph is separated from the paracone. The central valley of the tooth consists of two long centrolophs and three well-developed extra ridges. Each of these five ridges may end freely at the labial border so that no distinction between centrolophs and accessory ridges can be made any more. Additionally, some specimens may have short, low and narrow extra ridges, which tend to be situated in the middle of the central valley. The three main extra ridges and the centrolophs may fuse lingually to form an irregular ridge pattern. The posteroloph is connected to the protocone, but it is isolated from the metacone. Extra ridges outside the trigone are only present in M[2]; 3 specimens have one between the anteroloph and protoloph and one between the metaloph and posteroloph; 2 specimens have only the anterior one, and 1 tooth only the posterior extra ridge.

M[3] – The endoloph is continuous in 6 out of 8 specimens. The remaining dental pattern is of the same complexity as that of M[2].

P$_4$ – The anterolophid is connected to the protoconid in the majority of the specimens. The long centrolophid reaches the labial tooth border. The labial cusps are longitudinally elongated towards the anterior part of the tooth, thus nearly forming an ectolophid. Extra ridges are frequent; all teeth have at least three, some have four, and one specimen has 5 extra ridges. Generally the ridges in the anterior part of the tooth are chaotically arranged.

M$_1$ – The anterolophid is either connected to the protoconid or a tiny furrow is present, which may disappear with progressive wear. The metalophid is either connected to the metaconid or it is separated from this cusp. The centrolophid is long and it reaches the labial tooth border, where it may fuse with the anterior prolongation of the mesoconid. The mesolophid is isolated from the entoconid in 12 out of 16 specimens. The posterolophid curves forward along the labial border but without reaching the mesoconid. In 7 specimens the posterior central extra ridge is connected to the hypoconid. Six extra ridges are present; one at either side of the metalophid; one between centrolophid and mesolophid; and three in the posterior valley.

M$_2$ – This element has a similar dental pattern as that of M$_1$.

M_3 – The complexity is of the same degree as in $M_{1,2}$, although some specimens may only have two accessory ridges in the posterior valley. Furthermore the dental pattern of M_3 corresponds to that of $M_{1,2}$.

Discussion – The type species of *Vasseuromys* Baudelot & de Bonis, 1966 is *V. rugosus* Baudelot & de Bonis, 1966 from the Lower Miocene of Laugnac. The translated generic diagnosis is as follows: A medium-sized glirid of which the cheek teeth have a concave occlusal surface. The lower molars are characterized by a centrolophid reaching the external border, and by a prolongation of the labial cusps forming a nearly continuous external wall. The diagnosis of *V. rugosus* (translated: *Vasseuromys* characterized by numerous extra ridges) in Baudelot & de Bonis, 1966, was slightly emended by de Bonis in 1973. He added that the upper molars are provided with an endoloph, basing this observation on one specimen only. In the collections of the University of Utrecht *V. rugosus* from Laugnac is represented by several specimens which lack the endoloph however.

Cuenca Bescós (1985) characterized *Ebromys* as having a strongly concave occlusal surface, by the presence of numerous extra ridges and by the absence of an endoloph in M^1 and M^2. In her differential diagnosis of *Ebromys autolensis* she distinguishes this species from *Vasseuromys rugosus* from the Lower Miocene of its type locality Laugnac by the absence of an endoloph, by the absence of posterior branches of the labial cusps of M_1 and M_2 (Cuenca Bescós, 1985, p. 61, erroneously says lingual cusps), and by the lack of paralellism among the extra ridges in the posterior valley of all lower molars. Another typical feature of *E. autolensis* is the labial fusion of the mesolophid and centrolophid.

Vasseuromys rugosus from Santa Cilia differs from *E. autolensis* from Autol in the following features: Its size is somewhat larger. Its dental pattern is slightly more complicated; it is of the same complexity as *V. rugosus* from Laugnac. The labial cusps of the lower cheek teeth are longitudinally elongated, as is the case in *V. rugosus* from Laugnac.

Six out of 19 M^2 have an endoloph, and various other specimens have a nearly complete endoloph. In *V. rugosus* from Laugnac this feature is variable also. Although de Bonis (1973) characterizes this species as having a continuous endoloph (on the basis of one worn specimen), several $M^{1,2}$ without endoloph are present in the collections of the University of Utrecht. The specimens from the Utrecht collections have a long anteroloph whose lingual end descends toward the base of the protocone. This feature is also present in Santa Cilia and Autol.

It thus appears that the only difference between *V. rugosus* from Santa Cilia and from Laugnac is the slightly larger size of the former specimens. Because of general resemblances between *E. autolensis* and *V. rugosus*, it is probable that the former species is the ancestor of the latter one. We do not consider the few differences between *Ebromys* and *Vasseuromys* to be sufficient for generic separation. Hence, *Ebromys* is a junior synonym of *Vasseuromys*. *Vasseuromys? priscus* represents a separate line, and is not considered to be the ancestor of *V. rugosus* as suggested by de Bonis (1973).

Another off-shoot of *V. autolensis* is *V. bacchius* (Martínez-Salanova, 1988)

from the Lower Miocene (zone Y1) of Fuenmayor-2 (La Rioja, Spain). In this species from a more modern level than that of Santa Cilia, the teeth are of much larger size, the dental pattern is slightly more simple, the centrolophids are somewhat shorter than in Autol, and the labial cusps of the lower molars are not longitudinally elongated.

Lacomba & Martínez-Salanova (1988) mention *Ebromys autolensis* in the faunal list of Santa Cilia. This should be changed into *Vasseuromys rugosus*.

Vasseuromys? priscus de Bonis,1973
Pl. 11, figs. 1-20.

Locality – Santa Cilia, Province of Huesca.

Material and measurements

	Length				Width			
	n	min	mean	max	n	min	mean	max
P4	3	7.6	7.8	8.0	3	9.4	9.7	9.9
M1	14	10.4	11.0	11.8	14	11.1	12.0	12.9
M2	26	10.4	11.1	11.8	27	11.1	12.3	13.3
M3	11	8.5	9.3	11.0	11	9.6	11.0	11.5
P_4	1	—	8.9	—	1	—	8.1	—
M_1	18	11.1	11.6	12.6	21	9.6	10.3	10.7
M_2	23	11.1	11.6	12.2	22	10.7	11.4	11.8
M_3	11	9.2	9.8	11.1	11	9.6	10.1	10.5

Description

P4 – The short anteroloph is connected to the base of the protocone. In 2 out of 3 specimens the protoloph is interrupted in its central part. A small extra ridge in the central valley joins the labial portion of the protoloph. The posteroloph is connected to the metacone in 2 out of 3 specimens.

M1 – The anteroloph is separated from the paracone by a narrow and shallow furrow. Two out of 21 specimens have an endoloph. A short accessory ridge is present between the protoloph and the anterior centroloph. The anterior centroloph is very long and nearly reaches the protocone. The shorter posterior centroloph joins the anterior one in 7 out of 21 specimens. The posteroloph is connected to the metacone in 15 out of 17 cases. The trigone has an oblique V-shape.

M2 – The anteroloph is connected to the paracone in 4 out of 26 cases. An endoloph is present in 6 out of 28 specimens. The anterior extra ridge is always present. The anterior centroloph is very long and it joins the protocone in 7 out of 30 specimens. The shorter posterior centroloph is connected to the anterior one in 10 out of 30 cases. Only 1 specimen has a tiny extra ridge between the posterior centroloph and the metaloph. The posteroloph joins the metacone in 13 out of 26 specimens. The trigone has a U-shape.

M^3 – All specimens have an endoloph. In 10 out of 20 cases the anteroloph is connected to the paracone. In 10 out of 13 specimens the anterior centroloph is longer than the posterior one, and reaches nearly the endoloph. The anterior extra ridge is always present. In 10 out of 12 cases the posteroloph joins the metacone.

P_4 – The short centrolophid is connected to the metalophid. The mesolophid is separated from the mesolophid at the entoconid. In the posterior valley a short extra ridge is present.

M_1 – The anterolophid joins the protoconid in 7 out of 22 specimens. A well-developed extra ridge is present in the anterior valley. The metalophid is connected to the metaconid. The long centrolophid reaches the base of the anterior prolongation of the mesoconid, which in turn joins the base of the protoconid. An endolophid is present in 13 out of 18 specimens. The mesolophid is separated from the posterolophid at the entoconid in 12 out of 19 cases. The posterior extra ridge extends from the base of the entoconid to that of the hypoconid. In 6 out of 9 specimens the posterior valley is labially closed.

