

Rodents, Insectivores and Paleoenvironment Associated to the First-Appearing Hipparionine Horses in the Vallès-Penedès Basin (Northeastern Spain)

by

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Abstract

The insectivores and rodents from Creu Conill 20 and Creu Conill 22 are described. These are the earliest Vallesian sites of the Vallès-Penedès Basin and record the First Appearance Datum of the equid *Hipparion* s.l. at the base of chron C5r.1n (11.1 Ma). The rodent fauna is largely dominated by *Megacricetodon ibericus*, while the rest of the species are minor components. This faunal composition contrasts with the ones observed in other latest Aragonian and Early Vallesian sites (Can Missert, Upper Hostalets de Pierola, Can Ponsic) from the same basin, where the assemblage is dominated by the hypsodont cricetid *Hispanomys* and the ground squirrel *Spermophilinus*. However, all the sites close to the Aragonian/Vallesian boundary are characterized by low diversity levels and a rodent assemblage which indicates the existence of open areas. Thus, the dispersal of the hipparionine horses in the area is associated to a short-lasting shift towards dryer conditions. In the Calatayud-Daroca Basin (east-central Spain) the entry of *Hipparion* s.l. does not seem to coincide with an specially dry phase.

Keywords: Rodentia, Insectivora, paleoenvironments, Vallesian, Miocene, Spain

Kurzfassung

In der vorliegenden Arbeit werden die Insektivoren und Nagetiere aus den Fundstellen Creu Conill 20 und 22 beschrieben. Es handelt sich dabei um die ältesten Fundstellen des Vallesiums im Vallès-Penedès Becken, die das FAD von *Hipparion* s.l. an der Basis von Chron C5r.1n (11,1 MA) widerspiegeln. Die Nagetierfauna ist stark von *Megacricetodon ibericus* dominiert, während die übrigen Arten nur Begleitfaunencharakter haben. Diese Faunenzusammensetzung steht im Gegensatz zu dem, was aus anderen Fundstellen (Can Missert, Upper Hostalets de Pierola, Can Ponsic) in diesem Becken bekannt ist. Dort dominieren *Hispanomys* und *Spermophilinus*. Alle diese Fundstellen an der Grenze von Aragonium/Vallesium zeigen eine geringe Faunendiversität und eine für Offenlandschaften typische Nagetierassoziation. Das bedeutet, dass die Verbreitung der Hipparionen in diesem Gebiet mit einer kurzfristigen Trockenphase einher geht. Im spanischen Calatayud-Daroca Becken hingegen scheint die Einwanderung von *Hipparion* s.l. nicht mit einer Trockenphase zusammenzufallen.

1. Introduction

The Vallesian Mammal Stage was established by CRUSAFONT (1950) in the Vallès-Penedès Basin, where the first hipparionine horses entering Europe are still associated with a typical Middle Miocene mammalian fauna. The dispersal of *Hipparion* s.l. across the Old World was possible because of a global sea level fall of about 100 m (HAQ et al., 1987) that connected North America and Asia through Beringia. Surprisingly, such important global changes had little effect on terrestrial mammalian communities both in Spain (AGUSTÍ et al., 1999, AGUSTÍ et al., 2001) and the Paratethys realm (STEININGER et al., 1985, BERNOR et al., 1988), since no major turnovers have been recorded. Apparently the first hipparionine horses encountered an environment very similar to that existing in the late Middle Miocene.

In the last decade, the findings in the Can Guitart 1 section enabled to accurately date for the first time the First

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Appearance Datum (FAD) of *Hipparion* s.l. in the Vallès-Penedès Basin at the base of chron C5r.1n (11.1 Ma; GARCÉS et al. 1996). This age is congruent with the radiometric dating of key sites in Central Europe that suggest ages close to 11.5 +/- 0.5 Ma for the *Hipparion* s.l. FAD (BERNOR et al., 1988). RÖGL & DAXNER-HÖCK (1996) estimated the age of this event to be 11.2, based on Central-Eastern Paratethys correlations. However, the chronologic estimates of this event in the Daroca area (east-central Spain; GARCÉS et al., 2003), in Sinap (Turkey; KAPPELMAN et al., 1996), Siwaliks (Pakistan; BARRY et al., 1982; BARRY et al., 1985) and Ngororo formation (Kenya; PICKFORD, 2001) provide somewhat younger dates, ranging from 10.7 to 10.3 Ma, which might indicate that this dispersal was somewhat diachronic.

The Can Guitart 1 section is placed southeast of the city of Terrassa (UTM 4180-45990) and consists in a short series of about 50 meters dominated by conglomerates and alternating thinner brown-grey lutite layers, which have been interpreted as medial facies of an alluvial fan. Besides *Hipparion* and other large mammals, this section provided two fossiliferous levels with abundant microfauna: Creu Conill 20, in the lower part, and Creu Conill 22, about 20 meters above the former. The locality of Creu Conill 20 is especially relevant since it records the FAD of *Hipparion* s.l. in the basin, together with a small mammal assemblage which is described in this paper. Apart from *Hippotherium primigenium*, the large mammal assemblage from Creu Conill 20 also includes *Sansanosmilus jordani*, *Listriodon splendens*, *Proptamochoerus palaeochoerus*, *Parachleuastochoerus crusafonti*, *Miotragocerus pannoniae* and Cervidae indet. (AGUSTÍ et al., 1997). As stated, Creu Conill 20 is placed at the base of chron C5r.1n (GARCÉS et al., 1996). Above the level of Creu Conill 20, Creu Conill 22 delivered a richer and similar small mammal assemblage, in this case associated with *Hippotherium primigenium*, *Machairodus aphanistus* and *Miotragocerus pannoniae* (AGUSTÍ et al. 1997). This level is placed in the last reversed interval of chron C5r (GARCÉS et al., 1996). From a paleoherpetological point of view, testudinids (Creu Conill 20 and 22) and anguids (Creu Conill 22) are also frequent in the section (J. RENOM, pers. com.). A provisional faunal list of the small mammals present in both sites was given by AGUSTÍ et al. (1997), but a description of the fauna has not been published until date. This is one of the purposes of the present paper, where we will describe the rodents and insectivores of Creu Conill 20 and 22. In order to investigate the existence of faunal or environmental changes associated to the *Hipparion* s.l. dispersal, we will also focus in the changes in the composition and structure of the small-mammal assemblages throughout the latest Aragonian and the earliest Vallesian in Spain.

2. Material and Methods

The material described here is stored in the collections of the Institut de Paleontologia Miquel Crusafont in Sabadell,

Barcelona (abbreviated as IPS preceding the collection number). The first number denotes the box that contains the specimen, while the second number refers to the specimen itself. Dental nomenclature and measures for Erinaceidae following MEIN & MARTÍN-SUÁREZ (1993), Dimylidae after MÜLLER (1967), Soricidae following REUMER (1984), Talpidae after HUTCHISON (1974). Concerning the rodents, dental nomenclature and measurements for the Sciuridae follow CUENCA (1988), Cricetidae after MEIN & FREUDENTHAL (1971) and DAAMS & FREUDENTHAL (1988), Gliridae after DAAMS (1981), and Castoridae after STEHLIN & SCHAUB (1951), CRUSAFONT et al. (1948) and ALDANA CARRASCO (1991). All the measurements are in millimeters; L indicates length and W indicates width. For the Castoridae we have also classified the teeth in the age classes (AC) by ALDANA CARRASCO (1991) and measured crown high (AL3) and the distance from the tooth basis to the basis of the hypostria or hypostriid (AL1). In the tables, n indicates the number of specimens measured, and s.d. the standard deviation.

3. Systematic Palaeontology

Ordo Insectivora BOWDICH, 1821

Familia Erinaceidae FISCHER VON WALDHEIM, 1817

Genus *Parasorex* VON MEYER, 1865

Parasorex cf. *socialis* VON MEYER, 1865
(Plate 1, figs. 4-6)

Locality: Creu Conill 22

Material and measurements: 3 p4 (L = 1.85, W = 1.08; L = 1.84, W = 1.15; L = 1.85, W = 1.07), 1 broken M1 or M2 (no measurements can be taken), 3 M3 (L = 1.13, W = 1.77; L = 1.12, W = 1.66; L = 1.18, W cannot be measured).

Description:

M1/2: The tooth is broken and lacks the labial side. The protocone is slightly higher than the hypocone. The metaconule is strongly weathered but clearly isolated from the entoloph. There is no connective postprotocrista. The end of the posterior arm of the metaconule is missing, but the beginning seems to go in direction to reach the posterolabial corner of the tooth. The lingual face is softly orange-pigmented.

M3: The teeth show their typical triangular shape. Ridges connect the three main cusps. The paracone and the protocone are the highest cusps. There is a small interruption of the crest that connects these two cusps. The anterolabial zone of the tooth especially protrudes the outline in one of the specimens. There is an anterior cingulum at the base, running from the parastyle until the middle part of the tooth. The central basin is completely closed.

p4: The protoconid is the highest and biggest cusp. A small valley interrupts the connection with the metaconid. The trigonid basin is short and completely open by its lingual side. The talonid is relatively long. There is a broad cingulum at its distal end. A thin and short climbing crest runs

from the central part of this cingulum until the center of the talonid. No lateral cingula are observed.

