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Original article

The rodents from Santpedor-2 (Ebro Basin, NE Spain) confirm the Oligocene age of the latest primates from the Paleogene of Europe[☆]

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ABSTRACT

This paper provides a revised and updated description and identification of the rodents from Santpedor-2 (northeastern Spain). The age of this locality is particularly relevant, because it is one of the few European sites assigned to the early Oligocene that has yielded primate remains. However, the rodent assemblage from this site has never been described in detail, and therefore the Oligocene age of this locality remained tentative. Despite the scarcity of the material, the rodents from Santpedor-2 are characteristic enough either to be identified as already known species, or at least compared with close species. Eight different rodent taxa were recognized. Among them, the theridomyid *Ectropomys exiguus*, which is recorded only in late Eocene localities, and the glirid *Glamys devoogdi*, which is known in both latest Eocene and early Oligocene localities. The other taxa are found only in Oligocene localities, and consist of the theridomyid *Paratheridomys margaritae* and members of two families that arrived in Europe at the beginning of the Oligocene: eomyids (*Eomys* sp.) and cricetids (*Eucricetodon atavus*, cf. *Heterocricetodon* sp., cf. *Pseudocricetodon* sp.). Finally, another theridomyid (Issiodoromyinae) seems to correspond to a new species and new genus, the main features of which correspond to early Oligocene evolutionary grades. This rodent assemblage from Santpedor-2 is assigned to the early Oligocene, mainly on the basis of the presence of immigrant rodents that reached Europe in relation with the Grande Coupure (cricetids and eomyids). This dating is notably supported by the presence of *P. margaritae* together with *Glamys devoogdi*, both being found in Hoogbutsel (early Rupelian, MP21). Only one rodent (*E. exiguus*) represents an Eocene relict, as is the case of *Pseudoloris*, the only primate recorded in this locality. Therefore, this study supports the Oligocene age of Santpedor-2 and then the persistence of omomyid primates in the Iberian Peninsula (at least locally) after the Grande Coupure.

1. Introduction

The fossil site of Santpedor (Ebro Basin, NE Spain), originally named as “Costa de la Vila”, was first mentioned in the 1950’s, when Masachs et al. (1954) briefly described the presence of two perissodactyls and an artiodactyl: *Paleotherium medium*, *Plagiolophus annectens*, and an undetermined Anoplotheriidae (later referred to *Anoplotherium commune* by Golpe, 1982). These authors assigned the locality to the late Eocene. In the 1980’s, the teams of the Institut de Paleontologia de Sabadell (now Institut Català de

Paleontologia Miquel Crusafont, ICP) and the Universidad de Barcelona decided to resume the study of this locality. On the one hand, they revisited the macromammal remains first reported by Masachs et al. (1954), noting that the material was so scarce that it could not be determined at the specific level and did not allow for a precise dating of the locality. Therefore, according to Arbiol and Sáez (1988), the faunal list of the classical site of Santpedor consisted of *Paleotherium* sp., *Plagiolophus* sp. and Anoplotheriidae indet. On the other hand, these teams returned and prospected the area in order to find levels with micromammal remains. Agustí et al. (1987) and Arbiol and Sáez (1988) described a rodent-bearing site that they called Santpedor-2, placed 350 m east from the classical locality of Santpedor, and situated in the same stratigraphic level (Fig. 1). These authors reported in Santpedor-2 the presence of four different rodents: *Theridomys*

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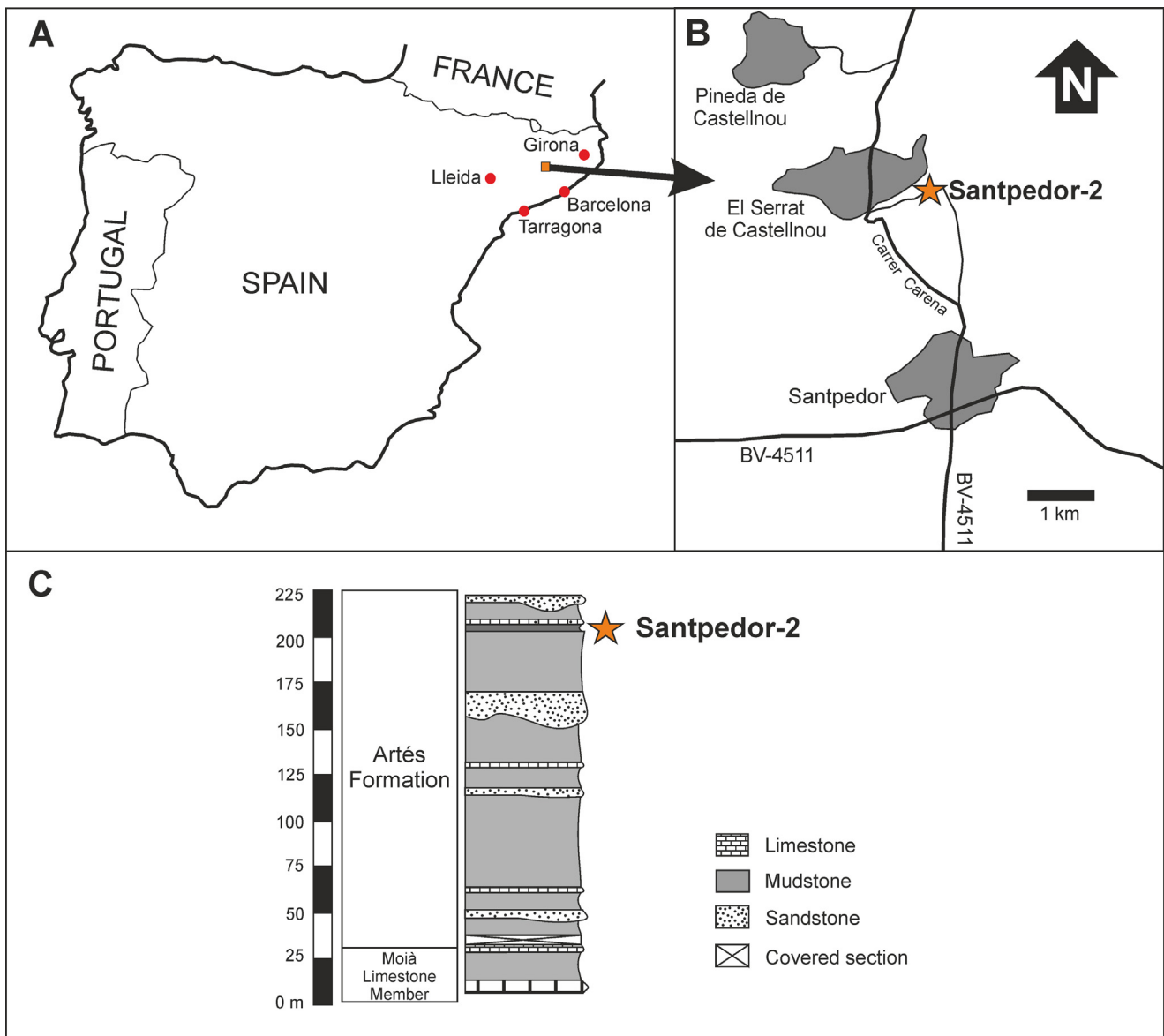


Fig. 1. Geographic and geological setting of the Santpedor-2 fossil locality. **A.** Situation of the studied section in the Iberian Peninsula. **B.** Detailed map showing the position of Santpedor-2 (modified from Arbiol and Sáez, 1988). **C.** Simplified column of the Santpedor section indicating the stratigraphic position of the sampled level (modified from Costa et al., 2011).

aff. *aquatilis*, *Gliravus* aff. *priscus*, *Eucricetodon atavus*, and *Pseudotimomys gaillardi*. Based on this rodent assemblage, they assigned the locality to the early Oligocene, an age maintained in several later works (Cuenca et al., 1992; Aguilar et al., 1997; Köhler and Moyà-Solà, 1999; Barberà et al., 2001; Hooker et al., 2007; Hooker, 2010; Minwer-Barakat et al., 2010, 2012, 2013, 2015; Costa et al., 2011; Marigó et al., 2014; Sanjuan et al., 2014). Even more, Agustí et al. (1987) proposed a biozone based on the rodent assemblage from Santpedor-2. They defined the *Theridomys* aff. *aquatilis* zone, which would represent the earliest Oligocene mammal level (MP21), thereby being correlated with the locality of Hoogbutsel in Belgium. However, neither Agustí et al. (1987) nor Arbiol and Sáez (1988) provided descriptions, measurements or illustrations of the rodent material from Santpedor-2, and their taxonomic ascriptions remained non verifiable as a result.