M_2 – In 17 out of 23 specimens the anterolophid is connected to the protoconid. The anterior extra ridge is always present. The metalophid is connected to the metaconid in 24 out of 25 specimens. The long centrolophid joins the mesolophid at the labial border in 4 specimens. The anterior prolongation of the mesoconid is not as well developed as in M_1, and only in some cases it descends towards the base of the protoconid. The mesolophid is a sinuous ridge. In 8 out of 26 specimens it is interrupted at the entoconid. The posterior extra ridge is always present. In specimens where the mesolophid joins the centrolophid, the posterior extra ridge joins the posterolophid at the entoconid (Pl. 11, fig. 18).

M_3 – In 5 out of 9 specimens the anterolophid is connected to the protoconid. In 8 teeth there is a short anterior extra ridge, and in all specimens the metalophid is connected to the metaconid. The short centrolophid joins the mesolophid in 3 specimens. An endolophid is present in 6 cases. A short posterior extra ridge is present, and in one case this ridge meets the entoconid. In two specimens the hypoconid joins the mesoconid, and in an other tooth the interrupted mesolophid is connected to the posterolophid.

Discussion – De Bonis (1973) described *V. priscus* from Moissac 1, characterizing it as follows (translated): *Vasseuromys* of which the teeth have few accessory ridges. The labial wall of the lower molars is hardly developed. The upper molars tend to form a continuous endoloph. According to his own descriptions the endoloph is only present after a certain degree of attrition.

Hugueney (1974) described *V. priscus* from the Lower Miocene of Carrière Cluzel and noted that measurements and dental pattern agree perfectly with those of the type material. In her material there is an apparent difference between the M^1 and M^2; the M^1 has an oblique V-shaped trigone and lacks an endoloph, whereas the M^2 has a U-shaped trigone, and an endoloph in various specimens. It was impossible for us to study the type material as it appears to be lost (M. Hugueney, pers. com.).

Our material from Santa Cilia agrees well with that of *V. priscus* from Carrière Cluzel. As our material is more abundant, it showed a larger variation than

the material from Carrière Cluzel. Therefore it was inevitable to change the diagnosis of this species into 'A small-sized *Vasseuromys* with generally one extra ridge in the upper molars and two in the lower ones. M^1 has an oblique V-shaped trigone, the M^2 a U-shaped one. M^1 generally without endoloph, M^2 shows tendency to form a lingual wall. The lower molars may have an endolophid and an irregular ridge pattern.'

On the other hand we doubt that *V. priscus* is a representative of *Vasseuromys*. The type material of *V. rugosus*, the type species of the genus, consists only of 14 lower and 4 upper cheek teeth, and that of *V. priscus* consists of 5 cheek teeth. This is really too poor to confirm possible phylogenetic relationships.

Aguilar (1974) considered the possibility that *V. priscus* and *P. jaegeri* Aguilar, 1974 from the Lower Miocene of France are synonymous. But the presence of endoloph(id)s and the extremely long anterior centroloph joining the endoloph in various M^2 in the former species, in our opinion excludes this possibility.

Biostratigraphy

The fauna from the base of the Sariñena Formation at Santa Cilia (Fig. 10) contains abundant *Rhodanomys oscensis* (Fig. 11) and was assigned to the upper part of zone X (Oligocene/Miocene boundary interval) by Alvarez Sierra (1987). Other elements supporting this correlation are *Vasseuromys*? *priscus* and *Piezodus* cf. *tomerdingensis*.

The fauna of San Juan in the upper part of the Sariñena Formation contains few elements for a solid age determination. The presence of one specimen of *Rhodanomys* or *Ritteneria* points at a pre-Ramblian age (probably zone Y). The Gliridae, the most abundant mammal group in this locality, are not very useful for biostratigraphic correlation, although *Quercomys daamsi* represents a more primitive morphological stage than the Ramblian representatives (see Daams, 1991).

The fauna of La Galocha 5 near the top of the Sariñena Formation, some 80 m stratigraphically above San Juan, contains *Quercomys parsani* and *Ligerimys* cf. *fahlbuschi* and therefore belongs to zone Z.

Other European faunas that may be correlated to these Spanish faunas are the following. The faunas from Gans (Aquitaine Basin, Ringeade, 1978) and Tomerdingen near Ulm (Tobien, 1976) may be correlated with the one from Santa Cilia on the basis of its Lagomorpha (López Martínez, 1984). According to Alvarez Sierra (1987), *Rhodanomys schlosseri* from Carrière Cluzel (Hugueney, 1974) would represent a more evolved stage of the *Rhodanomys-Ritteneria* lineage than its specific name indicates and may correspond to its descendant *Rh. oscensis* from Santa Cilia. *Vasseuromys*? *priscus* is another species in common between these two localities.

As for San Juan and La Galocha 5, the correlation is more problematic. San Juan may be correlative with Bouzigues and Laugnac, if these two French localities are really of the same age, as assumed by de Bonis (Baudelot & de Bonis, 1968). It appears that *Eucricetodon* is not a reliable genus for correlation, as the demonstrated morphological differences between the French species on the one hand, and the

Lithology	Fossiliferous localities	Local zones	Series
Clays and sand-stones of the Sariñena Formation	La Galocha 5 La Galocha 1-4 San Juan	Z / Y2	Lower Miocene
	Santa Cilia	Y1 / X	Oligo-Miocene bound. interval
Sandstones, clays and basal limestone of the Peraltilla Formation			Upper Oligocene
	Peraltilla		Lower Oligocene
Gypsums of Barbastro			

Fig. 10. Stratigraphical context of the fossiliferous localities studied .

Spanish species on the other, may be due to geographical variation. Geographical variation may also be present in *Prolagus vasconiensis*, thus reducing its value for long-distance correlation.

Agustí et al. (1985) presented a biozonation for the Oligocene-Miocene conti-nental sediments in the southeastern part of the Ebro Basin. Their two upper bio-zones are those of *Rhodanomys schlosseri* and *Ebromys autolensis* with Torrente de Cinca-68 and Santa Cilia as their respective type localities. From our study it ap-peared that the dormouse with complicated dental pattern from Santa Cilia, referred to as *Ebromys autolensis* by Agustí et al. (1985), is in fact *Vasseuromys rugosus*. *Ebromys autolensis* has also been misidentified in Santa Cilia (Lacomba & Martínez-Salanova, 1988; Lacomba Andueza, in press) and it seems clear now that it is absent in this fauna. On the other hand, the *Rhodanomys schlosseri* Zone is based on the presence of 7 teeth of this species (only P4 and M3) from Torrente de Cinca-68; unfortunately these teeth are the less characteristic elements for this spe-cies, as they appear to fall in both the size and morphological variation of *Rhoda-nomys transiens*, *Rh. schlosseri* and *Rh. oscensis*. Moreover, in the fauna of Autol *Ebromys autolensis* and *Rhodanomys schlosseri* are both present. Therefore we do not consider that the upper part of the biozonation of the central-eastern Ebro Basin of Agustí et al. (1985) has a basis sound enough to be applied also to the northern and western part of the Ebro Basin.

Series		Lower Miocene					Oligo-Miocene bound. interval
Continental (st)ages		Rm	Agenian				
Local zones		N				Y2	X
N of rodent M1,2		70	1	1	1	188	803
Lagomorpha	Prolagus vasconiensis aff. *fortis*	9				90	21 4
	Prolagus vasconiensis *fortis*						
	Piezodus cf. *tomerdingensis*						
	Titanomys visenoviensis						
Rodentia	Quercomys parsani	14				•	8
	Ligerimys cf. *fahlbuschi*	1 3				3	11
	Heteroxerus cf. *rubricati*	26 1				43 3	3
	'Peridyromys' brailloni		X	X	X	3	14
	Peridyromys turbatus						8
	Eucricetodon sp.					26 3	
	Eucricetodon aff. *aquitanicus*					3	
	Palaeomys castoroides	56					
	Quercomys daamsi					2	
	Pseudotheridomys sp.						
	Rhodanomys or *Ritteneria*					19 •	
	Peridyromys murinus						
	Pseudodryomys ibericus						2
	Quercomys bijmai						49 •
	Vasseuromys priscus						
	Vasseuromys rugosus						
	Castoridae gen. et sp. indet.						
	Palaeomys dehmi						
	Heteroxerus paulhiacensis						
	Palaeosciurus feignouxi						
	Rhodanomys oscensis						
Genera and species of Lagomorpha and Rodentia / Localities		La Galocha 5	La Galocha 3	La Galocha 2	La Galocha 1	San Juan	Santa Cilia

Fig. 11. Distribution chart of genera and species of micromammals from the localities studied in this paper. The rodents are given in percentages of the total rodent fauna; the number in the column of the Lagomorpha refers to the quantity of dental remains.