Remarks: The lack of connection between the protocone and the metaconule indicates that the species belong to the genus *Parasorex*. According to the available data, *P. socialis* is the unique known species of *Parasorex* during the Early Vallesian in Spain (VAN DEN HOEK OSTENDE 2001). Nevertheless, the classification *P. cf. socialis* seems more apt, since not enough diagnostic material has been recovered to determine the species with certainty.

Familia Dimylidae SCHLOSSER, 1888

Genus *Plesiodimylus* GAILLARD, 1899

Plesiodimylus sp.
(Plate 1, fig. 3)

Locality: Creu Conill 20

Material and measurements: Fragment of a dentary bone with a m2 (L = 2.56, Trigonid length = 1.57, Talonid length = 0.99, W = 1.24, Mesialmost side of the tooth to Protoconid position-orthogonal length ("V" in MÜLLER, 1967) = 1.30, Distalmost side of the tooth to Protoconid position-orthogonal length ("H" in MÜLLER, 1967) = 1.26).

Description:

m2: The protoconid and the metaconid are the highest cusps. They are connected by a continuous ridge that is slightly depressed on its central part. This ridge makes a perfect right angle with the lingual face. The hypoconid and the entoconid are not very high. The talonid is noticeably narrower than the trigonid. Both trigonid and talonid basins are open by their lingual side. The paraconid is apparently divided into two minor cuspules. The paralophid runs from the cuspule placed more anterolabially until the protoconid. A well-delimited buccal cingulum runs from anterolingual cuspule of the paraconid until the entoconid, thus covering the base of the tooth by the buccal and distal faces.

Remarks: The presence of the genus *Plesiodimylus* in the Vallès-Penedès area is rather frequent in Vallesian and Late Aragonian localities (GIBERT, 1975). VILLALTA & CRUSAFONT (1944) identified the species present in those localities as *P. chantrei*. The ascription is not so evident, and must bear in mind that the identification of the species was done when only *P. chantrei* was formally described, and consequently the genus was monospecific. Since then, no deep overview of the *Plesiodimylus* material from the Vallès-Penedès area has been done, and so the species has been always referred as *P. chantrei* in all the faunal lists of the localities from that basin. Nowadays five more species are included within the genus (*P. huerzeleri*, *P. crassidens*, *P. bavaricus*, *P. johanni* and *P. gaillardi*; although *P. huerzeleri* and *P. bavaricus* are not accepted by some authors). The diversity within the genus is wide enough to consider the question whether the species present at the Vallès-Penedès area is actually *P. chantrei* or not. Unfortunately, only an m2 is available

in this sample, and so any identification should better stay preliminary. In any case, it must be noticed that the molar has a more "squared-shape" of the occlusal outline and a wider trigonid than any other figured m2 of a *Plesiodimylus* species. According to the scatter diagram given by KÄLIN & ENGESSER (2001:22, fig. 18), the measurements of this tooth fit better within the range for *P. johanni* than for *P. aff. chantrei* from Can Llobateres. For all these reasons, it has been considered better to leave the identification as *Plesiodimylus* sp., till further research on larger samples will shed light on how many species, and which ones, were present in the Vallès-Penedès area during Aragonian and Vallesian times.

Familia Soricidae FISCHER VON WALDHEIM, 1817

Genus *Miosorex* KRETZOI, 1959

Miosorex sp.
(Plate 1, figs. 1-2)

Locality: Creu Conill 22

Material and measurements: 1 m1 (L = 1.26, TAW = 0.90, TRW = 0.80), 1 M1 (AW = 1.04, PW = 1.16, PE = 0.84, LL = 1.07, BL = 1.09).

Description:

m1: The buccal cingulum is very close to the paraconid. The protoconid is placed at the middle part of the anterior side. The endoloph stands at a right angle on this anterior part. The anterior margin of the tooth is convex, thus producing a strongly curved outline.

M1: In occlusal view, the tooth has a sub-quadrate shape, slightly wider than long. There is a moderate posterior emargination. The ectoloph is continuous. The metacone is the highest cusp. The metacrista is larger than the post-mesocrista. The paramesocrista is shorter than the postmesocrista, but longer than the paracrista, thus producing an asymmetrical aspect of the ectoloph. The endoloph is not continuous. There is a soft valley interrupting the connection between the protocone and the hypocone. The hypocone and the posterior part of the hypoconal flange are somewhat worn. The paraloph makes almost a right angle at the anterior part. The anterior border of the tooth is convex, thus producing a strongly curved outline.

Remarks: The current specimens are similar in size to those of *Miosorex desnoyersianus* described by BAUDELLOT (1972) for the MN 6 locality of Sansan, and slightly smaller in general terms than those of *M. aff. grivensis* from all the localities reported by DE JONG (1988) of the Calatayud-Daroca Basin. Nor *M. grivensis*, neither *M. desnoyersianus* lack the buccal cingulum on m1. The unique M1 is not extremely well preserved, and so it is not helpful on the taxonomical determination. For these reasons, the ascription has been kept at *Miosorex* sp.

Familia Talpidae FISCHER VON WALDHEIM, 1817

Genus *Talpa* LINNAEUS, 1758

***Talpa minuta* BLAINVILLE, 1838**

(Plate 1, fig. 7)

Locality: Creu Conill 20**Material and measurements:** Distal fragment of humerus (Distance between external margin of the capitulum and external margin of the fossa for muscle flexor digitorum – (measurement “9” in HUTCHISON, 1974) = 5.51, Diaphysal width (measurement “13” in HUTCHISON, 1974) = 2.68).**Description:****Humerus:** The capitulum is rounded in anterior view. In posterior view it shows a rather convex surface. The ectepicondylar width is similar to that of the entepicondyle. The trochlea is well delimited in the anterior view, but not in the posterior view. The oval olecranon fossa is relatively wide in comparison with the visible part of the diaphysis.**Remarks:** The distal fragment of humerus is similar in size to the remains reported by AGUSTÍ & GIBERT (1982) for *T. minuta*. The distribution of *Talpa minuta* in the Vallès-Penedès Basin is restricted to Castell de Barberà, Sant Quirze and Hostalets de Pierola (GIBERT, 1974, AGUSTÍ & GIBERT, 1982).

Ordo Rodentia BOWDICH, 1821

Familia Cricetidae FISCHER VON WALDHEIM, 1817

Genus *Hispanomys* MEIN & FREUDENTHAL, 1971***Hispanomys dispectus* AGUSTÍ, 1981**

(Plate 2, figs. 1-6)

Distribution: Creu Conill 20, Creu Conill 22**Locality:** Creu Conill 22.**Material and measurements:** Table 1**Description:****M1:** There is a deep groove between the two lobes of the anterocone, but they remain joined by a short and narrow ridge in most cases. In 53 % of the teeth there is a lingual anteroloph, which partially closes the valley. In one case the protosinus is completely closed by the lingual anteroloph, while in the remaining teeth it is less developed and ends in a small protostyle obstructing the protosinus. In about 26 % of the teeth there is no lingual anteroloph and the valley is wide and open, but in one tooth it is narrow and appears closed by a well-developed protostyle. Most teeth do not present a true mesoloph; in its place a small protuberance corresponding to this ridge is observed in

the ellipse-shaped posterior valley. In one case only this valley is rounded and no trace of this protuberance is observed. In four cases there is a lingual spur at the end of the posterior ectoloph of the paracone which points towards a short mesoloph without joining it. In its turn the posterior ectoloph never fuses with the metacone in these cases. In nearly half of the molars the anterior ectoloph is complete, although the connection anterocone-paracone consists only of a weak and straight ridge. In three cases this connection is formed by an irregular ridge consisting of an anterior spur departing from the paracone and the ectoloph of the anterocone. In only two cases the anterior ectoloph is not complete, and the anterocone has a posterior arm directed to the paracone, which lacks any anterior crest. There is a straight sinus usually closed by a low cingulum, but rarely an entostyle is observed. Usually the anterosinus and mesosinus remain open, but in few cases they appear closed by cingula. A poor, very short lingual arm of the posteroloph is present in about 75 % of the material.

M2: A short lingual anteroloph is present in nearly half of the molars; in the remaining there is no anteroloph. The anterior and the posterior ectolophs are always present. There is never a true mesoloph, but a small protuberance on the longitudinal ridge coinciding with its position. The sinus is straight and, as the mesosinus, it is usually open. The anterosinus and protosinus are always open.**M3:** There is no anteroloph. The anterior ectoloph is always complete except in two teeth. In these cases there is a ridge formed by the posterior arm of the anterocone, which in one tooth points towards an anterior spur of the paracone, but without connecting to it. The posterior ectoloph is always complete and closes an elliptic valley. The mesoloph is usually long, nearly joining the posterior ectoloph.**m1:** There is always a labial anterolophid, which is usually long closing the protosinusid. The metalophulid is always anterior and it may connect directly to the posterior wall of the anteroconid without joining the anterolophulid. In some teeth the metalophulid is joined to the anterior end of the anteroloph at the posterior wall of the anteroconid. In more than half of the teeth there is no mesolophid, and in the remaining ones it is very reduced. The sinusid is closed by low cingula in 64 %, whereas the anterosinusid and mesosinusid remain generally open and are obstructed by a poorly developed cingulum only in few cases. The posterosinusid is always open and it is usually a wide valley.