The relevance of this locality increased when Köhler and Moyà-Solà (1999) reported the presence of scarce primate

remains in Santpedor-2 and in the nearby and somewhat younger locality of Fonollosa-13. The fossil primates from Santpedor-2 consisted of two fragments of lower molars, whereas those from Fonollosa-13 documented an upper tooth row, the dental morphology of which allowed to undoubtedly assign them to the genus *Pseudoloris*. Interestingly, primates were so far supposed to have disappeared from Europe in relation to the drastic cooling recorded at the Eocene–Oligocene transition and the subsequent faunal turnover that dramatically affected continental vertebrate fauna, known as the “Grande Coupure”. The finding of *Pseudoloris* (*P. godinoti*) from Santpedor-2 and Fonollosa-13 represented the unique record of Oligocene primates in the continent, a presence that was shortly after confirmed by the discovery of a single lower molar of the genus *Microchoerus* in the early Oligocene locality of Aguatón, also in Spain (Peláez-Campomanes, 2000). However, the age proposed for Santpedor was based only on the faunal list

provided by Agustí et al. (1987) and Arbiol and Sáez (1988) and, despite the fact that the interest of the locality lies precisely on its Oligocene age, a detailed study of its rodents was never developed.

In this paper we present a thorough study of the rodents from Santpedor-2. The rodent assemblage from this site includes eight different forms of theridomyids, eomyids, cricetids and glirids, and is therefore more diverse than previously thought. The detailed study of these rodents supports the early Oligocene age of the locality.

2. Geological setting

The Ebro Basin is the southern foreland basin of the Pyrenean Range, which was formed in response to convergence and collision between the Iberian and European plates from the Late Cretaceous to the Miocene (Puigdefàbregas et al., 1992; Busquets et al., 2003). This basin is delimited by three mountain ranges formed during the Eocene-Oligocene compression: the Pyrenees to the North, the Iberian Range to the Southwest, and the Catalan Coastal Ranges to the Southeast. The marine connection of the Ebro Basin was interrupted during the Priabonian (the marine-continental transition has been precisely dated at ~36.0 Ma by Costa et al., 2010). From the late Eocene to the late Miocene, the Ebro Basin displayed a closed drainage system, and its depositional framework consisted of distributive alluvial systems fed from the tectonically active surrounding ranges, laterally changing to shallow lacustrine zones (Agustí et al., 1987; Barberà et al., 2001; Sáez et al., 2007). The basin infill (up to 2000 m thick) consists therefore of alluvial, fluvial and lacustrine deposits, in which several vertebrate sites have been identified (Agustí et al., 1987; Anadón et al., 1987; Cuenca et al., 1992). Nevertheless, mammal sites corresponding to the earliest phase of endorheic sedimentation are relatively scarce: the only two localities assigned to the late Eocene (Priabonian, MP19/20) are Sant Cugat de Gavadons (Crusafont-Pairó, 1967; Hooker et al., 2009; Minwer-Barakat et al., 2013, 2016) and Rocafort de Queralt (Anadón et al., 1987), while the first mammal site that, according to the published data, postdates the “Grande Coupure” is Santpedor (Köhler and Moyà-Solà, 1999; Barberà et al., 2001; Costa et al., 2011).

3. Material and methods

The described rodent specimens from Santpedor-2 consist of 33 isolated teeth, housed in the collections of the *Institut Català de Paleontologia Miquel Crusafont* (Sabadell, Barcelona, Spain). The nomenclature used in the descriptions (Fig. 2) follows Vianey-Liaud and Marivaux (2017) for theridomorphs, Dienemann (1987) for cricetids, Vianey-Liaud (1994) for glirids, and Maridet et al. (2010) for eomyids. Measurements (Table 1) were taken using an optic calliper “Nikon measuroscope 10” connected to a monitor “Nikon SC112”; measured parameters include the mesiodistal maximum length and the maximum width perpendicular to the length, taken in keeping the wear surface horizontal. Micrographs were obtained using the Environmental Scanning Electron Microscope (ESEM) at the *Universitat de Barcelona*.

4. Systematic paleontology

Class Mammalia Linnaeus, 1758
 Order Rodentia Bowdich, 1821
 Family Theridomyidae Alston, 1876
 Subfamily Oltinomyinae Hartenberger, 1971
 Genus *Ectropomys* Bosma et Schmidt-Kittler, 1972
Ectropomys exiguus Bosma et Schmidt-Kittler, 1972

Fig. 3(A–C)

Material: DP4: IPS 105269; p4: IPS 105286, m2: IPS 105287.

Description:

Upper teeth. The unique upper tooth is a DP4 (Fig. 3(A)), the lingual side of its crown being relatively high and narrow with respect to the buccal one; it is not anteriorly reduced. The postprotocrista makes the high endoloph, which does not join the hypocone, and then the syncline II communicates with the shallow and narrow sinus. The high anteroloph joins the paracone to the protocone, closing the syncline I (anteroflexus) buccally. The continuous protoloph joins the apex of the protocone. The mesoflexus (syncline II + syncline I) is closed buccally by the mesostyle and the extensions of the postparacrista mesially and of the premetacrista distally. The mesoloph is lower than the other loph and breaks at mid-length. Its buccal part weakly attaches its lingual part, which fuses with the thicker lingual metaloph. The mesoloph separates the long buccolingually syncline II and the shorter syncline III. The buccal metaloph is transverse but slightly mesially oriented, connected to the lingual metaloph, and separated from the long posteroloph. As a result, the syncline IV is more developed than on the known populations of *E. exiguus* or *E. monacensis*. This syncline IV could be subdivided into a much worn DP4, since a very low bead is visible at its bottom both on the distal flank of the buccal metaloph and on the lingual flank of the posteroloph.

Lower teeth. The p4 from Santpedor-2 (Fig. 3(B)) is more worn than that of Rocafort de Queralt, the front part of the latter being incomplete. It shows a break from the entoconid to the sinusid. On this p4, the protoconid and the larger metaconid are linked by a complete transverse metalophulid I. The latter is notched mesially by a short antesisinusid, limited mesially by a low anterolophid. A high postmetacristid joins the mesostylid. The mesostylid is connected to a mesolophid that reaches the mesoconid swelling at the distal end of a strong postprotocristid. The synclinid II is divided by a short mesiodistal cristid, extending from the mesolophid to the metaconid. The synclinid III is closed lingually. The short distal ectolophid is separated by a notch from the mesoconid swelling. The entolophid and posterolophid are high and complete, between the strong entoconid and hypoconid. The morphology of m2 (Fig. 3(C)) is reminiscent to that of the tooth from San Cugat de Gavadons, in which the small anteroconid is framed by the anterolophid and anterocingulid, which delimit narrow anteroflexid and antesisinusid. The sinusid is slightly deeper transversely, and the mesolophid is complete, reaching the mesostylid-postmetacristid junction.

Remarks: The teeth are larger than those of *Ectropomys exiguus* from the Isle of Wight, Rocafort de Queralt and San Cugat de Gavadons, but they are clearly smaller than *Oltinomys platyceps* (Bosma and Schmidt-Kittler, 1972; Vianey-Liaud et al., 1994). The general features of these teeth are compatible with the species *E. exiguus*, whereas the few differences are more derived than in the material from the above mentioned localities (larger size, much more marked lophodonty, higher crown, deeper sinusid). These characteristics argue for a form younger than the late Eocene populations of *E. exiguus*.

Subfamily Theridomyinae Alston, 1876

Genus *Paratheridomys* Vianey-Liaud et Marivaux, 2017

Paratheridomys margaritae (Vianey-Liaud, 1972)

Fig. 3(D–F)

Material: M2: IPS 18941; M3: IPS 105257; m3: IPS 105284.