The zones X and Y were correlated with the latest Oligocene and earliest Miocene by Alvarez Sierra et al. (1987). As there is no possibility to draw the Oligocene/Miocene boundary in our continental successions, these authors refer to an Oligocene/Miocene boundary interval. The unconformity separating the Peraltilla Formation from the Sariñena Formation just below the locality of Santa Cilia (Crusafont et al., 1966; Riba et al., 1983) may be situated in the Upper Oligocene or in the above mentioned boundary interval. Another unconformity may be present between the folded sediments of the Santa Cilia locality at the north flank of the Barbastro Anticline, and the subhorizontal sediments of the San Juan - La Galocha section towards the centre of the basin. Hitherto this unconformity has not been described by any author, although a general rupture in zone Y has been demonstrated in other parts of the Ebro Basin by López Martínez et al. (1987). The identification criteria of 'ruptures' were briefly discussed by López Martínez et al. (1987).

Palaeoecology

Between Santa Cilia on the one hand and San Juan and La Galocha 5 on the other, some significant changes in faunal composition are evident. The fauna of Santa Cilia consists predominantly of Eomyidae (53 %), and the faunas of San Juan and La Galocha 5 are dominated by Gliridae (76 % and 97 %, respectively). These percentages refer to the rodent fauna only; lagomorphs are not included.

Elements that are characteristic for a humid environment in Santa Cilia are *Rhodanomys oscensis*, *Vasseuromys rugosus* and Castoridae, which together constitute more than 60 % of the assemblage. Elements representative for more arid biotopes, *Heteroxerus*, *Quercomys* and *Pseudodryomys*, constitute 21 % of the assemblage. The sedimentological setting of the locality is that of a flood plain.

The fauna of San Juan contains *Peridyromys turbatus* and 'P'. *brailloni*, which are considered to be representatives of humid biotopes, according to the model of van der Meulen & de Bruijn (1982), slightly emended by Daams & van der Meulen in 1984. Other elements of humid environments are the Castoridae and Eomyidae. *Quercomys* and *Eucricetodon* are more characteristic for dry biotopes. The fauna of San Juan was recovered from the bottom of a fine-grained sand, set in a cross-bedded channel filling.

In La Galocha 5 the number of representatives of humid biotopes is less than in San Juan, although 'P.' *brailloni* constitutes 32 % of the rodent fauna. The Eomyidae only constitute 2 % of the fauna. Furthermore La Galocha 5 is characterized by its impoverished rodent fauna; only 5 species are present, whereas San Juan contains 11 and Santa Cilia 9.

Daams & van der Meulen (1984) constructed a temperature curve for part of the Neogene of Spain on the basis of the relative abundance of *Peridyromys murinus* within the Gliridae family, *Armantomys* omitted. They reasoned that increasing relative abundance would coincide with a decrease in temperature and compared their curve with the one made by Muller (1984) on the basis of oxygen isotopes in nannoplankton from the Mediterranean and Atlantic regions. The agreement be-

tween the curves was so good that further elaboration of their method seems worthwile.

The relative abundance of *Peridyromys murinus* in Santa Cilia, San Juan and La Galocha 5 is 17 %, 30 % and 59 %, respectively, implying a tendency toward temperature decrease. In north central Spain the faunas from Cetina de Aragon (zone Y1 of the Almazán Basin), Alcocer 3B (zone Y2 of the Loranca Basin) and zone Z in the Calamocha area (Calatayud-Teruel Basin) show relative abundances of 23 %, 26 % and 67 % respectively, implying the same tendency. The fauna from Cetina is intermediate in age between those of Santa Cilia and San Juan, that from Alcocer 3B is probably somewhat older than the fauna from San Juan, and the one from La Galocha 5 belongs to zone Z. In the microfauna from Loranca (zone Z, Loranca Basin) the relative abundance of *P. murinus* is 67 %. It is striking that the tendencies are so similar in the distinct areas, and that the relative abundances seem to agree also. If the method, developed by Daams & van der Meulen is reliable, it implies that temperature decreased in the time interval covered by the faunas from Santa Cilia to La Galocha 5 (zones X-Z), which was accompanied by a trend toward more aridity.

Palaeobiogeography

Other faunas of the age of Santa Cilia are not known in Spain. In France an equivalent fauna could be that of Carrière Cluzel in the Massif Central (Hugueney, 1974). *Vasseuromys*? *priscus, Rhodanomys oscensis, Palaeosciurus feignouxi, Heteroxerus paulhiacensis*, and *Piezodus* cf. *tomerdingensis* are the most important species in common between these two faunas. But Carrière Cluzel also contains *Pseudotheridomys parvulus* and *Plesiosminthus myarion*, elements which are absent in Santa Cilia. The fauna of Santa Cilia contains *Vasseuromys rugosus, Pseudodryomys ibericus, Quercomys bijmai*, and *Palaeomys*, which are in turn absent in Carrière Cluzel. Characteristic is the absence of *Eucricetodon* in both faunas. Elements of northern origin in the fauna of Santa Cilia may be *Vasseuromys*? *priscus, V. rugosus, Titanomys visenoviensis*, and *Piezodus* cf. *tomerdingensis*.

Prae-Ramblian faunas contemporaneous with San Juan are probably not known in Spain. The nearest one in age may be that of Alcocer 3B (Alvarez Sierra, 1987; Lacomba Andueza, in press) in the Loranca Basin of Guadalajara. But there are very few diagnostic species in common between these two faunas. On the other hand there appears to be some resemblance with the French fauna of Poncenat (Hugueney, 1974). In this French locality the following rodent species are present; *Vasseuromys rugosus*?, *Pseudotheridomys*, some teeth belonging to the *Rhodanomys-Ritteneria* group, *Steneofiber eseri* (*Palaeomys castoroides*), and *Eucricetodon gerandianus*. Although not all of these species correspond to those in San Juan, the general resemblance at the generic level is striking. An other French element in the San Juan fauna is '*Peridyromys*' *brailloni*, hitherto only known from Bouzigues and perhaps from Laugnac. A typical Spanish element in the fauna of San Juan is *Quercomys*, and the variation of the dental pattern of *Peridyromys murinus* is more in

agreement with that of the Spanish representatives than with that of the French ones.

French equivalents of the fauna of La Galocha 5 are not known, but Lower Ramblian faunas in Spain are. The La Galocha 5 fauna also presents a mixture of French and Spanish elements. *Quercomys* is present in the Ramblian of Central Spain, but '*P.*' *brailloni*, which at La Galocha 5 amounts to 32 % of the rodent fauna, is not (see above). The upper molars of *Peridyromys murinus* have an extra ridge in 30 % of the cases, which would rather be a French feature (see Daams, 1981).

It is remarkable that the few faunas studied contain French elements, which never have been encountered in the rich contemporaneous faunas of Central Spain. At this moment we do not know if these differences are due to latitudinal differences only, or due to a geographical barrier between the north and the centre of Spain. We think that at least from the age of Santa Cilia to that of La Galocha 5, there has been a faunal exchange from the Spanish pre-Pyrenees toward both the north and the south, but with certain limitations.

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Plate 1

Titanomys visenoviensis von Meyer, 1843, Santa Cilia
a: occlusal view, large scale; b: side view, small scale.
1. D^4 sin., SC-LO 14.
2. P^2 sin., SC-LO 11.
3. P^3 sin., SC-LO 2.
4. M^2 sin., SC-LO 26.
5. P$_3$ dext., SC-LO 1.
6. P$_3$ dext., SC-LO 21.
7. M$_2$ sin., SC-LO 8.

Piezodus cf. *tomerdingensis* Tobien, 1975, Santa Cilia
8. P^2 sin., SC-LO 10.
9. M^2 dext., SC-LO 4.