	Length					Width				
	n	min	mean	max	s. d.	n	min	mean	max	s. d.
M¹	17	2.90	3.12	3.35	0.11	17	1.65	1.76	1.88	0.14
M²	16	2.11	2.52	2.77	0.16	17	1.63	1.81	2.00	0.09
M³	14	1.74	1.74	1.94	0.12	14	1.37	1.64	1.85	0.14
M₁	11	2.47	2.65	2.82	0.11	14	1.46	1.64	1.81	0.10
M₂	11	2.40	2.53	2.69	0.09	12	1.74	1.87	1.98	0.08
M₃	7	2.17	2.29	2.41	0.09	8	1.65	1.76	1.88	0.07

Table 1: Measurements taken for *Hispanomys dispectus* from Creu Conill 22.

m2: The labial anterolophid is well developed and connected to the base of the protoconid in many cases, but this ridge is absent in 27 %. There is no lingual anterolophid. A very short mesolophid is present in about half of the teeth. In 72 % of the teeth the sinusid is closed by a low cingulum formed by two ridges departing from the basis of protoconid and hypoconid, respectively. Generally the sinusid is straight but in some cases it may point slightly forwards. The posterosinusid is always open.

m3: There is a long labial anterolophid that nearly reaches the labial margin of the tooth in 75 %, whereas in the remaining teeth it is poorly developed. The mesolophid is generally absent. The cusps are always placed in an alternate position.

Remarks: *Hispanomys dispectus* from Creu Conill 22 is morphologically very similar to the material of the type-locality Lower Hostalets, although there are many characteristics, such as the less developed mesolophids and mesolophids, which resemble the population of Upper Hostalets. As in Upper Hostalets the protosinus in the M1 is not completely closed in a larger number of teeth than in Lower Hostalets. In this aspect the material of Creu Conill 22 is almost equal to that of Upper Hostalets. From the metrical point of view the material from Creu Conill 22 is not significantly different from that of Lower and Upper Hostalets. The only difference with the material of those sites is that the specimens from Creu Conill 22 present slightly more elongated second and third molars, in both the upper and lower dentition.

Locality: Creu Conill 20

Material and measurements: Table 2

Description:

M1: The material is not significantly different from that of Creu Conill 22 except for ectoloph development. The anterior ectoloph is always absent, and the labial lobe of the anterocone shows a short ectoloph pointing to the paracone, which in its turn does not present any trace of an anterior spur. The posterior ectoloph is always present though it is weak, formed by a narrow and long posterior spur of the paracone that reaches the metacone.

M2: The material is very similar to that of Creu Conill 22, but the sinus is closed in all teeth either by an entostyle (1) or by low cingula (3). The remaining valleys are open.

M3: The material is not significantly different from that of Creu Conill 22.

m1: There is only one molar and it exhibits a rounded

anteroconid with a well-developed labial anterolophid which delimits a narrow and open protosinusid. The anterolophid and the metalophid reach the posterior wall of this anteroconid separately. There is a long mesolophid. All valleys except for the anterosinusid appear closed by cingular formations (protosinusid, mesosinusid and posterosinusid) or stylids (sinusid).

m2: The material of Creu Conill 20 is not significantly different from that of Creu Conill 22.

m3: The teeth strongly resemble the material of the locality described above, but there are small differences. There is a mesolophid in two teeth, while in the remaining tooth it is absent. The sinusid is never closed by cingular formations.

Remarks: The Creu Conill 20 material is very similar from the metrical point of view to that of Creu Conill 22 and Upper Hostalets. Morphologically it is also very close, although in Creu Conill 20 the mesolophids are usually longer and a greater number of valleys appear closed. However, this material is very scarce, so the differences may be due to a sampling bias.

Genus *Megacricetodon* FAHLBUSCH, 1964

Megacricetodon ibericus (SCHAUB, 1944)

(Plate 2, figs. 7-12)

Localities: Creu Conill 20, Creu Conill 22

Locality: Creu Conill 22.

Material and measurements: Table 3

Description:

M1: There is a cingular ridge at the anterior border in front of the anterocone in more than 80 % of the teeth. This ridge can be fused either with labial or lingual ridges. Frequently the valleys are closed by well-developed cingular formations. Small cusps (styles) at the end of the valleys are present frequently, in the same position as the cingula. These styles can appear in all the valleys, especially in the sinus (70 %) and the mesosinus. Cingula may be observed closing any valley, but they are more frequent in the lingual side. Nearly 80 % of the teeth possess a cingulum closing the protosinus and an entostyle in the sinus. In many cases there is a cingulum closing the sinus fused to the one closing the protosinus, which in its turn joins the anterior ridge on the base of the anterocone defining a continuous antero-lingual cingulum. Both patterns may be associated with the presence of a mesostyle. In other cases there is

	Length					Width				
	n	min	mean	max	s. d.	n	min	mean	max	s. d.
M ¹	3	2.97	3.11	3.32	—	4	1.97	2.01	2.04	0.03
M ²	4	2.26	2.36	2.57	0.14	4	1.79	1.81	1.88	0.06
M ³	5	1.60	1.73	1.75	0.06	5	1.36	1.56	1.82	0.17
M ₁	1	—	2.45	—	—	1	—	1.64	—	—
M ₂	3	2.10	2.36	2.50	—	3	1.68	1.82	1.92	—
M ₃	3	2.13	2.17	2.19	—	3	1.72	1.76	1.78	—

Table 2: Measurements taken for *Hispanomys dispectus* from Creu Conill 20.

only one anterior ridge at the base of paracone and several styles in the valleys (usually three: protostyle, mesostyle and entostyle). The anterocone is deeply split in most teeth. The labial anterolophule is absent. Nearly all the molars have a poorly developed posterior spur on the paracone pointing towards the mesostyle. There is no mesoloph. The metaloph departs from behind the hypocone, nearly at the posterior margin of the teeth. This implies the absence of the posteroloph and the posterosinus. Only 7 % of the teeth have a vestigial posteroloph and a narrow posterosinus.

M2: A low lingual anteroloph closes the protosinus and joins the protocone at its base. The labial anteroloph is not as developed as the lingual one, but it is long and joined to the paracone, closing the anterosinus. Thus the branches of the anteroloph form a continuous anterior ridge closing the lingual and labial valleys. As in M1 many molars tend to develop small styles in the valleys. Nearly 74 % shows an entostyle, whereas the mesostyle is rarer than in the M1 and it is only present in about 2 % of the molars. In some cases there is not an entostyle, and there is a low ridge closing the sinus. The longitudinal crest is connected to the protocone indirectly through paracone and protolophule. The latter in its turn is joined to the longitudinal crest behind the protocone. The sinus is mostly transverse and slightly pointing forwards at its labial end. In most cases (about 67 %) the paracone has a long ectoloph reaching the bottom of the mesosinus. The remaining teeth show a less developed posterior spur at the paracone, and only 7 % lack the posterior spur. There is no mesoloph. The metalophule is obliquely directed forwards, and it joins a short posteroloph behind the hypocone. For that reason the posterosinus is very narrow, except in one molar where the posterosinus is absent. In about 7 % there is a double metalophule.

M3: More than half of the molars is rounded, while the remaining ones are slightly square-shaped. The anteroloph is long. The protocone and paracone are oppositely rather than alternately placed. The protolophule is posterior in 53 %, but it can be transverse or point obliquely forward. The paracone usually has an ectoloph, which is frequently long, and in about 30 % it is joined with an anterior spur departing from the metacone. In several cases (20 %) there is a short anterior spur at the metacone that does not reach the ectoloph. The paracone may also have an anterior ectoloph, but it is a quite rare feature. Nearly all molars lack the mesoloph. The posteroloph is usually absent.

m1: The anteroconid is deeply split, forming an X-pattern with the metaconid and protoconid. The cusps are placed

alternately, so all the valleys point forwards. Two low cingular ridges departing from the labial and lingual ends of the anteroconid close the protosinusid and the anterosinusid, respectively. Lingual cingula are more developed than the labial ones. In many cases cingular formations close the sinusid and more rarely the mesosinusid. The mesolophid is absent.

m2: The morphology resembles that of m1 with alternate cusps and the valleys curved forwards. The labial anterolophid is long and reaches the base of the protoconid. There is a short (nearly vestigial) lingual anterolophid in 28 % of the molars, whereas this ridge is absent in the rest of the molars. A low ridge may close the sinusid. The mesolophid is absent in all molars. The posterolophid is short and joins the entoconid.