Description:

Upper molars. The mesial and distal flanks of the crown are relatively flat, vertical and parallel on M2 (Fig. 3(D)). This tooth is worn, and the wear reduces the posterosyncline (syncline IV) to an islet. The paracone, mesostyle and metacone are slightly bulged.

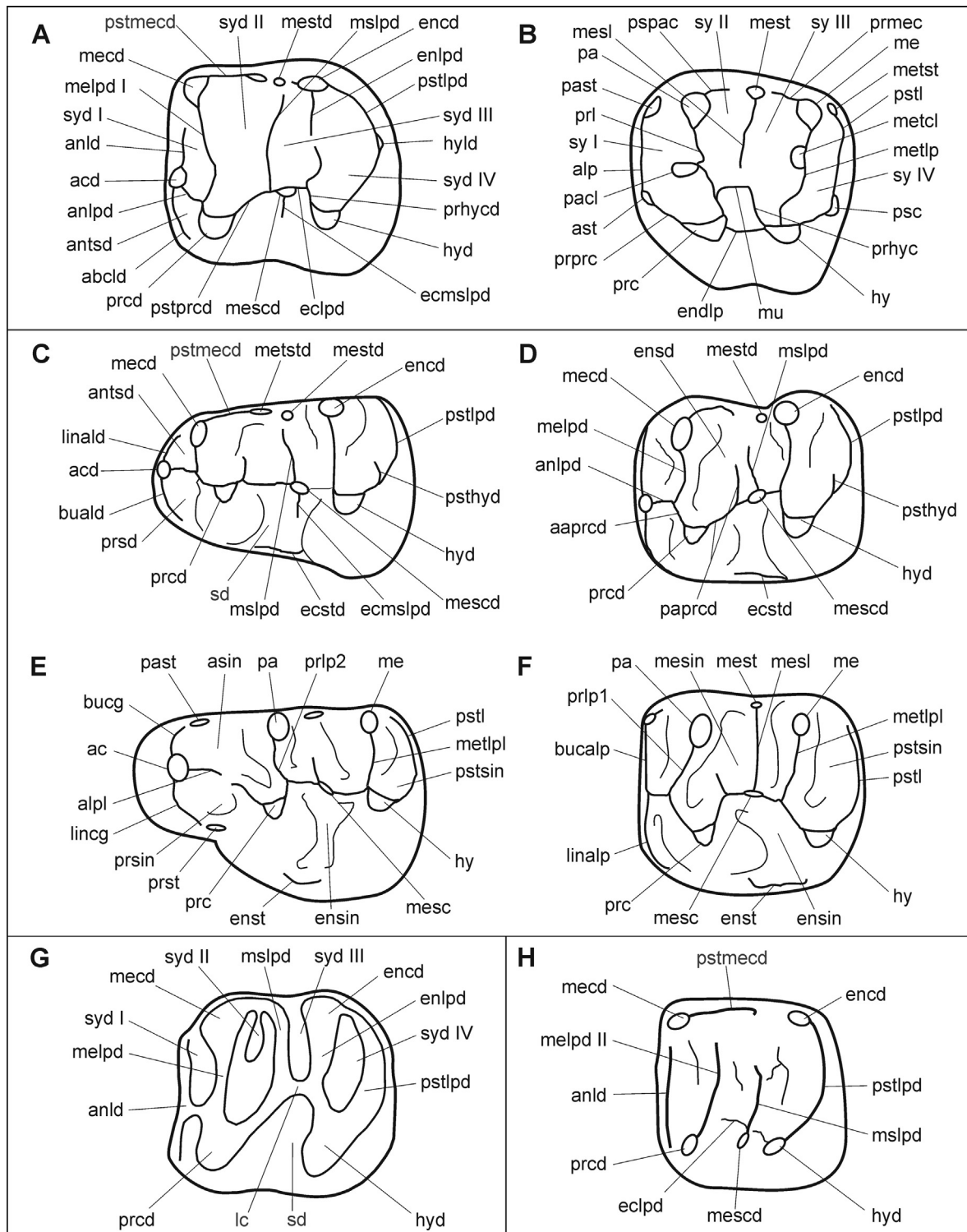


Fig. 2. Dental nomenclature employed for the description of the teeth of Theridomyidae (A, B), Cricetidae (C–F), Eomyidae (G) and Gliridae (H). A, C, G and H represent m1; B and E represent M1; D corresponds to a m2, and F to a M2. A and B are modified from [Bonilla-Salomón et al. \(2016\)](#); G is modified from [Daxner-Höck and Höck \(2009\)](#); the rest of figures correspond to original drawings. Abbreviations for lower molars: aaprcd: anterior arm of protoconid; abclcd: anterobuccal cingulid; acd: anteroconid; anld: anterolophid; anlpcd: anterolophulid; antsd: anterosinusid; buald: buccal anterolophid; eclpcd: ectolophid; ecmslpcd: ectomesolophid; ecstd: ectostylid; encd: entoconid; enlpcd: entolophid; ensd: entosinusid; hyd: hypoconid; hyld: hypoconulid; lc: longitudinal crest; linald: lingual anterolophid; mecd: metaconid; melpcd: metalophid; melpcd I: metalophid I; melpcd II: metalophid II; mescd: mesoconid; mestd: mesostylid; mestd: metastylid; mslpcd: mesolophid; paprcd: posterior arm of protoconid; prcd: protoconid; prhycd: prehypocristid; prsd: protosinusid; psthyd: posterior arm of hypoconid; pstlpcd: posterolophid; pstmeccd: postmetacristid; pstprcd: postprotocristid; sd: sinusid; syd I: synclinid I; syd II: synclinid II; syd III: synclinid III; syd IV: synclinid IV. Abbreviations for upper molars: ac: anterocone; alp: anteroloph; alp1: anterolophule; asin: anterosinus; ast: anterostyle; bucalp: buccal anteroloph; bucg: buccal cingulum; me: metacone; mesc: mesocone; mesin: mesosinus; mesl: mesoloph; mest: mesostyle; metcl: metaconule; metpl: metaloph; metpl1: metalophule; metst: metastyle; mu: mure; pa: paracone; pacl: paraconule; past: parastyle; prc: protocone; prhyc: prehypocrista; prl: protoloph; prlp1: protolophule 1; prlp2: protolophule 2; prmec: premetacrista; prprc: preprotocrista; prsin: protosinus; prst: protostyle; psc: posterocone; pspac: postparacrista; pstl: posteroloph; pstsin: posterosinus; sy I: syncline I; sy II: syncline II; sy III: syncline III; sy IV: syncline IV.

Table 1
Measurements (in mm) of the rodent teeth from Santpedor-2.

Taxon	Catalogue number	Tooth	Length	Width
<i>Ectropomys exiguus</i>	IPS 105269	DP4	1.66	1.86
	IPS 105287	m2	1.91	1.80
	IPS 105286	p4	1.75	1.44
<i>Paratheridomys margaritae</i>	IPS 18941	M2	1.94	2.63
	IPS 105257	M3	1.96	2.23
	IPS 105284	m3	–	1.72
Issiodoromyinae nov. gen., nov sp.	IPS 105276	P4	2.23	2.69
	IPS 105275	M1-2	2.16	2.72
	IPS 105277	M1-2	2.03	2.75
	IPS 105278	M1-2	–	–
	IPS 105279	M3	2.20	2.69
	IPS 105280	M3	2.03	2.42
	IPS 18940	dp4	2.14	1.41
	IPS 105281	p4	2.35	1.97
	IPS 105282	m2	2.39	2.07
	IPS 105283	m3	2.30	1.93
	IPS 105285	m3	–	–
	IPS 105265	p4	1.08	1.03
	IPS 105262	m1-2	–	1.09
<i>Eucricetodon atavus</i>	IPS 105268	M1	1.92	1.23
	IPS 105266	M2	1.32	–
	IPS 105264	M3	–	–
cf. <i>Heterocricetodon</i> sp.	IPS 105273	M1	–	–
	IPS 105258	M2	1.50	1.48
	IPS 105260	M2	1.51	–
	IPS 105267	M3	1.18	1.24
	IPS 105259	m1	1.72	1.23
	IPS 105261	m2	–	–
	IPS 105263	m3	1.58	1.33
	IPS 105274	m2	–	1.19
cf. <i>Pseudocricetodon</i> sp. <i>Glamys devoogdi</i>	IPS 105272	p4	0.93	0.86
	IPS 105270	m2	1.01	1.11
	IPS 105271	m2	–	–

The protocone is not strongly pinched, and rather appears only slightly stretched obliquely (mesiobuccal to distolingual), giving the same orientation to the sinus. The syncline I and syncline II are equally long and shorter than syncline III. The enamel of the distal flank of the protocone is only a little thinner than on the mesial flank; the enamel of the hypocone and of its arms is particularly thick, and as thick as the distal border of the crown.