Compare figs. 4 and 9 to note the relatively wider teeth and the less curved shaft of *Titanomys* in relation to *Piezodus*. The stronger curvature of the *Piezodus* teeth is also evident comparing figs. 2b and 8b.
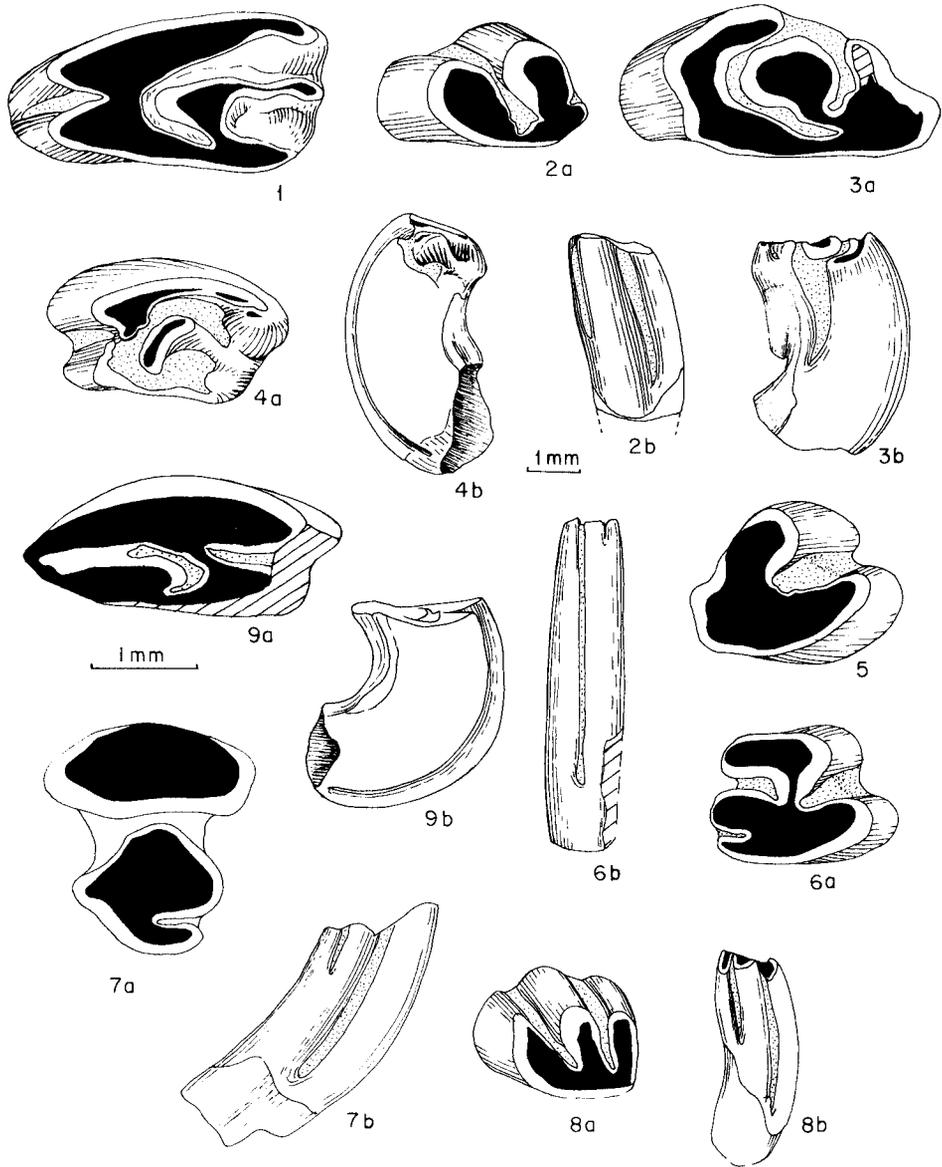
Plate 2

Prolagus vasconiensis fortis López Martínez & Sesé, subsp. nov., San Juan
  1. D^2 dext., SJ-LO 45b.
  2. D^4 sin., SJ-LO 45a.
  3. D_3 sin., SJ-LO 62.
  4. P^2 dext., SJ-LO 59.
  5. P_3 dext., SJ-LO 33 (holotype); a: occlusal view; b: labial view.
  6. P^3 dext., SJ-LO 75.
  7. P^4 dext., SJ-LO 27.
  8. M^1 dext., SJ-LO 72.
  9. P_3 sin., SJ-LO 34.
10. Fragment of M_2 sin., (talonid with hypoconulid), SJ-LO 138.

Prolagus vasconiensis aff. *fortis* López Martínez & Sesé subsp. nov., La Galocha 5
11. D_3 sin., LG5-LO 5.
12. P^4 sin., LG5-LO 3.
13. P^2 sin., LG5-LO 10.
14. P^2 sin., LG5-LO 11.

Bar length is 10 mm.
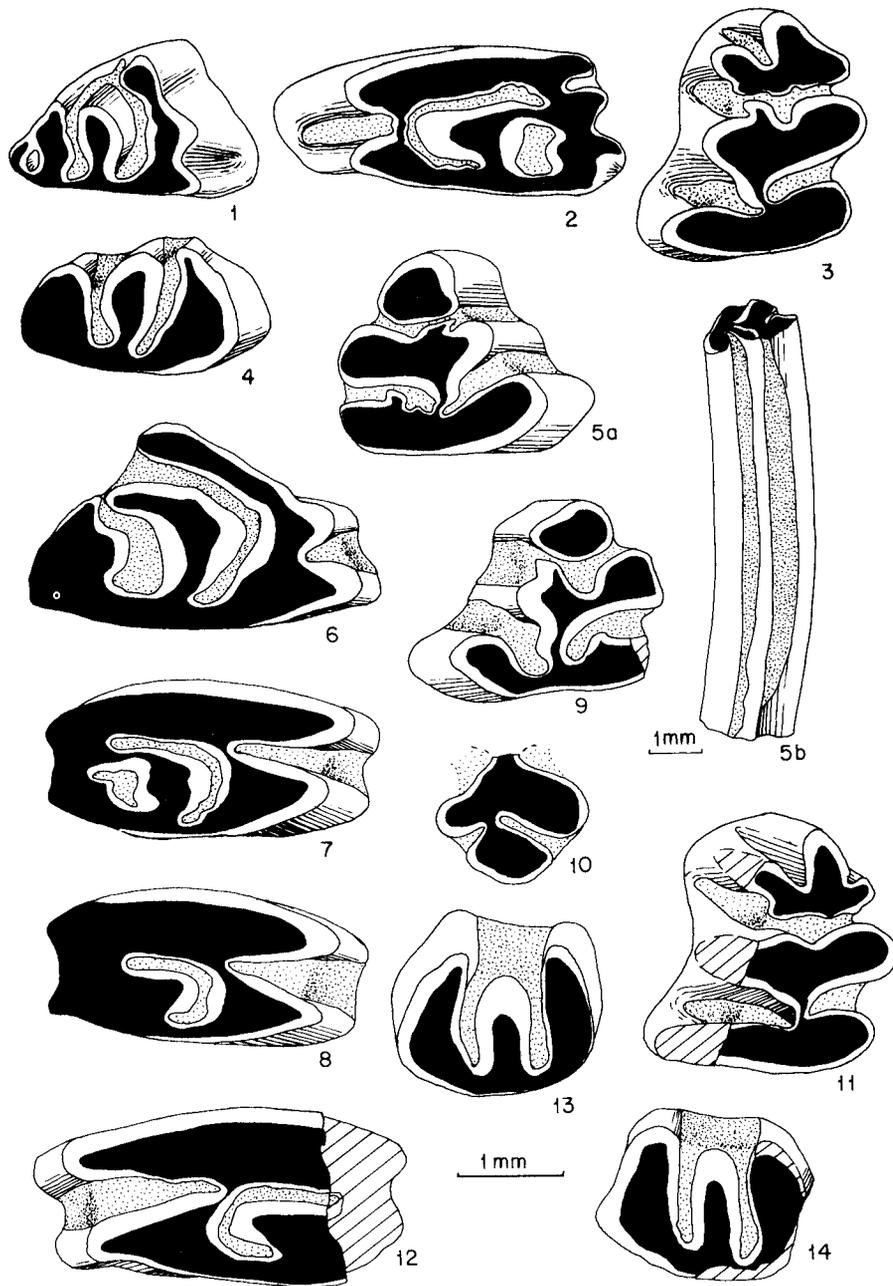
Plate 3

Palaeomys dehmi Freudenberg, 1941, Santa Cilia
1. $M^{1,2}$ dext., SC-C 4.
2. M^3 sin., SC-C 6.
3. idem, posterior view.
4. $M_{1,2}$ sin., SC-C 5.
5. idem, labial view.

Palaeomys sp., Santa Cilia
6. $M^{1,2}$ dext., SC-C 2.
7. idem, lingual view.