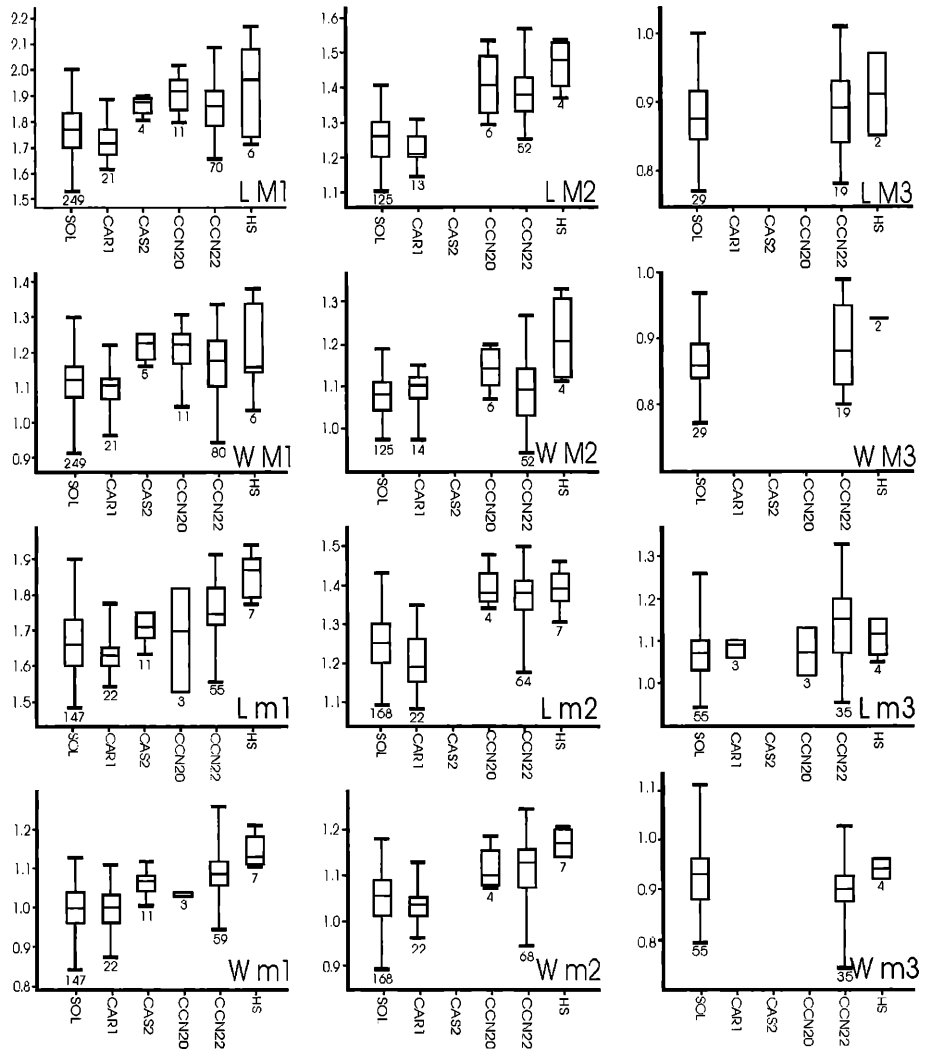
m3: Triangular shaped molar. There is a long anterolingual ridge closing the protosinusid. The sinusid is open. The mesosinusid may be closed by a low ridge. There is no mesolophid.

Remarks: The material from Creu Conill 22 represents the largest sample of *Megacricetodon ibericus* ever recovered in the Vallès-Penedès Basin, consisting of 338 molars. A considerable intrapopulation variation would be expected in such a large sample, but the result is the opposite. The population of Creu Conill 22 is very homogeneous and less diverse in morphotypes than the ones from Hostalets de Pierola (lower and upper levels) in the same basin and Nombrevilla and Carrilanga 1 (DAAMS & FREUDENTHAL, 1988) in the Calatayud-Daroca Basin. The size of the molars is close to the values observed for the ones of Hostalets de Pierola (AGUSTÍ, 1980) and only slightly smaller (Fig. 1). Figure 1 also shows that the molars of the populations from the Vallès-Penedès Basin are considerably bigger than the ones from the Calatayud-Daroca Basin, and they are closer in size to that of Casasola 2 (Duero Basin). Their morphology resembles that of the late populations of this species: upper levels of Hostalets de Pierola, Nombrevilla, Carrilanga 1 and Ampudia 9 and 10. The characters considered as advanced by one of us (AGUSTÍ, 1981) are observed in the *M. ibericus* of Creu Conill 22. These features consist of a larger size; reduction of longitudinal ridges; trend towards an alternate position of the cusps; presence of an X-pattern in the m1 defined by the anteroconid with the protoconid and the metaconid; and a tendency to a transformation of the cingular ridges that close the valleys in small cusps. This last character deserves particular interest in the population studied, because in many teeth (especially M1

	Length					Width				
	n	min	mean	max	s. d.	n	min	mean	max	s. d.
M¹	70	1.64	1.85	2.10	0.078	80	0.94	1.17	1.34	0.058
M²	52	1.25	1.38	1.57	0.062	52	0.94	1.09	1.26	0.063
M³	19	0.78	0.89	1.01	0.082	19	0.80	0.88	0.99	0.057
M₁	55	1.55	1.76	1.92	0.091	59	0.94	1.09	1.26	0.085
M₂	64	1.17	1.37	1.50	0.071	68	0.94	1.12	1.25	0.071
M₃	35	0.95	1.14	1.28	0.067	35	0.74	0.89	1.03	0.062

Table 3: Measurements taken for *Megacricetodon ibericus* from Creu Conill 22.

Figure 1: Box plots comparing length and width of the lower (lower-case letters) and upper molars (capital letters) of *Megacricetodon ibericus* from Creu Conill 20 and 22 to other Spanish sites. The box indicates the array of data between 25 and 75 percent quartiles and the horizontal line drawn inside the box shows the median. The minimal and maximal values are shown with thin horizontal lines outside the box. Below each individual box plot a number indicates the amount of teeth in each sample. Locality abbreviations are as follows: SOL, Solera; CAR1, Carrilanga 1; CAS2, Casasola 2; CCN20, Creu Conill 20; CCN22, Creu Conill 22; HS, Upper Hostalets de Pierola. SOL and CAR1 are placed in the Calatayud-Daroca Basin, and are dated as Late Aragonian and Early Vallesian, respectively. CAS2 is an Early Vallesian site from the Duero Basin. CCN20, CCN22 and HS are Early Vallesian sites from the Vallès-Penedès Basin. Data for SOL and CAR1 have been taken from DAAMS & FREUDENTHAL (1988), while data for CAS2 are from GARCÍA MORENO (1987). The material from SOL is identified as a transitional population between *M. crusafonti* and *M. ibericus* in DAAMS & FREUDENTHAL (1988).



and M2) some of the ridges have been modified into small cusps. This usually happens in the sinus, which shows an entostyle instead of a ridge closing the lingual end. A singular ridge is mostly observed in *M. ibericus* of the Upper Hostalets. Contrary to in this last locality, the labial valleys are usually open in Creu Conill 22.

Locality: Creu Conill 20

Material and measurements: Table 4

Description:

M1: The material is very similar to that of Creu Conill 22.

Nevertheless, there are some differences concerning the development of elements closing the valleys. Valleys are usually closed by styles, not by singular formations. An entostyle is present in 80 %, a parastyle and mesostyle in 60 %, whereas the protostyle is rarer, and is only present in 30 %. The paracone usually has a short ectoloph that reaches the base of the metacone, but it is absent in 20 % of the molars.

M2: These molars have no significant differences with the ones of Creu Conill 22 except for the development of styles in the lingual and labial valleys. The presence of a

	Length					Width				
	n	min	mean	max	s. d.	n	min	mean	max	s. d.
M¹	11	1.79	1.90	2.02	0.146	11	1.04	1.21	1.31	0.008
M²	6	1.29	1.41	1.54	0.059	6	1.07	1.14	1.20	0.064
M³	1	—	0.85	—	—	1	—	0.90	—	—
M₁	5	1.53	1.68	1.82	0.072	3	0.94	1.21	1.26	—
M₂	4	1.34	1.39	1.48	0.106	4	1.07	1.11	1.19	0.051
M₃	3	0.95	1.07	1.28	0.079	2	0.92	—	1.00	—

Table 4: Measurements taken for *Megacricetodon ibericus* from Creu Conill 20.

mesostyle is rarer (about 33 %), whereas the entostyle is more frequently present.

M3: There is only one right molar, which is rounded and very similar to the material of Creu Conill 22. The paracone has a short anterior ectoloph that is directed towards the anteroloph. The protolophule is anterior.

m1: The description of these molars is analogous to that of Creu Conill 22.

m2: There is no lingual anterolophid. The labial branch of the anterolophid is connected to the base of the protoconid and closes the protosinusid. A low ridge often closes the sinusid. The mesolophid is absent. The rest of characters as in the material of Creu Conill 22.

m3: The material is not significantly different from that of Creu Conill 22.