Lower molar. Only one m3 can be referred to this species (Fig. 3(F)). There is no synclinid I; the metalophid I is mesial and the synclinid II is not compressed. The postmetacristid is high and joins the mesostylid at the lingual extremity of the transverse mesolophid. The postprotocristid is not markedly oblique and it joins the (pseudo)mesoconid at the mesial extremity of the short and slightly oblique buccomesial to distolingual short ectolophid. The synclinid II is nearly as long as the synclinid IV, but wider. Synclinid III and synclinid IV are equal in width.

Remarks: The characters of the upper molars described above are found on the M2 of the type population from Hoogbutsel (Belgium, MP21; Vianey-Liaud, 1972, 1989). These teeth differ from those of *Blainvillimys langei* in their more regular enamel thickness, their lower crown, less pinched protocone and less oblique sinus. The features of the m3 described above are very similar to those of the m3 of *P. margaritae* lacking synclinid I from Hoogbutsel (Vianey-Liaud, 1972). The m3 from Santpedor is lower crowned, with a more regular enamel thickness and less oblique postprotocristid than the m3 of *B. langei*. The teeth from Santpedor differ from *Theridomys aquatilis* in their smaller size.

?Issiodoromyinae Tullberg, 1899

?Issiodoromyinae nov. gen., nov. sp.

Fig. 3(G–Q)

Material: P4: IPS 105276; M1-2: IPS 105275, 105277, 105278; M3: IPS 105279, 105280; dp4: IPS 18940; p4: IPS 105281; m2: IPS 105282; m3: IPS 105283, 105285.

Description:

Upper teeth. The crowns of the P4 and M1-2, and probably of the worn M3, show a constriction of the outline at the levels of the termination of the anterior arm of the protocone (at the junction with the anteroloph) and of the posterior arm of the hypocone (at its junction with the posteroloph). These shrinkings, well distinct on the less worn teeth only, are never observed on the M1-2 of *Paratheridomys margaritae*, *Theridomys aquatilis*, and *Blainvillimys langei*, as well as on M1-2 of any species of *Pseudoltinomys*. On the P4 and M1-2, the paracone and metacone are markedly bulged and the protoloph and metaloph are thick. The mesoloph is thinner and lower than these lophes. On P4 (Fig. 3(G)), the anteroloph is short but the anterosyncline (syncline I) is longer than in the late Eocene and Oligocene species of *Pseudoltinomys*. The posteroloph is short, and the posterosyncline is particularly reduced, even on the weakly worn M1-2 IPS 105275 (Fig. 3(H)). The sinus is shorter buccolingually than the opposite syncline II, or has similar length in the most worn teeth. Contra what is seen on *Pseudoltinomys*, the sinus and the syncline II are not communicating: they are separated by a very short mure as seen on the weakly worn M1-2 (Fig. 3(H)).

Lower teeth. The dp4 (Fig. 3(M)) is slightly shorter than p4 (Fig. 3(N)), and the latter is similar in length then that of the m2 and m3. On dp4, the weak protoconid and the following post-protocristid are lowered by wear, and then the metaconid and entoconid remain higher. There is a very low mesiodistal ridge descending from the metaconid to the middle of the mesolophid. The latter is complete, and joins the postmetacristid at the mesostylid level. The lingual opening of the synclinid III is narrow. The sinusid is buccolingually short. The long and curved posterolophid is thickened at the hypoconulid level, lingually to the oblique posthypocristid. On the unworn p4, the metaconid connects to the protoconid by a high mesial metalophid. There is no antesinusid. The mesolophid is slightly lower than the meta- and ento- lophids. The mesolophid is broken before joining the mesostylid level by a short and narrow notch. The synclinid II displays a short and weak mesiodistal ridge. The ectolophid is short, showing a very shallow and narrow break in its middle. The synclinid III is lingually open. The sinusid is buccolingually shorter than the synclinid III. The entolophid is as high as the other lophids, and the posterolophid is long, without distinct swelling at the hypoconulid level.

The m2 (Fig. 3(O)) is worn and the enamel shows a similar thickness on the mesial, buccal and distal surfaces of the crown. There is an indication of the presence of an antesinusid as an angle on the mesial face of the metalophid I. The synclinid II is divided by a mesiodistal ridge. The sinusid is oblique and directed to the buccal end of the synclinid IV. The synclinid II is closed lingually, the synclinid III open, and the synclinid IV shallowly and narrowly open. The m3 IPS 105283 (Fig. 3(P)) displays the same features as those of the m2, and, as it is more worn, the synclinid III and synclinid IV are weakly closed lingually. A very narrow break is observed between the oblique sinusid and the synclinid IV. As for the m2, an angle of enamel on the metalophid I indicates the presence of a possible antesinusid. It is well marked on the m3 IPS 105285 (Fig. 3(Q)).

Remarks: This material documents the best represented species of theridomyid from Santpedor-2. It was previously referred to *Pseudoltinomys gaillardi* (see Section 1). Nevertheless, these teeth show strong differences with this species, and moreover, with the genus *Pseudoltinomys*, like the absence of break of the longitudinal crest on upper teeth, the reduced antesinusid or the relatively larger p4. It would be necessary to get more material to define a new species, as it appears to be, and probably also a new genus. The teeth have been directly compared with several theridomyid species from the late Eocene and early