Palaeomys castoroides Kaup, 1832, San Juan
8. Left lower incisor, SJ-C 12.
9. idem, frontal view.
10. $M^{1,2}$ sin., SJ-C 11.
11. $M^{1,2}$ sin., SJ-C 14.
12. idem, lingual view.
13. M^3 sin., SJ-C 1.
14. P_4 sin., SJ-C 10.
15. $M_{1,2}$ dext., SJ-C 2.
16. idem, lingual view.
17. idem, labial view.
18. idem, labial view.
19. $M_{1,2}$ sin., SJ-C 25.
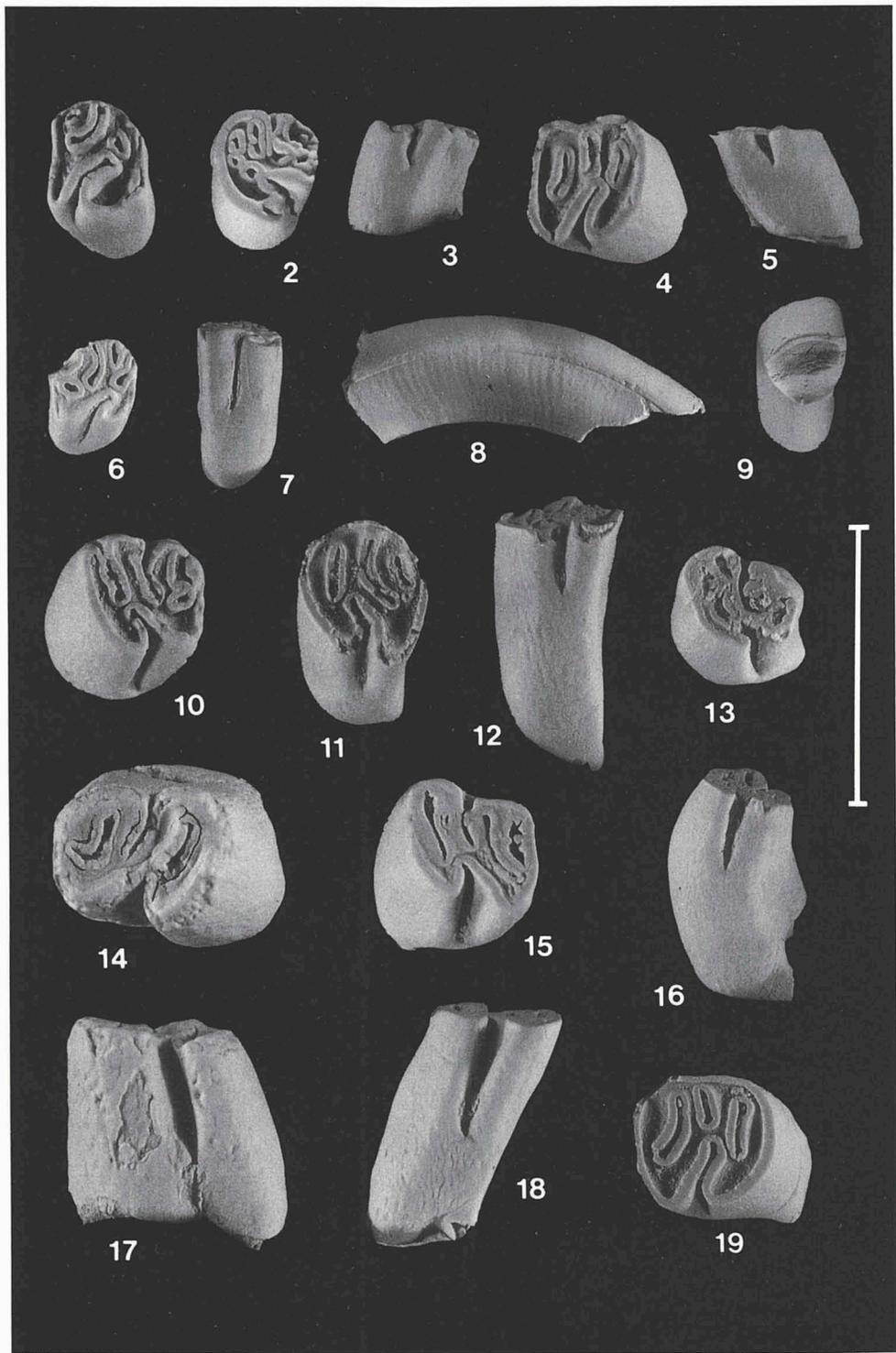
Plate 4

Palaeosciurus feignouxi Pomel, 1853, Santa Cilia
  1. M^2 sin., STC 1047.

Heteroxerus paulhiacensis Black, 1965, Santa Cilia
  2. M^1 sin., STC 1042.
  3. M^1 dext., STC 1006.
  4. $M^{1,2}$ dext., STC 1010.
  5. M^2 sin., STC 1007.
  6. M^2 dext., STC 1041.
  7. M^3 sin., STC 1012.
  8. M^3 dext., STC 1045.
  9. P_4 sin., STC 1017.
10. P_4 dext., STC 1016.
11. M_1 sin., STC 1029.
12. M_1 dext., STC 1019.
13. M_2 dext., STC 1021.
14. M_3 sin., STC 1034.
15. M_3 dext., STC 1031.
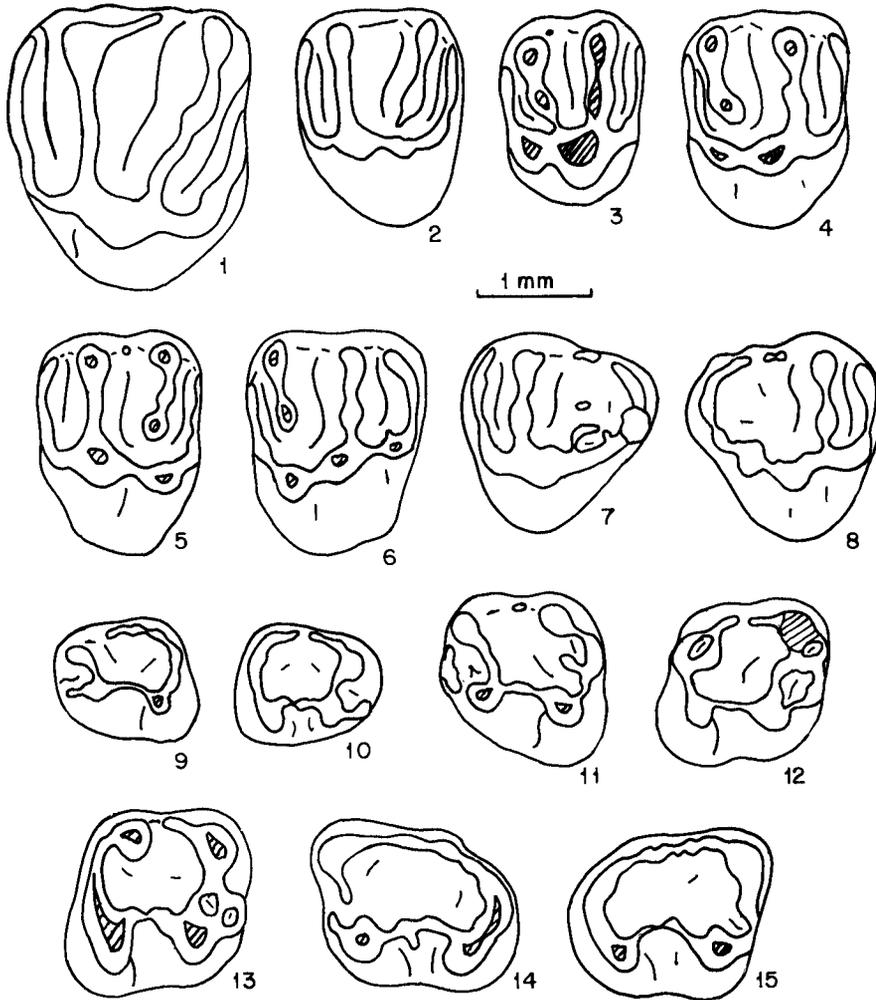
Plate 5

Eucricetodon aff. *aquitanicus* Baudelot & de Bonis, 1968, San Juan
1. M_1 dext., SJ 406.
2. M_1 sin., SJ 407.
3. M_2 dext., SJ 408.
4. M^2 dext., SJ 404.
5. M^3 sin., SJ 405.

Eucricetodon sp., San Juan
6. M^1 dext., SJ 403.

Pseudotheridomys sp., San Juan
7. D^4 dext., SJ 507.
8. M^1 dext., SJ 311.
9. M^3 sin., SJ 509.
10. M^3 sin., SJ 310.
11. D_4 sin., SJ 503.
12. $M_{1,2}$ dext., SJ 508.
13. $M_{1,2}$ dext., SJ 501.

Eomyidae gen. et sp. indet., San Juan
14. P_4 sin., SJ 504.