Remarks: The material does not significantly differ from that of Creu Conill 22 and, as in that site, there is little morphological variation, although in the case of Creu Conill 20 this may be an effect of the smaller sample size.

Genus *Democricetodon* FAHLBUSCH, 1964

Democricetodon cf. *sulcatus* FREUDENTHAL, 1967 (Plate 2, figs. 13-14)

Locality: Creu Conill 22

Material and measurements: 1 M1 (L = 1.62, W = 1.05), 1 eroded m2 (no measurements were taken).

Description:

M1: The anterocone is slightly subdivided in two lobes. The labial lobe is broader than the lingual one. There is a double protolophule. The mesoloph is short. The metalophule is very short and placed rather labially, directly connecting the metacone to a well-developed posteroloph, which in its turn closes the posterosinus. The sinus is straight. The remaining valleys are closed by moderately developed cingula.

m2: A well-developed labial anterolophid closes the protosinusid. The lingual ridge is very short. The metalophulid and the hypolophulid are anterior. There is no mesolophid. The sinusid is slightly proverse. Both the sinusid and the mesosinusid are open. The posterolophid joins the posterior side of the entoconid, closing the posterosinusid.

Remarks: The size of these molars seems close to that of larger-sized later *Democricetodon* such as *D. sulcatus* (FREUDENTHAL, 1967). Some morphological traits also appear in *D. sulcatus* such as the presence of a slightly subdivided anterocone in the M1. Other resemblances are the presence of a short mesoloph in the M1 or the absence of mesolophid in the m2. However, the material is too scarce to unquestionably ascribe it to *D. sulcatus*.

Genus *Cricetulodon* HARTENBERGER, 1965

Cricetulodon n.sp. (Plate 2, fig. 15)

Locality: Creu Conill 22.

Material and measurements: 1 M2 (L = 1.02, W = 0.87), 1 m1 (L = 1.21, W = 0.73).

Description:

M2: This tooth presents a lingual anteroloph closing the protosinus. The labial ridge of the anteroloph is also well developed and closes the anterosinus. The protolophule is anterior. The longitudinal ridge does not depart from the protocone, but from the posterior side of the paracone. The mesoloph reaches the labial margin and its labial end points to the anterior side of the metacone, where it joins the cingulum that closes the mesosinus. A posterior metalophule is present, joining the posteroloph. The posteroloph is connected to the posterior side of the metacone, closing the posterosinus. All the valleys appear closed by well-developed cingular formations.

m1: Small and elongated molar. The anteroconid is small and only slightly divided by a weak anterior groove. The lingual cusp of the anteroconid is more developed than the labial one. Two lophes depart from both lingual and labial ends of the anteroconid closing the protosinusid and the anterosinusid, respectively. The labial loph is shorter due to the proximity of the metaconid. The anterolophulid is low and has a central position, although its anterior end points slightly lingually and is connected to the lingual lobe of the anteroconid. There is no mesolophid. The sinusid and mesosinusid are closed by very low cingular formations. The hypolophulid is very short and the entoconid contacts the longitudinal ridge. The posterolophid closes the posterosinusid.

Remarks: The studied material differs from all the described *Cricetulodon* species by its much more smaller size. It is also smaller than many small-sized *Democricetodon* species. The presence of a short hypolophulid in the m1 and the absence of mesolophid in the same molar strongly resemble *C. sabadellensis*, but the molars also show a slightly divided anteroconid with the lingual lobe broader such as *C. hartenbergeri*. The M2 is closer to *C. hartenbergeri*, and it has a long mesoloph reaching the labial margin of the molar. A larger sample is required to adequately characterize *Cricetulodon* n. sp. from Creu Conill 22.

Familia Gliridae MUIRHEAD, 1819

Genus *Miodyromys* KRETZOI, 1943

Miodyromys hamadryas (FORSYTH MAJOR, 1899) (Plate 2, figs. 16-17)

Locality: Creu Conill 22

Material and measurements: 2 M1 or M2 (L = 1.16, W = 1.25; L = 0.99, W = 1.15).

Description:

M1/2: Square-shaped teeth with concave wear surface. Six main ridges can be observed: anteroloph, protoloph, anterior centroloph, posterior centroloph, metaloph and posteroloph. The protoloph, the metaloph and the posteroloph reach the endoloph separately. The anteroloph points backwards but it is not connected to the endoloph. The protoloph also points backwards, whereas the metaloph is approximately transverse. There are five narrow

synclines. The posteroloph and the metaloph are also connected labially so the fifth valley is completely closed. The anterior centroloph is always long and points backwards without reaching the endoloph. The posterior centroloph is transverse and short in one case, reaching the midpoint of the tooth. In the other tooth there is a long and transverse posterior centroloph that is connected to the end of the anterior centroloph. There are always extra ridges, but their development is variable. In one tooth there is only a small anterior extra ridge that is weakly joined to the centroloph. The other tooth shows three extra ridges. An anterior extra ridge is connected to the paracone, and reaches the midpoint of the molar; a posterior extra ridge, shorter than the anterior one, connects weakly with the metacone; and finally, a very small and low extra ridge is placed in the valley defined by the centrolophs.

Genus *Muscardinus* KAUP, 1829

Muscardinus hispanicus DE BRUIJN, 1966

Locality: Creu Conill 20

Material and measurements: 1 m1 (L = 1.19, W = 1.11).

Description:

m1: Low-crowned molar with flat wear surface. The posterior margin is wider than the anterior one. Six main transverse ridges and their corresponding five synclines are present. The anterolophid is joined to the protoconid and the metaconid. There is a metalophid departing from this last cusp that joins the protoconid and completely closes the first valley. The centrolophid is long and reaches the labial margin. The termination of this ridge consists in a cusp comparable in size to the main cusps of the molar. There is a long and isolated mesolophid, which joins the mesoconid with a small lingual cusp. The posterolophid is fused both at its lingual and labial ends with a posterior extra ridge; thus the fifth syncline is also completely closed.

Remarks: The size and general morphology of this molar strongly resembles the *Muscardinus hispanicus* material from Castell de Barberà (AGUILAR et al., 1979).

Familia Castoridae HEMPRICH, 1820

Genus *Trogotherium* FISCHER, 1809

Subgenus *Euroxenomys* SAMSON & RADULESCO, 1973

Trogotherium (Euroxenomys) minutum (VON MEYER, 1838)

(Plate 2, fig. 18)

Localities: Creu Conill 20, Creu Conill 22

Locality: Creu Conill 22

Material and measurements: Table 5

Description:

M2: Small-sized molars with high crowns, which present

Element	AC	L	W	AL1	AL3
M2	AC0	2.94	2.72	2.51	9.20
	AC3	2.76	2.68	3.36	6.392
	AC5	3.08	—	—	—
	AC1	3.14	—	—	—
	AC4	—	2.96	3.18	6.25
M3	AC3	2.83	2.70	4.31	7.36
	AC4	2.66	2.80	0.98	4.27
	AC4	2.62	2.63	2.33	5.38

Table 5: Measurements taken for *Trogotherium (Euroxenomys) minutum* from Creu Conill 22.

three grooves on the labial side: parastria, mesostria and metastria. The mesostria is the deepest and longest one. The teeth possess a long hypostria, which, however, does not reach the crown basis. The occlusal surface is flat. The hypoflexus reaches the midpoint of the molar, whereas the mesoflexus, which is very curved, covers all the surface of the tooth up to the lingual side, nearly reaching the posterior side. There is a long and narrow parafofsete separated from the hypoflexus. This fofofsete is transverse in almost all the teeth, although it points slightly backwards on its lingual side. An oblique and narrow metafofofsete can also be observed. Its orientation is parallel to that of the mesoflexus. In one case the metafofofsete is wider on both its lingual and labial ends than in its central part.

M3: The teeth have high crowns with a flat and rounded occlusal surface. Only one groove can be observed on the labial side, the mesostria, which is well developed. The hypostria is long, but as in the M2 it does not reach the crown basis. The hypoflexus is short and more or less transverse, separated from a long, narrow and curved parafofofsete. The mesoflexus may be open or closed on its labial side. It is always long and points backwards. There may be a metafofofsete or, when it is open on both labial and lingual sides, a sinuous metafofofsete. There may be up to three small conules at the posterior side, and those on the lingual side are joined by a small ridge. The third conule, when present, is isolated and placed on the posterior side of the metacone. The metafofofsete or the metafofofsete encircles a circular submetafofofsete or submetafofofsete situated at the postero-lingual corner of the teeth.

Locality: Creu Conill 20

Material and measurements: 1 broken M1 or M2, measurements cannot be taken.

Description:

M1/2: The posterior side of the tooth is broken. There is a long and deep hypostria that does not reach the base of the molar. The hypoflexus is wide and reaches the midpoint of the molar. There is a small, strongly curved parafofofsete. There is an elongated and curved mesofosfofsete with the lingual end strongly pointing backwards. There is a reduced oval-shaped metafofofsete, placed at the medial plane of the molar. The mesofosfofsete partially surrounds the metafofofsete. The remaining characters cannot be observed.