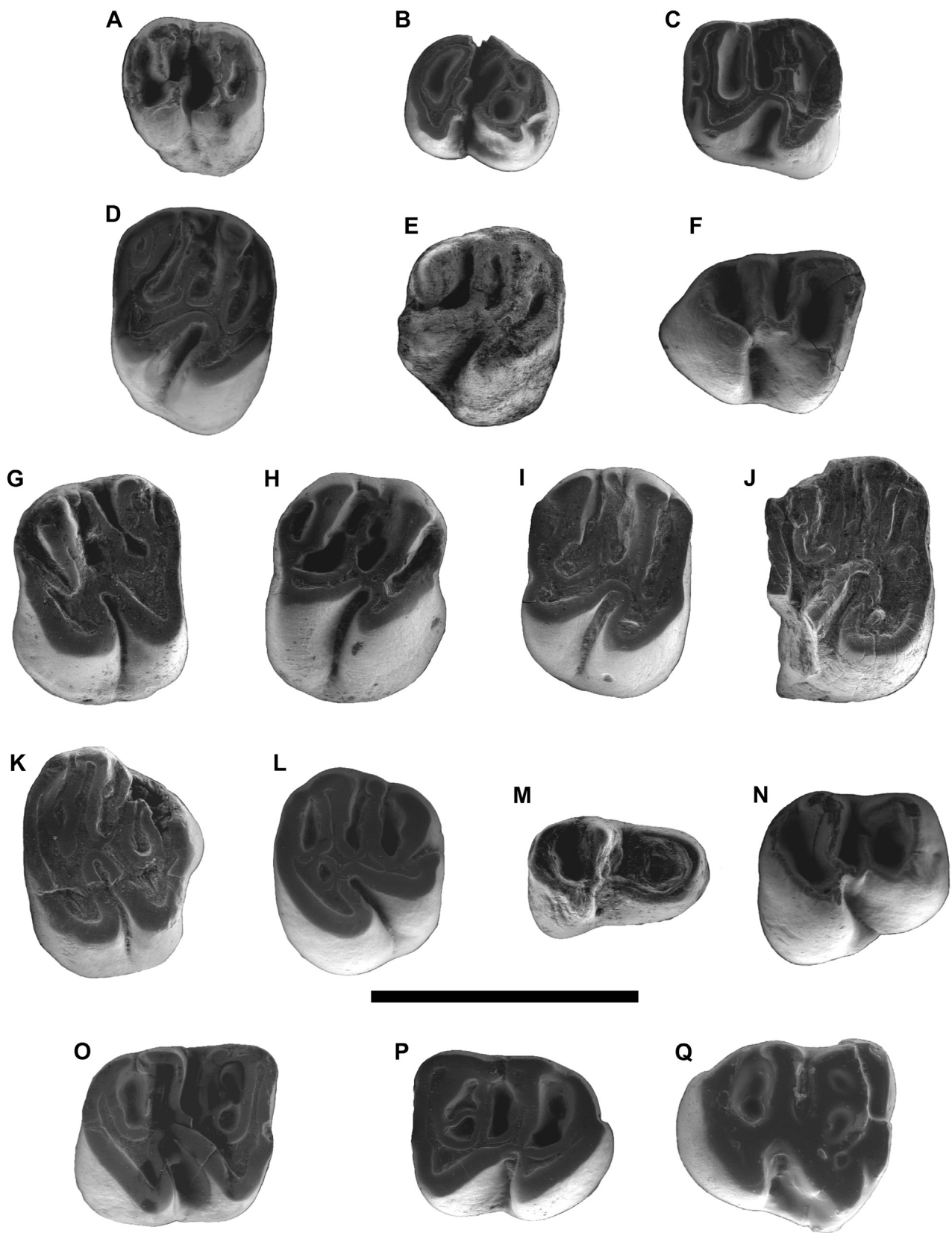


Fig. 3. ESEM pictures of the teeth of Theridomyidae from Santpedor-2. **A–C.** *Ectropomys exiguus* Bosma et Schmidt-Kittler, 1972. A: right DP4 (IPS 105269); B: right p4 (IPS 105286); C: left m2 (IPS 105287). **D–F.** *Paratheridomys margaritae* (Vianey-Liaud, 1972). D: right M2 (IPS 18941); E: right M3 (IPS 105257); F: right m3 (IPS 105284). **G–Q.** ?*Issidoromyinae* nov. gen., nov. sp. G: left P4 (IPS 105276); H: right M1-2 (IPS 105275); I: right M1-2 (IPS 105277); J: right M1-2 (IPS 105278); K: left M3 (IPS 105279); L: left M3 (IPS 105280); M: right dp4 (IPS 18940); N: right p4 (IPS 105281); O: right m2 (IPS 105282); P: left m3 (IPS 105283); Q: right m3 (IPS 105285). Scale bar: 3 mm.

Oligocene localities of Spain and Southern France: San Cugat de Gavadons, Calaf and Los Barros (Ebro Basin, Spain); Civrac, Saint-Capraise-d'Eymet and Soumaillies (Aquitaine Basin); Escamps, Sainte-Néboule, Aubrelong 1 and Ravet (Quercy Phosphorites); Ronzon (Auvergne). The size is larger than that of *Pseudoltinomys* aff. *cuvieri* from San Cugat de Gavadons and *P. gaillardi* from Soumaillies, Ronzon, or from the Quercy localities (Vianey-Liaud, 1976). The deciduous lower molar is simpler than that of *P. gaillardi*; it is less hypsodont and simpler than that of *P. amblesi* (Garzon Heydt and López Martínez, 1978). The p4 has its mesial width less reduced with respect to the distal width compared with p4 of *P. cuvieri*, *P. gaillardi*, *Paratheridomys margaritae* and *Blainvillimys langei*. The crown is lower than in *P. gaillardi*. Compared to the species of *Theridomys*, it is close to the size of the smallest teeth of *T. aquatilis*, and smaller than *T. golpei* and *T. calafensis* (Anadón et al., 1987). In addition, the dp4 and p4 are simpler and shorter than in *Theridomys*.

Family Eomyidae Depéret et Douxami, 1902

Genus *Eomys* Schlosser, 1884

Eomys sp.

Fig. 4(A, B)

Material: p4: IPS 105265; fragment of m1-2: IPS 105262.

Description and remarks: The size of these teeth is larger than that of *Eomys antiquus*, close to that of *E. molassicus* (Engesser, 1987), and slightly smaller than that of *E. zitteli* (Comte and Vianey-Liaud, 1989). However, some features of these two teeth differ from the latter two species. The p4 of *Eomys* sp. (Fig. 4(A)) is less elongated, and its metaconid and protoconid are more robust than on *E. zitteli*. Contrary to *E. antiquus*, *E. molassicus* and *E. zitteli*, in the teeth from Santpedor the anteroconid/anterolophid is absent: there is only a high mesial connection between the protoconid and the metaconid, which is the metalophulid I. These cusps are closer to each other than on *E. molassicus*, on which the 'trigonid' appears less short buccolingually than on the species from