Ligerimys cf. *fahlbuschi* Alvarez Sierra, 1987, La Galocha 5
15. P_4 sin., LG5 1.
16. M_1 dext., LG5 2.
17. M_1 sin., LG5 3.
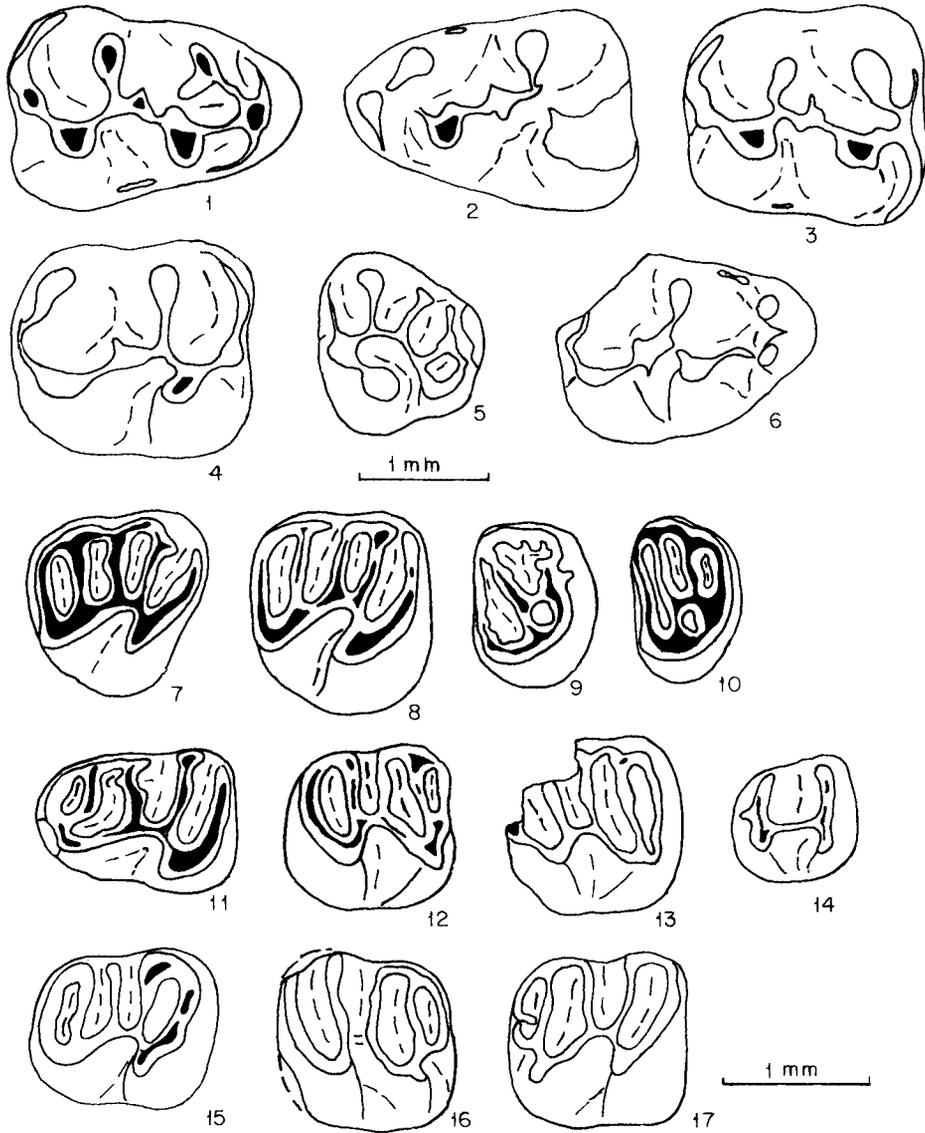
Plate 6

Peridyromys turbatus Daams & de Visser, sp. nov., San Juan

1. D^4 dext., SJ-G 261.
2. P^4 dext., SJ-G 283.
3. P^4 dext., SJ-G 277.
4. M^1 sin., SJ-G 27.
5. M^1 sin., SJ-G 21.
6. M^2 dext., SJ-G 30.
7. M^2 sin., SJ-G 8.
8. M^2 dext., SJ-G 28.
9. M^2 sin., SJ-G 14.
10. M^3 sin., SJ-G 68.
11. M^3 sin., SJ-G 60.
12. M^3 sin., SJ-G 65.
13. P_4 sin., SJ-G 295.
14. P_4 sin., SJ-G 305.
15. P_4 sin., SJ-G 294.
16. M_1 sin., SJ-G 82.
17. M_1 sin., SJ-G 81.
18. M_1 sin., SJ-G 89.
19. M_1 sin., SJ-G 87.
20. M_2 dext., SJ-G 113.
21. M_2 dext., SJ-G 118 (holotype).
22. M_3 dext., SJ-G 149.
23. M_3 sin., SJ-G 127.
24. M_3 sin., SJ-G 130.
25. M_3 sin., SJ-G 131.
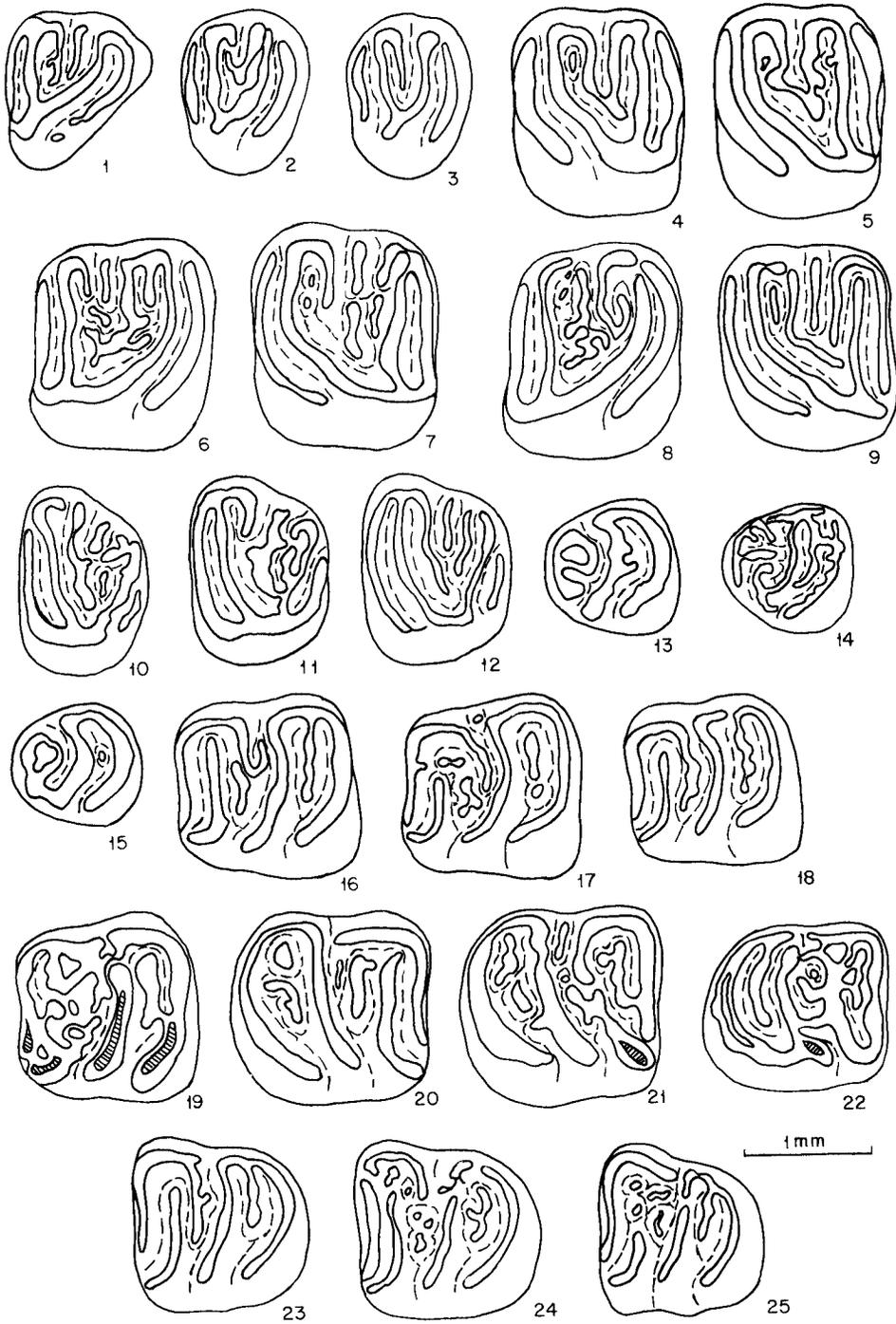
Plate 7