Familia Sciuridae FISCHER VON WALDHEIM, 1817

Genus *Spermophilinus* DE BRUIJN & MEIN, 1968

Spermophilinus bredai (VON MEYER, 1848)
(Plate 2, figs. 19-20)

Locality: Creu Conill 22.

Material and measurements: 1 M1/2 (L = 1.83, W = 2.23), 2 M3 (L = 2.07, W = 2.19 ; L = 2.09, W = 2.07), 2 m1/2 (L = 1.89, W = 1.84 ; L = 2.08, W = 1.83).

Description:

M1/2: The anteroloph is long and low on its lingual side. The labial side is higher and a crest-like parastyle can be distinguished. The protocone and the hypocone cannot be distinguished within the endoloph. A weak mesostyle may be present, fused to the posterior wall of the paracone. The metaloph is directed forward and becomes very weak at the point where it joins the endoloph. The protoloph is higher than the metaloph. The metaloph and the protoloph trace a "V" The posteroloph is low in the lingual side and it just touches the metacone with its terminal part. This morphology basically results in four transverse ridges that cross the whole surface of the tooth.

M3: A well-developed paracone and a lower protocone are the only cusps that can be distinguished. The anteroloph is long and connected to the protocone and paracone. The protoloph is also connected to the protocone, so both ridges enclose a narrow and shallow anterior valley. There is a posteroloph that covers the postero-labial side of the molar, although this ridge is weak compared to the anteroloph and protoloph.

m1/2: The entoconid is included into the posterolophid and it cannot be distinguished. There is a small anteroconulid joined to the protoconid in one case. In the other the anteroconulid is an isolated cusp placed quite posteriorly, displaced to the central valley. There is a small mesoconid that is joined to the posterior side of the protoconid in one case, while in the other it is isolated. The posterolophid reaches the metaconid in one case. The central valley is deep and rounded. The sinusid is transverse.

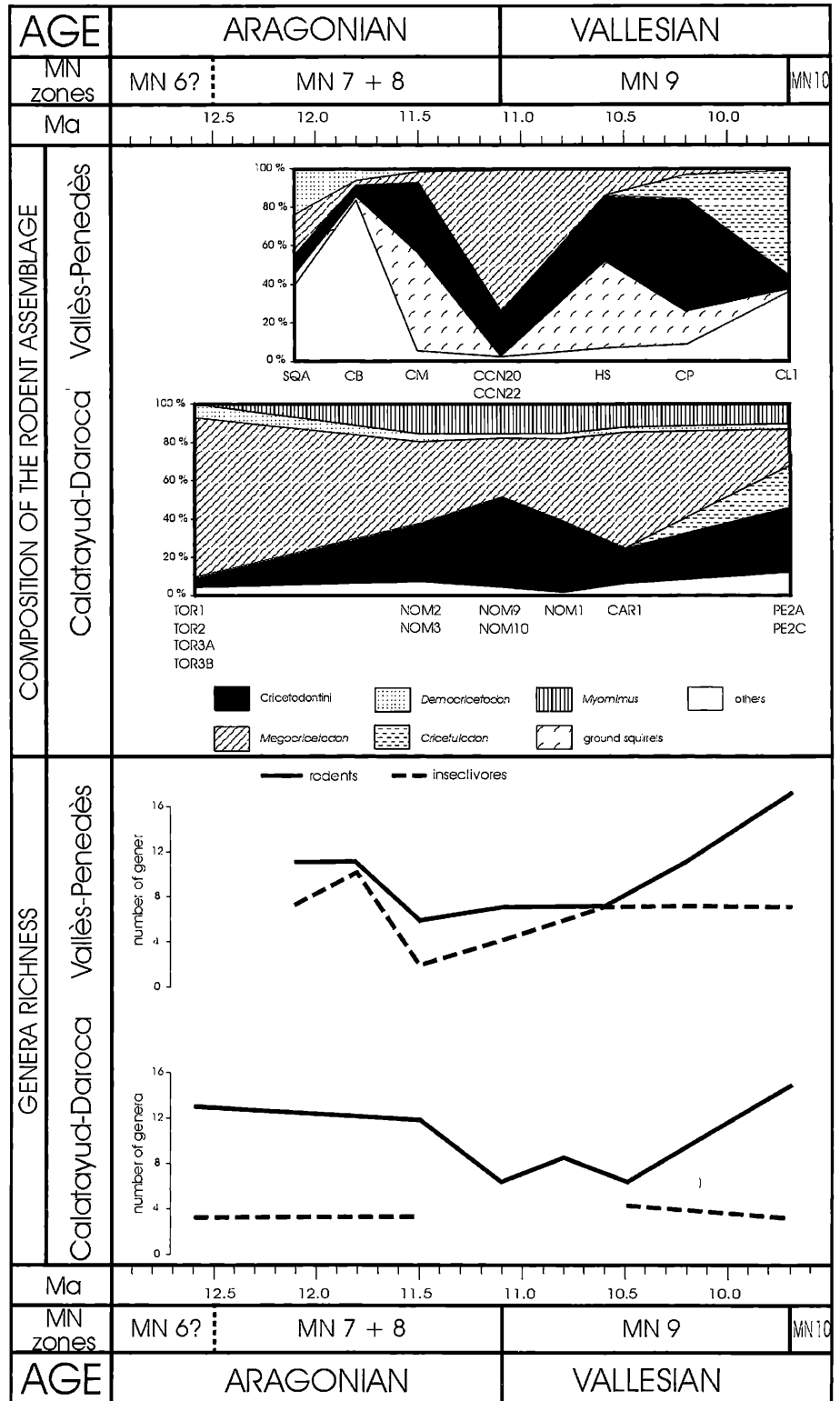
4. Discussion

The small mammal assemblages from Creu Conill 20 and Creu Conill 22 show relatively few species, a fact which in the case of Creu Conill 20 may be partly an effect of the small sample size. Nevertheless, the material from Creu Conill 22 includes nearly 450 specimens, and this sample size is comparable to other well-known localities from the Vallès-Penedès Basin (such as Castell de Barberà or Can Llobateres). Taphonomic factors might explain the differences in composition and diversity between the sites considered. However, since all these sites are placed in medial to distal facies of alluvial fans, we assume that no major taphonomical bias occurred, and that the differences observed thus result from changes in the environment. We have assessed this issue by comparing the insectivore

and rodent genera richness and the composition of the rodent assemblage throughout the latest Aragonian and the Early Vallesian (Fig. 2). We have also considered the extension of the changes observed in the Vallès-Penedès to other areas of Spain, and we have represented the temporal evolution of the same parameters for the small-mammal assemblages of the Calatayud-Daroca Basin. We have only included these two basins in the analysis because they are the ones which present the most continuous record for the studied time interval. Insectivore genera richness is based in the review of the Spanish insectivore record by VAN DEN HOEK OSTENDE & FURIÓ (2005), while rodent genera richness and abundance data for Calatayud-Daroca Basin are taken from ÁLVAREZ SIERRA et al. (2003). Rodent abundance data and genera richness for the Vallès-Penedès were compiled by one of us (J.A.). The assigned ages to the small mammal localities are based on the magnetostratigraphical data from GARCÉS et al. (2003) in the case of the Nombrevilla section sites. The Toril mammal sites are considered to be equivalent to Las Planas 5H, at the top of the Aragonian type section in Villafeliche (DAAMS et al., 1999; ALCALÁ et al., 2000; GARCÉS et al., 2003). The chronological position of the two Pedregueras sites (Toril section) is based on the lithostratigraphical correlation presented in ÁLVAREZ SIERRA et al. (2003:27, fig. 2), which shows that they are stratigraphically very close to Nombrevilla 19. This latter site is supposed to be close to 9.7 Ma (GARCÉS et al., 2003). The age of Carrilanga 1 is taken from VAN DER MEULEN et al. (2003). The assigned ages for the Vallès-Penedès sites are based on magnetostratigraphical data in the cases of Can Llobateres 1 and Creu Conill 20 and 22 (GARCÉS et al., 1996). The rest of ages have been interpolated according to the evolution of mammal faunas and unpublished magnetostratigraphical data. When two or more sites are stratigraphically very close (as in the case of the Toril or Creu Conill sites) they are united in a single fauna and genera richness and the rodent abundances are recalculated.