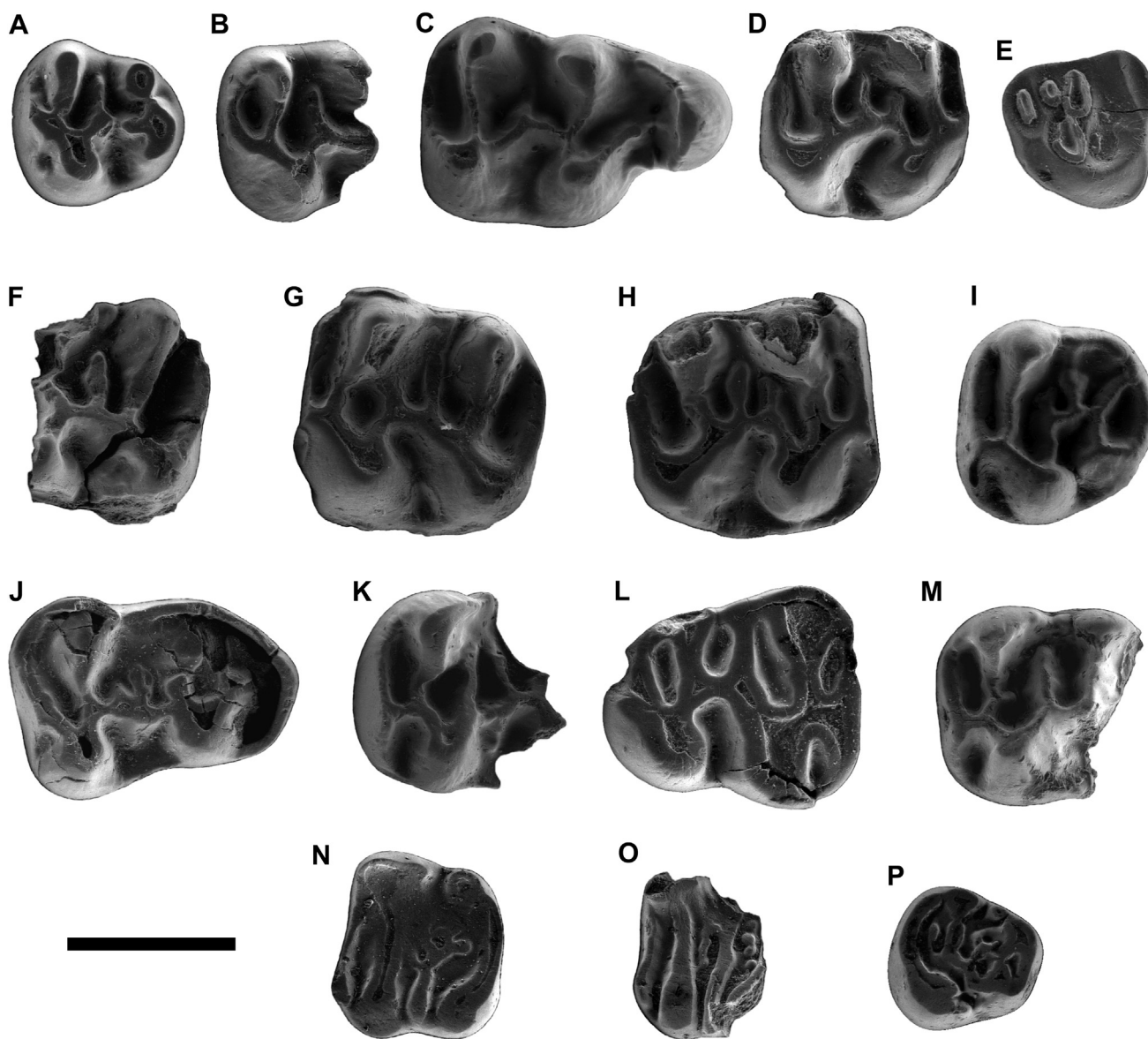


Fig. 4. ESEM pictures of the teeth of Eomyidae, Cricetidae and Gliridae from Santpedor-2. **A, B.** *Eomys* sp. A: right p4 (IPS 105265); B: right m1-2 (IPS 105262). **C-E.** *Eucricetodon atavus* Misonne, 1957. C: right M1 (IPS 105268); D: right M2 (IPS 105266); E: right M3 (IPS 105264). **F-L.** cf. *Heterocricetodon* sp. F: left M1 (IPS 105273); G: left M2 (IPS 105258); H: right M2 (IPS 105260); I: left M3 (IPS 105267); J: right m1 (IPS 105259); K: left m2 (IPS 105261); L: right m3 (IPS 105263). **M.** cf. *Pseudocricetodon* sp., left m2 (IPS 105274). **N-P.** *Glamys devoogdi* (Bosma et de Bruijn, 1979). N: left m2 (IPS 105270); O: left m2 (IPS 105271); P: right p4 (IPS 105272). Scale bar: 1 mm.

Santpedor. On p4 and m2, the mesolophid is moderately long as observed on *E. zitteli* or on the *Eomys* sp. from Möhren 20 (Maridet et al., 2010). It is longer than on the type of *E. zitteli*, but shorter and weaker than on *E. molassicus*. On the latter (type from Oensingen), it makes an angle, being firstly directed posteriorly before being transverse, whereas it is transverse since the mesoconid on *Eomys* sp. from Santpedor. On the fragment of m2 IPS 105262 (Fig. 4(B)), the attachment of the entolophid on the posterolophid is more buccal than on *E. molassicus*, and thus the posterosynclinid and the posterolophid are longer mesiodistally. Therefore, the species from Santpedor displays original features.

Family Cricetidae Rochebrune, 1883

Remarks: When studying the rare cricetid teeth from Santpedor-2, we were confronted with the absence or incompleteness of diagnosis for several Oligocene species or genera. The history of these European Oligocene cricetids, resulting from several phases of immigration and local developments in Western Europe, is complex. An exhaustive review with direct comparison of populations from numerous localities in this geographical area would be essential to achieve consistent results. It would be necessary to take into account all their features, dental (morphology and ultrastructure) and cranial.

Subfamily Eucricetodontinae Mein et Freudenthal, 1971

Genus *Eucricetodon* Thaler, 1966

Eucricetodon atavus Misonne, 1957

Fig. 4(C–E)

Material: M1: IPS 105268; M2: IPS 105266; M3: IPS 105264.

Description:

M1. The enamel of the outskirts of the crown is wrinkled. The buccal side is convex. There is only a single anterocone, from which a weak anterocone spur slopes and joins the long protocone spur. Lingually, the anteroloph slopes to the level of the protocone, from which it is separated by a notch. Buccally, the cingulum is longer and stronger than the anteroloph. The protolophule joins the short distal arm of the protocone, and the metalophule reaches the short mesial arm of the hypocone. The entoloph is long and angles at the level of the mesocone. The mesoloph is short and the mesostyle is reduced to short circular elements. Lingually, the entostyle is also reduced.

M2. The buccal anteroloph is well developed, reaching the buccal corner of the tooth. The lingual anteroloph is thinner, lower and long. The protoloph is oblique forwardly and joins the anterolophule. The posterior arm of the protocone is present. The mesoloph is short. The metalophule is directed anteriorly. A thin entostyle underlines the buccal border of the mesosinus. It differs from the M2 of cf. *Heterocricetodon* from Santpedor-2 in its smaller size, lophs and mesosinus less transverse and in the different wear pattern (horizontal only on the lingual half of *Eucricetodon*, the paracone and metacone being bulged and protruding, whereas the buccal cusps of *Heterocricetodon* are also flattened).

M3. This tiny tooth is too much eroded to depict its features.

Remarks: The small species of *Eucricetodon*, including *atavus*, have been referred to the genus *Atavocricetodon* by Freudenthal (1996), but this author did not give any differential diagnosis with respect to the genus *Eucricetodon*. A differential diagnosis is also missing in the redescription of the species *atavus* made by Freudenthal (1988). The validity of *Atavocricetodon* was then discussed and rejected by other authors (e.g., de Bruijn et al., 2003, Gomes Rodrigues et al., 2013), who “found no obvious reason, even pragmatism, to keep *Atavocricetodon* as a genus or even a subgenus”. This is the reason why we decide here to use *Eucricetodon* rather than *Atavocricetodon*. As this cricetid is poorly represented in the locality, we cannot contribute more to this discussion. Its size and morphology fit those of the genus *Eucricetodon*: bunodont teeth, larger than those of *Pseudocricetodon* and with simpler lophs and ridges; anterocone of the M1

generally simple, sometimes tending to be slightly duplicated, convex buccal contour of the M1 and posterior lobe of the M3 markedly reduced (Vianey-Liaud, 1972). The size and morphology of the M1 and M2 match those of the lower Oligocene populations of *E. atavus* (e.g., Hoogbutsel, Aubrelong 1, Ravet, Montalbán, Mège, Pech Crabit, Itardies; Vianey-Liaud, 1972, 1974; Freudenthal, 1988), better than to ‘*Atavocricetodon*’ aff. *nanus* from Valbro (Peigné et al., 2014: fig. 16). The more distinctive difference in size is between the lower m1 of these two species, but there is no available m1 in Santpedor-2. If considering the type population of *nanus* from Valdecollares (Peláez-Campomanes, 1995), the size of the M1 and M2 from Santpedor-2 is clearly larger. *Eucricetodon atavus* is recorded from MP21 to MP23 (Vianey-Liaud, 1972; Vianey-Liaud and Schmid, 2009).

Subfamily Pseudocricetodontinae Engesser, 1987

Genus *Heterocricetodon* Schaub, 1925

cf. *Heterocricetodon* sp.

Fig. 4(F–L)

Material: M1 (distal part): IPS 105273; M2: IPS 105258, 105260; M3: IPS 105267; m1: IPS 105259; m2: IPS 105261; m3: IPS 105263.

Description: We refer the teeth from Santpedor to a small primitive species of *Heterocricetodon* better than to *Pseudocricetodon*, on the basis of their rather lophodont dental pattern and the presence of a long mesoloph on one of the M2 (Fig. 4(G)) and on the M3 (Fig. 4(I)). Even if this latter feature is variably found in *Pseudocricetodon incertus*, it is observed in the material from Santpedor together with other features found in *Heterocricetodon*: the long lingual anteroloph of M2, the high lophs on the unworn M3; the flat wear surface of the M2 from the lingual edge of the crown to the 2/3 of the occlusal surface, with moderately prominent buccal upper main cusps; the long postmetacristid on m1 (Fig. 4(J)), the flat wear surface of the m3, with its long posterior arm of the protoconid, and the reduced width of its posterior lobe (Fig. 4(L)). The anteroconid and metaconid of m1 are strongly worn, and therefore the lophids are difficult to distinguish, except the occurrence of a long postmetacristid and a short thick posterior arm of the protoconid, weakly separated from the lingual metalophulid; there are two short mesolophids, the more mesial being the longest. There is no posterior arm of the hypoconid. The fragment of m2 shows a long postmetacristid ending in a small swelling as a metastylid; its posterior arm of the protoconid is long and oblique towards the base, and ends with a thickening against the middle of the buccal flank of the metaconid; the mesolophid has same length than the posterior arm of the protoconid. Flat and worn on its buccal two-third, its lingual cusps are not worn. The enamel of the surroundings of the crown is wrinkled.