'Peridyromys' brailloni Thaler, 1966, La Galocha 5
1. D^4 dext., LG5 78.
2. P^4 dext., LG5 81.
3. M^1 dext., LG5 86.
4. M^2 dext., LG5 89.
5. P_4 sin., LG5 101.
6. M^3 sin., LG5 96.
7. M^2 dext., LG5 93.
8. M^2 dext., LG5 92.
9. M^2 dext., LG5 90.
10. M^3 dext., LG5 99.
11. P_4 sin., LG5 104.
12. M_1 sin., LG5 108.
13. M_1 sin., LG5 111.
14. M_1 dext., LG5 110.
15. M_2 dext., LG5 117.
16. M_2 dext., LG5 119.
17. M_3 sin., LG5 124.
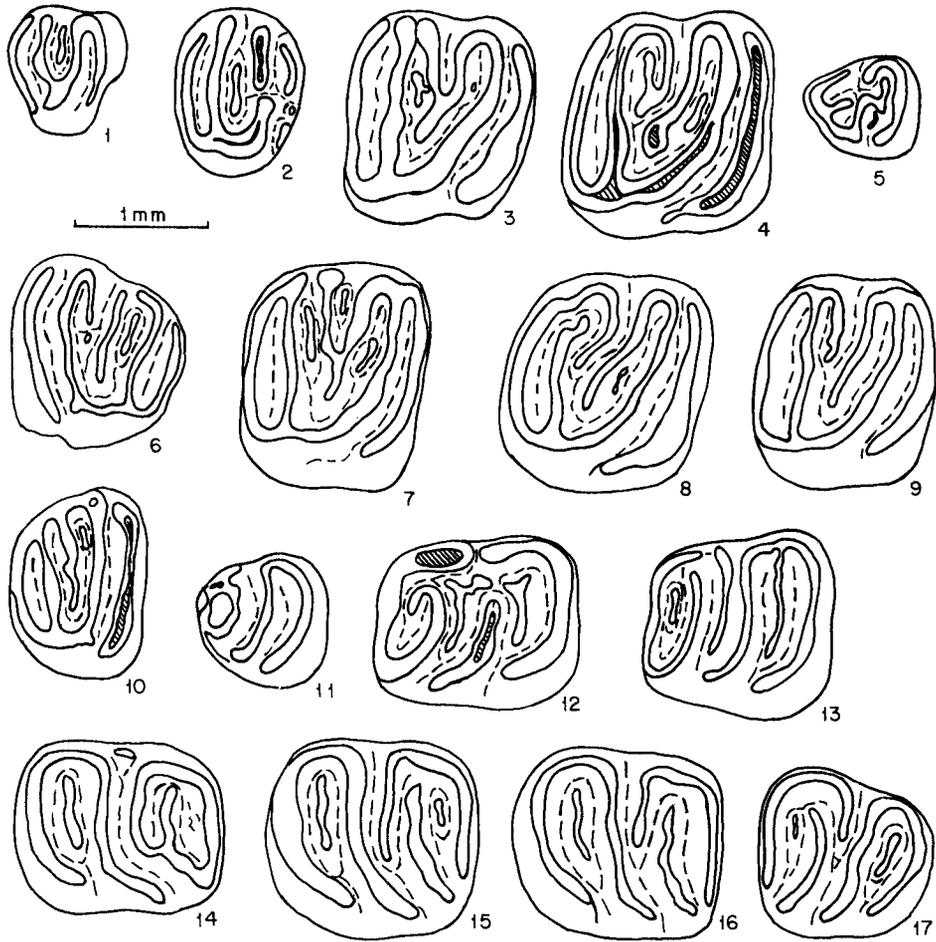
Plate 8

Quercomys daamsi de Visser, sp. nov., San Juan
  1. M^1 dext., SJ-G 201.
  2. M^1 sin., SJ-G 39.
  3. M^1 dext., SJ-G 193 (holotype).
  4. M^2 sin., SJ-G 206.
  5. M^2 sin., SJ-G 204.
  6. M^3 dext., SJ-G 217.
  7. D_4 dext., SJ-G 224.
  8. P_4 dext., SJ-G 223.
  9. P_4 dext., SJ-G 220.
 10. D^4 dext., SJ-G 307.
 11. P^4 dext., SJ-G 36.
 12. M_1 dext., SJ-G 233.
 13. M_1 dext., SJ-G 231.
 14. M_1 dext., SJ-G 234.
 15. M_2 dext., SJ-G 249.
 16. M_3 dext., SJ-G 257.
 17. M_3 dext., SJ-G 256.
 18. M_3 dext., SJ-G 259.
 19. M_3 dext., SJ-G 258.
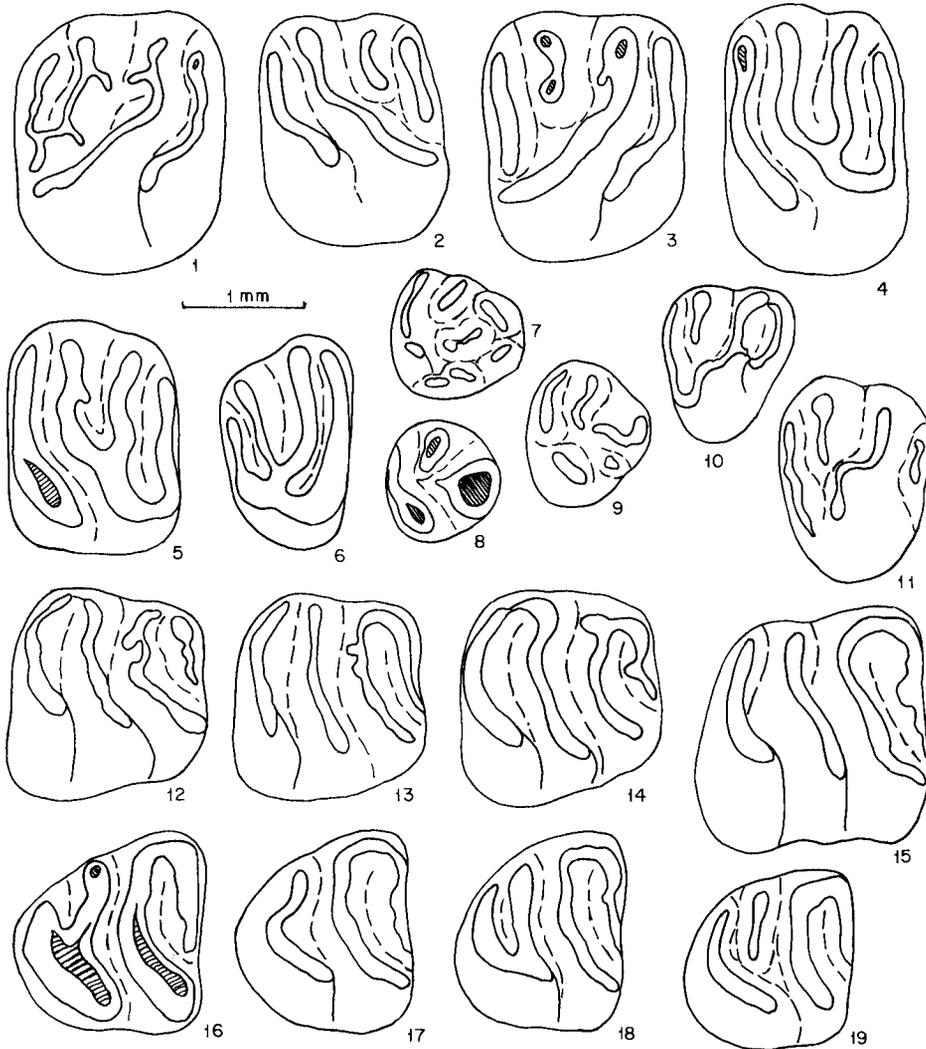
Plate 9

Quercomys parsani Daams, 1990, La Galocha 5
1. P^4 sin., LG5 52.
2. M^1 dext., LG5 54.
3. M^1 sin., LG5 55.
4. M^2 sin., LG5 56.
5. M^3 sin., LG5 65.
6. M$_1$ sin., LG5 66.
7. M$_2$ sin:, LG5 68.
8. M$_3$ sin., LG5 73.
9. M$_3$ sin., LG5 74.