The trends in rodent and insectivore genera richness in the Vallès-Penedès Basin seem to be correlated. Genera richness is high during the latest Aragonian (Sant Quirze A, Castell de Barberà) and also by the end of the Early Vallesian, when the number of rodent genera reaches a maximum (Can Llobateres 1). However, coinciding with the Aragonian/Vallesian boundary, both richness curves take lower values. If we take into account rodent composition, we observe that the cricetids are always the most abundant kind of rodents (except in the case of Castell de Barberà, where castorids are incredibly abundant). The cricetid *Eumyarion*, the dormice, flying squirrels and beavers are always present, though they are only abundant in certain sites. It is possible to broadly define three kinds of rodent assemblages. The first one would include a species rich fauna where the Gliridae, Pteromyidae, Castoridae are diverse and abundant. The cricetid *Eumyarion* may also be abundant as well as other cricetid genera such as *Cricetulodon* or *Democricetodon*. The small-sized *Megacricetodon* species are more frequent than the larger-sized ones. This kind of rodent assemblage, rich and equitative, is the one we find in some Late Arago-

Figure 2: Rodent and insectivore genera richness and composition of the rodent assemblage during the latest Aragonian and the Early Vallesian in the Vallès-Penedès and Calatayud-Daroca basins. See text for details on data sources and the chronologic position of the considered sites. The boundaries of the MN zones are taken from AGUSTÍ et al. (2001). In the section dedicated to the composition of the rodent assemblage we follow VAN DER MEULEN et al. (2003) and we include *Fahlbuschia*, *Pseudofahlbuschia* and *Renzimys* in the genus *Democricetodon*. The use of the term *Cricetodontini* follows MEIN & FREUDENTHAL (1971), so we only include the genera *Cricetodon* and *Hispanomys* within this group. The ground squirrels include the genera *Heteroxerus* and *Spermophilinus* in the Vallès-Penedès Basin. In the Calatayud-Teruel Basin this group has not been distinguished and is included in "others". By the way, the ground squirrels always represent a minor part of the rodent assemblage in this later basin. The group "others" includes the flying Pteromyinae, all the Gliridae except *Myomimus*, the Castoridae, the Anomalomyidae, the Eomyidae, the Muridae (which are only represented by a few remains in PE2C and CL1) and the Cricetidae *Eumyarion* and *Rotundomys* (present only in CL1, where it is extremely rare). The dashed line between MN 6 and MN 7 + 8 indicates the uncertain position of the lower boundary, which may be at 13 or 12.5 Ma (AGUSTÍ et al., 2001). Site abbreviations are as follows: CAR1 = Carrilanga 1; CB = Castell de Barberà; CCN20 = Creu Conill 20; CCN22 = Creu Conill 22; CL1 = Can Llobateres 1; CM = Can Missert; CP = Can Ponsic; NOM1 = Nombrevilla 1; NOM2 = Nombrevilla 2; NOM3 = Nombrevilla 3; NOM 9 = Nombrevilla 9; NOM10 = Nombrevilla 10; PE2A = Pedregueras 2A; PE2C = Pedregueras 2C; SQA = Sant Quirze A; TOR1 = Toril 1; TOR2 = Toril 2; TOR3A = Toril 3A; TOR3B = Toril 3B.



nian (Sant Quirze A, see AGUSTÍ, 1981; Castell de Barberà, see AGUILAR et al., 1979) and late Early Vallesian sites (Can Llobateres 1, see HARTENBERGER, 1965; HARTENBERGER, 1966, AGUSTÍ, 1981). The second kind of assemblage, which we see in some latest Aragonian (Can Missert; see AGUSTÍ

et al., 2005) and Early Vallesian localities (Upper Hostalets, see AGUSTÍ & GIBERT, 1982; Can Ponsic, see HARTENBERGER & CRUSAFONT, 1979), is characterized by lower diversity levels and the minority presence of dormice, beavers, flying squirrels and eomyids. The rodent fauna is dominated by

the cricetid *Hispanomys* and to a lesser degree by ground squirrels (mainly *Spermophilinus*). Finally, the third kind of association is the one that we find in Creu Conill 22, where *Megacricetodon ibericus* accounts for 70% of the assemblage, while *Hispanomys dispectus* represents only a 20%. This coincides with the nearly total absence of any other rodent genera. The pattern exhibited by the insectivores is not as clear as that shown by rodents.

Many of the genera present in the Vallès-Penedès assemblages are traditionally considered to be forest-dwellers. This applies to all the Gliridae except the Myomiminae (VAN DER MEULEN & DE BRUIJN, 1982), the Pteromyidae and probably the Eomyidae (VAN DE WEERD & DAAMS, 1978; DAAMS et al., 1988; VAN DAM & WELTJE, 1999). The presence of Castoridae is linked to the presence of stable water masses, since the European members of this family already presented the characteristic anatomical adaptations for a semi-aquatic life-style except the dorso-ventrally flattened tail (HUGUENEY & ESCUILLIÉ, 1995). The ground squirrels include two tribes: the Tamiini and the Xerini. VAN DAM & WELTJE (1999) consider the Xerini (such as *Heteroxerus*) as characteristic of dry habitats, while the Tamiini (such as *Spermophilinus*) would have inhabited humid forested areas. This interpretation is based in the observation that *Spermophilinus bredai* is quite abundant in very "humid" faunas (such as Anwil in Switzerland; see ENGESSER, 1972). However, many other studies suggest a preference for open and dry environments (VAN DE WEERD & DAAMS, 1978; DAAMS et al., 1988; VAN DER MEULEN & DAAMS, 1992). Since the abundance peaks of *Spermophilinus* and *Heteroxerus* in the Vallès-Penedès Basin are correlated, we interpret that the two genera preferred similar environments. These ground squirrels are quite rare when forest-dwellers are abundant, so they are considered to indicate the existence of dry and open habitats. The Anomalomyidae and the Muridae are very rare in the assemblages. A fossorial life-style has been proposed for the Anomalomyidae (BOLLIGER, 1999), while the first-appearing Muridae may have been ubiquitous (VAN DAM & WELTJE, 1999). The Cricetodontini show a tendency towards the development of hypsodont cheek teeth accompanied by the development of longitudinal connections between the labial cusps in the upper molars (ectolophs), and because of this morphology a preference for open, more arid environments has been suggested (DE BRUIJN et al., 1993; DE BRUIJN & ÜNAY, 1996). *Cricetodon lavocati* and all the species of the genus *Hispanomys* present in the sites show well-developed ectolophs and a medium hypsodonty. The environmental preferences of other cricetid genera are debated. A preference for moist biotopes is generally accepted for *Eumyarion* mainly because its abundance is correlated with that of forest-dwelling rodents (VAN DE WEERD & DAAMS, 1978; DAAMS et al., 1988). A preference for dry environments has also been proposed for *Megacricetodon ibericus*, as well as for other larger-sized *Megacricetodon* species (DAAMS & FREUDENTHAL, 1988). In contrast, small-sized *Megacricetodon* species would have preferred more humid habitats (DAAMS & FREUDENTHAL, 1988). The same has been proposed for larger-sized *Democricetodon* spe-

cies (that some authors include in the genus *Fahlbuschia*), that may have preferred dry and warm habitats (VAN DER MEULEN & DAAMS, 1992), while the smaller-sized ones may have inhabited wetter areas (DAAMS et al., 1988). However, it must be noted that the interpretation of the environmental preferences of these fossil cricetids is mainly based in their relative abundance in assemblages where forest-dwellers are common. Considering these remarks on the supposed ecological requirements of some fossil rodents, we interpret that the Aragonian/Vallesian boundary in the Vallès-Penedès coincided with a dry phase. First we have a succession of high-diversity assemblages with abundant forest-dwellers in the Late Aragonian that are followed by a set of sites where the rodents that indicate dryer habitats are dominant and the forest-dwellers are much less diverse and abundant. By the end of the Early Vallesian the rodent association is similar to that existing in Late Aragonian sites, though the cricetid *Cricetulodon* becomes a major component. Prior to the *Hipparion* s.l. FAD the Late Aragonian site of Can Missert shows a fauna dominated by *Hispanomys* and *Spermophilinus*. Similar faunal compositions are present in the Early Vallesian sites of Upper Hostalets de Pierola and Can Ponsic. Nevertheless, in Creu Conill 20 and 22, the ground squirrels are extremely rare, and though *Hispanomys* is the second most abundant rodent, it is outnumbered by *Megacricetodon ibericus*. The dominance of this cricetid species in these sites also supports the presence of dry and open habitats, but evidences a different community structure.

The pattern of rodent genera richness in the Calatayud-Daroca Basin follows the trends described in the case of the Vallès-Penedès, and an important decrease in the number of genera is observed at the Aragonian/Vallesian boundary and during the earliest Vallesian. By the late Early Vallesian, as it happened in the Vallès-Penedès, the maximum levels of rodent genera richness are achieved. The insectivore faunas are always poorer in Calatayud-Daroca than in the Vallès-Penedès since some genera (burrowing species of Talpidae and *Plesiodimylus* amongst others) are not recorded. Similarly, many dormice genera (*Bransatoglis*, *Glirulus*, *Myoglis*, *Glirudinus*), the eomyids *Eomyops* and *Keramidomys* and the anomalomyids are not recorded in this basin. The cricetid *Eumyarion*, the flying squirrels and the beavers are very rare in Calatayud-Daroca. This indicates that the environment in this basin was dryer than that of the Vallès-Penedès, which in its turn was more similar to Central Europe and France. The distribution of many large-mammal taxa (great apes, tapirids), which in Spain is restricted to the Vallès-Penedès, also supports this conclusion.