Remarks: The genus *Heterocricetodon* was so far unknown in the lower Oligocene. Until now, the earliest species referred to this genus were *H. landroveri* (Daams et al., 1989) from Pareja (MP 26, early Chattian; Aguilar et al., 1997) and *H. hausi* from Bumbach (MP24–25?, earliest Chattian; Engesser, 1987).

As noticed by Engesser (1987: p. 990) for the species *hausi*, it is difficult to refer isolated teeth to *Heterocricetodon*, and especially to differentiate them from the genus *Pseudocricetodon* until the discovery of more abundant material. It is even much more difficult to carry out such a distinction in an older Rupelian locality, where very few teeth are documented. Daams et al. (1989: pp. 47–48) propose to include the species *incertus* within the genus *Heterocricetodon* even if cranial features “prove the value of this genus”.

The teeth from Santpedor are larger than those of ‘*Pseudocricetodon incertus*’ from some lower Chattian localities (Vianey-Liaud et al., 2014: table 5, p. 594) but smaller than *H. hausi* from Bumbach, and similar in size to *H. landroveri* (m1 smaller than the smallest m1 from Pareja, m3 like the largest). The species from

Santpedor-2 differs from *H. landroveri* in the more reduced posterior lobe of m3 and the mesoconid more distinct on m1. Its morphology is closer to *H. hausi*, but the sinus seems less deep buccolingually. As the sample is scarce, we cannot define the morphological and size variability, and prefer to keep this *Heterocricetodon* sp. in open nomenclature. This species thus represents the earliest record of the genus documented so far.

Genus *Pseudocricetodon* Thaler, 1969
cf. *Pseudocricetodon* sp.

Fig. 4(M)

Material: An incomplete m2: IPS 105274.

Description and remarks: This fragment of tooth differs from that ascribed to *Heterocricetodon* in its slightly smaller size, the enamel smooth, and the more bulbous and rounded main cuspids, as well as in the different arrangement of the talonid basin area. The postmetacristid is shorter and the metastylid less distinct, by contrast there is a mesostylid blocking the opening of the entosinuid. There is no mesolophid distinct from the posterior arm of the protoconid. The latter is widely oblique and is connected to the mesial extremity of the ectolophid: at the junction it curves buccolingually. If this interpretation is right, the mesolophid is absent, because there is no distinct mesoconid, and no ectomesolophid, but only a faint vertical swelling on the buccal flank of the short ectolophid.

Family Gliridae Thomas, 1897

Subfamily Glamyiinae Vianey-Liaud, 1994

Genus *Glamys* Vianey-Liaud, 1989

Glamys devoogdi (Bosma et de Bruijn, 1979)

Fig. 4(N–P)

Material: p4: IPS 105272; m2: IPS 105270; m2 incomplete: IPS 105271.

Description: The wear surface of p4 (Fig. 4(P)) is nearly flat and the crown relatively low. The metaconid and protoconid are linked by two short and thick lophids: an anterolophid and a metalophid II. The anterior arm of the hypoconid is faintly developed; therefore, the sinusid is confluent with the posterosynclinid. The posterolophid is long and strong, ending against the bulged entoconid. On m2, the anterolophid is long, separates from the protoconid and joins the metaconid; the postmetacristid is present and slopes gently to the mesoflexid lingual opening; the metalophid is transverse and thick; the mesoconid is present, and the mesolophid is long, connected to the entoconid by a low entolophid. One extra-ridge (Fig. 4(N)) and granules (Fig. 4(O)) are present in the mesoflexid and posteroflexid.

Remarks: The size of the p4 and of the complete m2 fits the size range of *Glamys devoogdi* from Hamstead Beds and Hoogbutsel (Bosma and de Bruijn, 1979; Vianey-Liaud, 1994) and the morphology is also close to that of this species. On the p4 figured in Bosma and de Bruijn (1979: pl. 2, fig. 5), the mesial connection (anterolophid) is low and does not reach the top of the metaconid and protoconid, whereas this connection is higher and complete on the p4 from Santpedor. The paths of the other extra-ridges and granules, into the sinusid and the talonid, occupy similar positions but their connections vary. The species is recorded from the late Priabonian (MP19/20) to the early Rupelian (MP21).

5. Discussion

The Eocene-Oligocene transition was characterized by a drastic decrease in global temperatures, which involved a significant change in the faunas of both marine and terrestrial realms, known as the “Grande Coupure” (e.g., Stehlin, 1910; Prothero, 1994; Zachos et al., 2001; Hooker et al., 2004; Hooker, 2010; Hren et al., 2013). In the European continent this faunal turnover was marked,

among other changes, by the arrival of some immigrant groups, such as cricetid rodents (Vianey-Liaud, 1979; Hooker et al., 2004; Maridet and Ni, 2013; Freudenthal and Martín-Suárez, 2016), and by the nearly complete disappearance of primates. Until the end of the XXth century, it was generally accepted that microchoerine primates became extinct at the Eocene-Oligocene transition, but the identification of scarce remains of *Pseudoloris* in Fonollosa and Santpedor (Köhler and Moyà-Solà, 1999) and of *Microchoerus* in Aguatón (Peláez-Campomanes, 2000) testified to the persistence of this group in the Iberian Peninsula during the earliest Oligocene. For this reason, the detailed study of the fossil sites documenting this time window in Spain is particularly relevant, in order to ensure precise dating of such localities, and to analyze the mammal assemblages that coexisted with these last surviving Paleogene primates in Europe.

The reference faunas of the latest Priabonian (MP20, St-Capraise-d'Eymet) and earliest Rupelian (MP21, Soumailles) MP-levels are poor, and have been chosen mainly because they have provided both small and large mammals. However, the evolutionary stages of the documented lineages are not very discriminating, either for the MP20 or for the MP21 (Aguilar et al., 1997). The characterization of the MP20, which is mainly based on the terminal stage of *Palaeotherium curtum* (sub-species *frohntetense*), is not evident (e.g., Hooker, 2010). For the rodents, *Theridomys bonduelli* could be a good marker, but this species is only known from the Paris and Hampshire basins. This has a definite impact on the precise definition and correlations of faunas around the “Grande Coupure”.

The “Grande Coupure” would mark the base of the Rupelian, currently dated at 33.9 Ma (Vandenberghe et al., 2012). Several correlation attempts with respect to mammalian lineages have been made, using magnetostratigraphy and geochemistry (Solent Group, Whitecliff Bay, Isle of Wight, England; Gale et al., 2006; Hooker et al., 2009) or only magnetostratigraphy in the case of the Santpedor section (Barberà et al., 2001; Costa et al., 2011). According to the latter authors, the magnetostratigraphic location of the MP21 level, possibly represented at Santpedor at the upper part of the 13r chron, would date this MP around 33.4 Ma, but this datum needs to be confirmed. This locality contains both immigrant rodents, such as the Cricetidae, as well as native species of Gliridae and Theridomyidae. The scarcity of rodent material in the MP20 and MP21 reference levels, combined with the geographical differentiation observed between theridomyoids at the beginning of the Oligocene, does not facilitate precise correlations. Nonetheless, it is easy to identify the arrival of immigrant taxa and also to distinguish the evolutionary stages of certain lineages when they have represented by sufficient teeth.

There are currently few Rupelian and earliest Chattian MP, four in number (MP21 to MP24), over a total stage duration of ~6 myr. However, based on the evolutionary degrees of several Theridomyoidea lineages, at least one intermediate level MP23/24 can be inserted even if it has not yet been formally defined (Fig. 5). It would correspond to the evolutionary level of the fauna from St-Martin-de-Castillon (Vaucluse), in particular to the species *Protechimys truci* (Huguency, 1994; Vianey-Liaud, 1998; Vianey-Liaud and Marivaux, 2017). The standard locality of MP24 (Heimersheim) is located at the base of the Cyrenen Mergel, and correlated with the Kasseler Meeressand, which provided nannoplankton from the NP24 area (Bahlo, 1975: p. 12). Thus, the age of MP24 is close to the Rupelian-Chattian boundary (28.3 Ma; Vandenberghe et al., 2012) within the lowermost Chattian.