Pseudodryomys ibericus de Bruijn, 1966, Santa Cilia
10. P^4 dext., STC-G 514.
11. M^1 dext., STC-G 72.
12. M^1 dext., STC-G 104.
13. M^2 dext., STC-G 94.
14. M^2 dext., STC-G 113.
15. M^2 sin., STC-G 114.
16. M^3 sin., STC-G 609.
17. M^3 sin., STC-G 136.
18. P$_4$ sin., STC-G 1.
19. M$_1$ sin., STC-G 43.
20. M$_2$ sin., STC-G 28.
21. M$_3$ sin., STC-G 480.
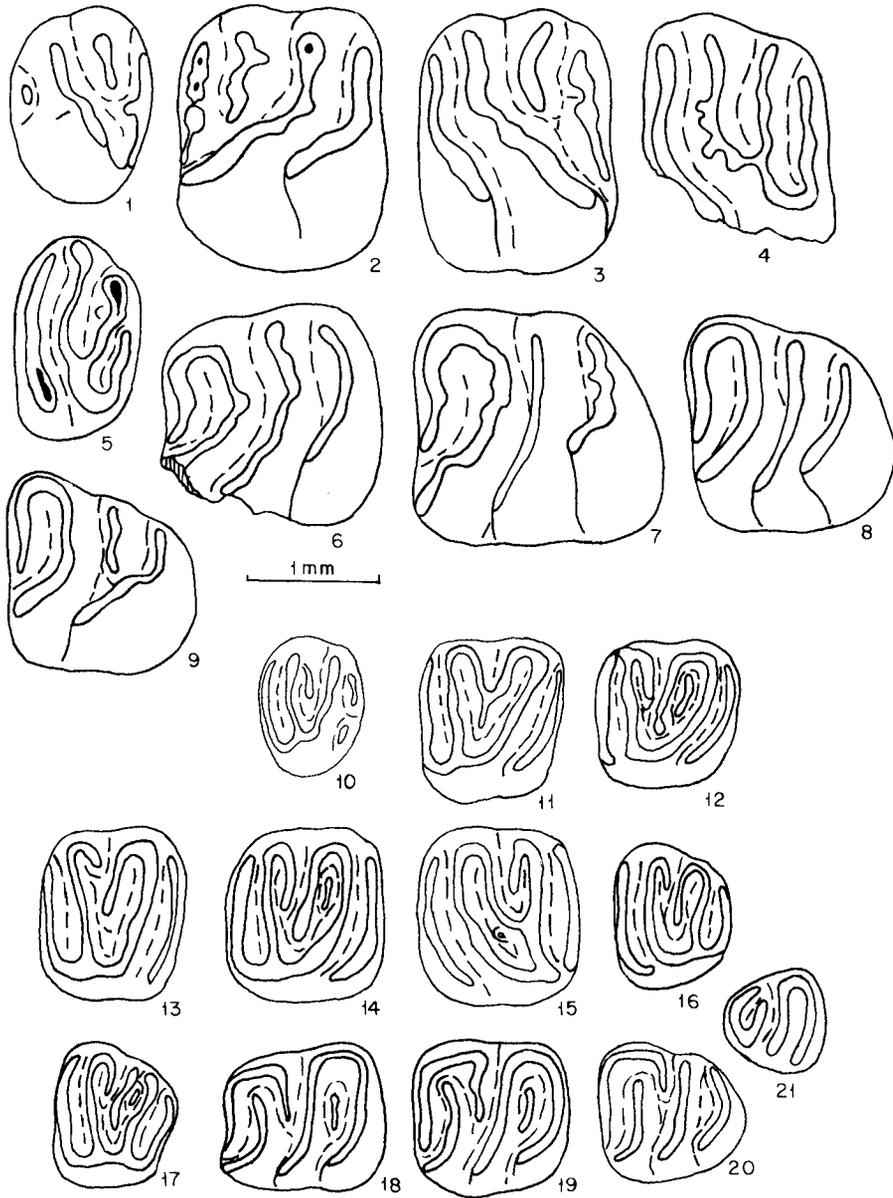
Plate 10

Vasseuromys rugosus Baudelot & de Bonis, 1966, Santa Cilia
  1. P^4 dext., STC-G 519.
  2. P^4 dext., STC-G 371.
  3. M^1 dext., STC-G 325.
  4. M^1 dext., STC-G 172.
  5. M^2 sin., STC-G 346.
  6. M^2 sin., STC-G 343.
  7. M^2 sin., STC-G 328.
  8. M^3 dext., STC-G 355.
  9. M^3 dext., STC-G 353.
10. M^3 sin., STC-G 188.
11. P_4 dext., STC-G 194.
12. P_4 sin., STC-G 196.
13. P_4 sin., STC-G 197.
14. M_1 dext., STC-G 288.
15. M_1 sin., STC-G 299.
16. M_1 sin., STC-G 295.
17. M_2 sin., STC-G 310.
18. M_2 sin., STC-G 313.
19. M_2 dext., STC-G 307.
20. M_3 dext., STC-G 316.
21. M_3 sin., STC-G 361.
22. M_3 sin., STC-G 360.

1 mm
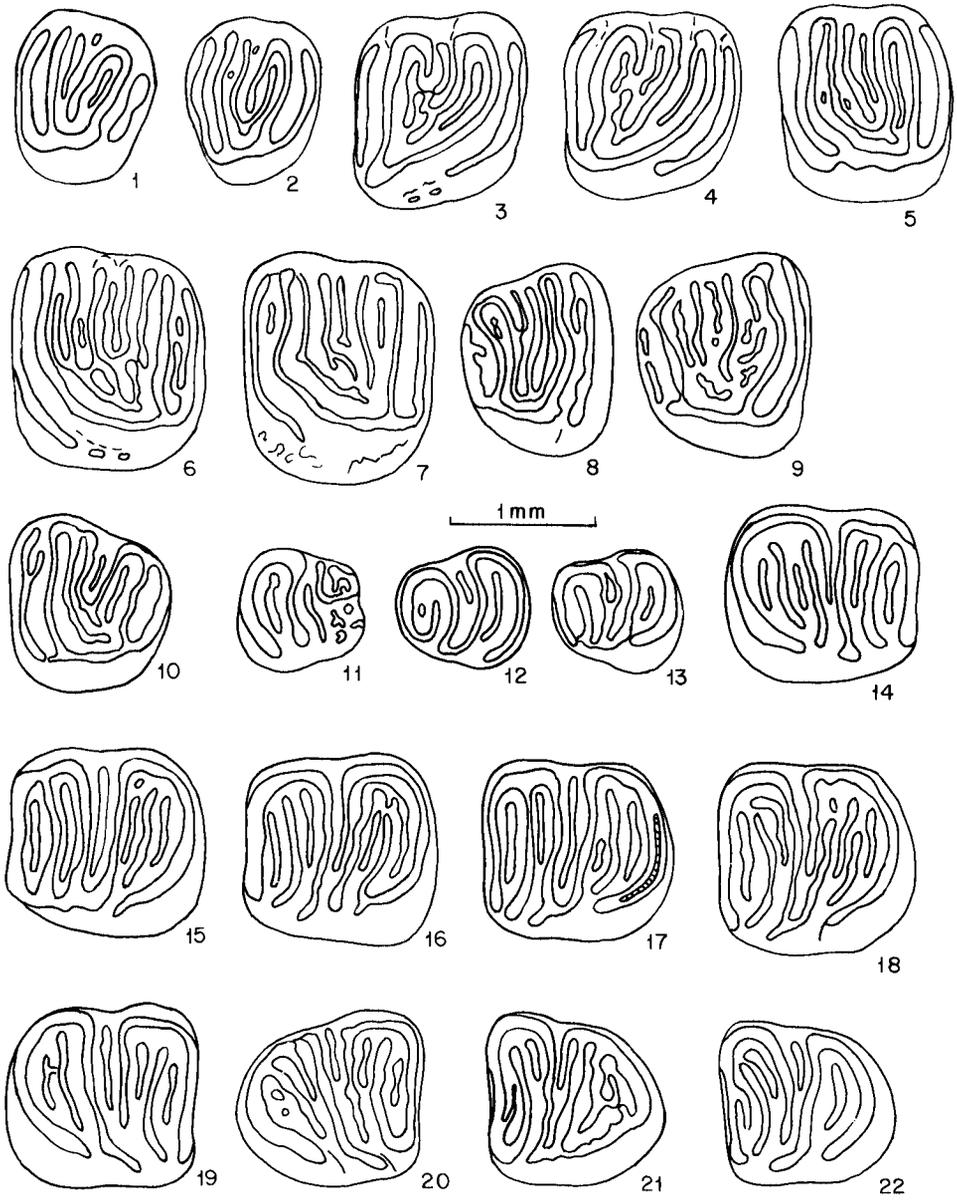
Plate 11

Vasseuromys? priscus de Bonis, 1973, Santa Cilia
  1. P^4 dext., STC-G 513.
  2. M^1 sin., STC-G 263.
  3. M^1 sin., STC-G 267.
  4. M^2 sin., STC-G 152.
  5. M^2 dext., STC-G 268.
  6. M^3 sin., STC-G 289.
  7. M^3 dext., STC-G 285.
  8. P_4 sin., STC-G 453.
  9. M_1 dext., STC-G 243.
 10. M_1 dext., STC-G 244.
 11. M_1 dext., STC-G 213.
 12. M_3 dext., STC-G 121.
 13. M_1 sin., STC-G 242.
 14. M_1 sin., STC-G 245.
 15. M_2 dext., STC-G 223.
 16. M_3 dext., STC-G 247.
 17. M_2 dext., STC-G 225.
 18. M_2 dext., STC-G 234.
 19. M_3 dext., STC-G 249.
 20. M_3 sin., STC-G 253.

1 mm