Until the late Early Vallesian the rodent assemblage is always dominated by the genus *Megacricetodon* (except in Nombrevilla 9 and 10). In Pedregueras 2A and 2C *Cricetulodon* represents an important proportion of the rodent fauna and *Megacricetodon* is only represented by the small-sized lineage. The members of the small-sized lineage are more abundant than the larger-sized ones from the Aragonian/Vallesian boundary onwards. During the Late Aragonian the larger-sized *Megacricetodon* over-

whelmingly dominate the assemblage, as it happened in the Vallès-Penedès in Creu Conill 22. The Cricetodontini always define an important proportion of the rodent faunas (except in the Toril sites), but the ground squirrels are very rare. The ground dormice *Myomimus* is quite common in all sites from the latest Aragonian onwards. Thus, during the Late Aragonian the rodent associations of Calatayud-Teruel differ from the ones of the Vallès-Penedès and, according to the supposed environmental preferences of the involved genera, indicate the existence of a dry and open biotope. From the Aragonian/Vallesian onwards the environment appears to have become increasingly wetter until reaching a maximum by the end of the Early Vallesian. Nevertheless, in the Early Vallesian sites *Hspanomys* and *Myomimus* are always abundant, suggesting the existence of dry and open areas too.

Thus, the FAD of *Hipparion* s.l. is associated to important changes in the small-mammal communities, although these changes were short-lasting ones. These changes may result from the shift towards more open and dryer environments in the Vallès-Penedès, while in Calatayud-Daroca the opposite situation seems to occur (which is in agreement with the results of VAN DER MEULEN & DAAMS, 1992). Nevertheless, we must stress that the environment in this basin is supposed to have been dryer than in the Vallès-Penedès during the whole time interval.

The earliest hipparionine horses of Europe are referable to the species *Hippotherium primigenium*, which is gracile build and presents axial skeleton adaptations for leaping and sprinting rather than high speed, sustained running. In contrast to their North American ancestors, which were mainly grazers, *Hippotherium primigenium* was a browser and it is supposed to have been well adapted to Central Europe's Vallesian subtropical to warm-temperate woodland environments (BERNOR et al., 1996; BERNOR et al., 1997). Furthermore, the environment appears to have been moist and densely forested in Central Europe coinciding with the FAD of hipparionine horses in the Vienna Basin (BERNOR et al., 1988). So the shift towards dryer conditions observed in the Vallès-Penedès Basin does not seem to have been a crucial point for the quick dispersal of this equid in Spain.

5. Conclusions

The FAD of *Hipparion* s.l. coincided with a decrease in rodent genera richness in the Calatayud-Daroca and the Vallès-Penedès basins (in the Vallès-Penedès insectivores appear to have been affected too). In addition to it the structure of the rodent assemblages changed markedly in the Vallès-Penedès, suggesting the existence of dryer and more open habitats. In Calatayud-Daroca the environment appears to have been always dryer than in the Vallès-Penedès during the Late Aragonian, and the beginning of the Early Vallesian coincides with a shift towards somewhat wetter conditions. Thus, in this later basin the FAD of *Hipparion* s.l. does not seem to coincide with a very dry phase. The structure of the rodent

assemblage associated to the first-appearing hipparionine horses in the Vallès-Penedès is more similar to that of the Late Aragonian sites of Calatayud-Daroca than to Early Vallesian ones.

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PLATE 1

SEM micrographs of the insectivore material from Creu Conill 20 and 22

- Fig. 1-2 *Miosorex* sp. from Creu Conill 22. 1. Left M1, IPS 29578-2. 2. Left m2, IPS 29578-1.
- Fig. 3 *Plesiodimylus chantrei* from Creu Conill 20, left m2, IPS 20907.
- Fig. 4-6 *Parasorex* cf. *socialis* from Creu Conill 22. 4. Right M3, IPS 20908-1. 5. Right M1 or M2, IPS 20908-3. 6. Left p4, IPS 20908-2.
- Fig. 7 *Talpa* cf. *minuta* from Creu Conill 20, humerus, IPS 29579. Anterior is to be right in the right teeth and to the left in the left ones.

PLATE 1

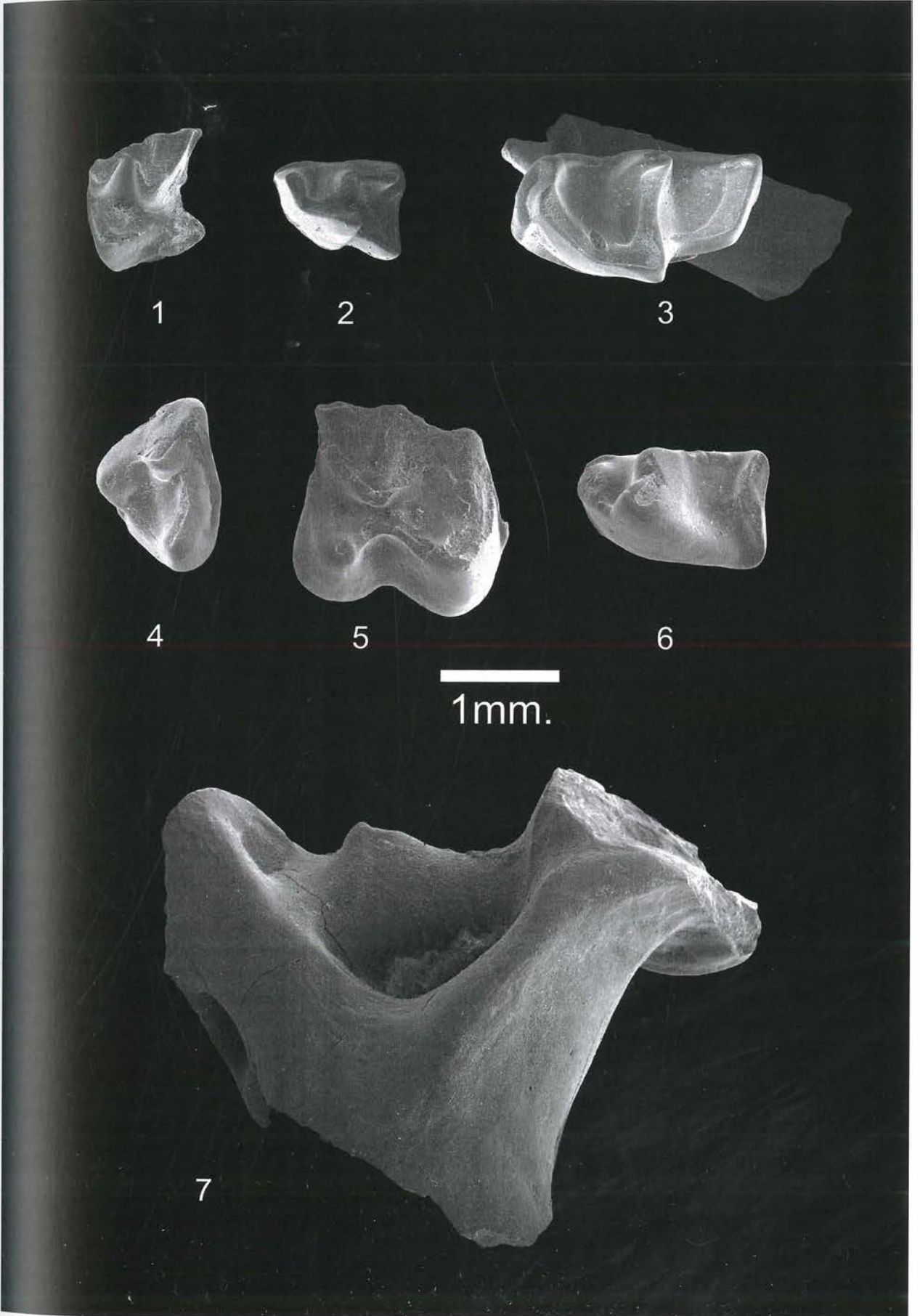


PLATE 2**SEM micrographs of the rodent material from Creu Conill 22**

- Fig. 1-6 *Hispanomys dispectus*. 1. Left M1, IPS 11523-393. 2. Left M2, IPS 11519-408. 3. Left M3, IPS 11520-417. 4. Left m1, IPS 11525-353. 5. Left m2, IPS 11526-527. 6. Left m3, IPS 11521-371.
- Fig. 7-12 *Megacricetodon ibericus*. 7. Left M1, IPS 11500-219. 8. Left M2, IPS 11512-268. 9. Left M3, IPS 11510-319. 10. Left m1, IPS 10995-60. 11. Left m2, IPS 10157-115. 12. Left m3, IPS 11506-160.
- Fig. 13-14 *Democricetodon* cf. *sulcatus*. 13. Left M1, IPS 11515-431. 14. Right m2, IPS 11515-430.
- Fig. 15 *Cricetulodon* n. sp., left m1, IPS 29576-1.
- Fig. 16-17 *Miodymomys hamadryas*. 16. Left M1 or M2, IPS 29577-1. 17. Right M1 or M2, IPS 29577-2.
- Fig. 18 *Trogotherium* (*Euroxenomys*) *minutum*, right M3, IPS 11516-449.
- Fig. 19-20 *Spermophilinus bredai*. 19. Right M1, IPS 11514-438. 20. Right m2, IPS 11514-437.

PLATE 2