The study of the rodents from Santpedor-2 reveals a higher diversity than previously thought. Even if the number of rodent teeth is small, they are characteristic enough either to be identified as already known species, or at least compared to morphologically close species. Among them, one species is known only from late

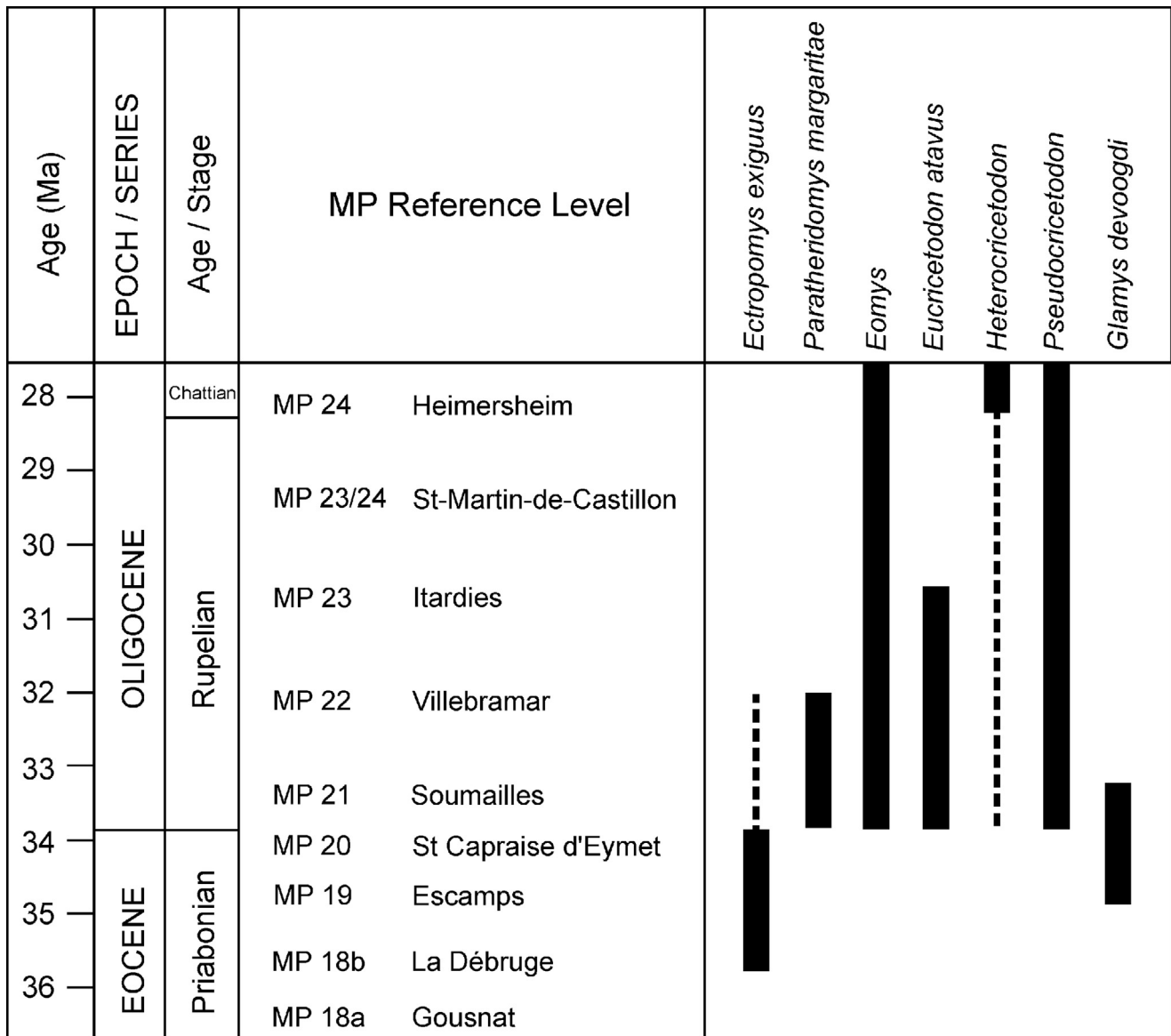


Fig. 5. Known stratigraphical extension of the rodents identified in Santpedor-2, after [Vianey-Liaud \(1994\)](#), [Freudenthal \(1996\)](#), [Hooker et al. \(2004\)](#), [Vianey-Liaud and Schmid \(2009\)](#), [Peigné et al. \(2014\)](#), and [Vianey-Liaud and Marivaux \(2017\)](#). Dotted lines indicate the extended ranges of some taxa after the identification of the rodents from Santpedor-2 (MP21 or MP22). The MP reference levels are correlated to the GTS scale ([Vandenbergh et al., 2012](#)), with position of these levels discussed in [Vianey-Liaud and Marivaux \(2017\)](#). The Theridomorpha from Gousnat (MP18a) represent evolutionary grades more primitive than those from La Débruge (MP18b) ([Vianey-Liaud and Marivaux, 2017](#)).

Eocene localities (MP18 to MP20): the Theridomyidae *Ectropomys exiguus* ([Vianey-Liaud et al., 1994](#)). The glirid *Glamys devoogdi* is known from late Priabonian to early Rupelian localities (MP19 to MP21; [Vianey-Liaud, 1994](#): table 2). The other identified rodents belong exclusively to Oligocene taxa ([Fig. 5](#)). One Theridomyidae (*Paratheridomys margaritae*) is known from the standard locality of MP21 (Hoogbutsel, Belgium; [Vianey-Liaud, 1972](#)), which is the type locality of the species, and from La Plante 2 (Quercy, France, MP22; [Vianey-Liaud, 1989](#)). The other Theridomyidae (?Issiodoromyinae) is probably a new species, and perhaps a new genus; its features (e.g., size of premolars) better indicate Oligocene rather than late Eocene evolutionary grades. Two immigrant families of the “Grande Coupure” are recognized: the Eomyidae and the Cricetidae, among which one species (*Eucricetodon atavus*) and one genus (*Pseudocricetodon*) are recorded since MP21. The other genera are represented by original species, a *Heterocricetodon* more

primitive, smaller, and plausibly older than the earliest species known until now, and an *Eomys* larger than the MP21 species *E. antiquus*, but with features different from all known *Eomys* species.

This rodent assemblage is most probably early Oligocene in age, with a certain diversity of well-characterized immigrant families, and Oligocene evolutionary grades of autochthonous lineages (i.e., *P. margaritae* and *G. devoogdi*). One rodent species (*Ectropomys exiguus*) represents an Eocene relict, as is the case of *Pseudoloris godinoti*, the only primate recorded in this locality. As there are only 33 teeth for eight rodent species found so far, some of them remain in open nomenclature, and therefore we cannot precise if the assemblage is close to MP21 or to MP22. Further field campaigns in this fossil site, leading to the recovery of more abundant material, will probably allow for more precise taxonomic determinations and a more accurate dating of the locality.

6. Conclusions

The rodent fossil material from Santpedor-2 (Ebro Basin, NE Spain) was described in detail for the first time. The assemblage includes eight different rodent taxa: *Ectropomys exiguus*, *Paratheridomys margaritae*, ?Ilsiodoromyinae nov. gen., nov. sp., *Eomys* sp., *Eucricetodon atavus*, cf. *Heterocricetodon* sp., cf. *Pseudocricetodon* sp., and *Glamys devoogdi*; it is notably different from that reported in the preliminary faunal lists provided by Agustí et al. (1987) and Arbiol and Sáez (1988). Although the locality has yielded one species that can be considered as an Eocene relict (*Ectropomys exiguus*), the presence of two rodent families that arrived in Europe as part of the “Grande Coupure” event (Eomyidae and Cricetidae), as well as the evolutionary grade of species of Gliridae and Theridomyidae, might indicate an early Oligocene age for this assemblage. Nevertheless, the scarcity of the material prevents a precise taxonomic determination of some taxa and a conclusive assignment to one of the earliest Oligocene standard levels (MP21 or MP22). In any case, this study confirms the early Oligocene age of Santpedor-2, one of the few European localities that documents the persistence of omomyid primates after the “Grande Coupure”.

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