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Three million years of “Terror-Shrew” (*Dinosorex*, *Eulipotyphla*, Mammalia) in the Miocene of the Vallès-Penedès Basin (Barcelona, Spain)



*Trois millions d'années de « musaraigne terrifiante » (*Dinosorex*, *Eulipotyphla*, Mammalia) dans le Miocène du bassin Vallès-Penedès (Barcelone, Espagne)*

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ABSTRACT

For the first time, the heterosoricid genus *Dinosorex* from the Iberian Peninsula has been studied in detail. Dental morphology and measurements match the original description of the species *Dinosorex grycivensis* Rzebik-Kowalska and Topachevsky, 1997. This is the first time that the species is reported in southwestern Europe. Biostratigraphically, the last occurrences of *Dinosorex* in the Vallès-Penedès basin coincide with the transition from early to late Vallesian, together with the first occurrences of the murid *Progonomys*, at about 9.6 Ma. This is close in time to the estimated moment of final extinction for the genus. From an evolutionary point of view, it is remarkable that in the more than forty localities in the Vallès-Penedès Basin, spanning three million years, there are no apparent morphological changes. Notably, to date, no occurrences have been reported in central Europe that could link the Ukrainian and Iberian assemblages biogeographically. These results clearly highlight the need of revision of other European forms to place the Iberian finds in a broader scenario in order to fully comprehend the factors driving the evolution and ultimately extinction of the “terror-shrews”.

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R É S U M É

Le genre d'Hétérosoricidé *Dinosorex*, de la péninsule Ibérique, est étudié en détail pour la première fois. La morphologie dentaire, ainsi que les mesures, correspondent à la description originale de l'espèce *Dinosorex grycivensis* Rzebik-Kowalska et Topachevsky, 1997, reconnue ainsi pour la première fois en Europe du Sud-Ouest. La dernière occurrence de *Dinosorex* dans le bassin Vallès-Penedès coïncide avec la transition du Vallésien basal à

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terminal, et correspond à la première occurrence du rongeur muridé *Progonomys*, à environ 9,6 Ma. Cette extinction est aussi proche de la date estimée de la disparition définitive du genre du registre fossile. D'un point de vue évolutif, il est remarquable qu'aucun changement morphologique ne puisse être observé dans plus de 40 sites couvrant 3 millions d'années. Aussi remarquable, aucune occurrence indiscutable de *D. grycivensis* ne peut être mise en évidence en Europe centrale, ce qui permettrait de lier biogéographiquement les faunes ukrainiennes et ibériques. Ces résultats soulignent clairement le besoin de réviser les autres formes européennes pour placer les fossiles ibériques dans un plus large contexte, et pouvoir comprendre les facteurs dirigeant l'évolution et l'extinction de la « musaraigne terrifiante ».

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1. Introduction

Compared to central Europe, the Spanish record of insectivores is rather scanty in terms of species diversity (Van den Hoek Ostende and Furió, 2005). One exception is the early Late Miocene (Vallesian) of the Vallès-Penedès. It is, therefore, no coincidence that the first Iberian insectivores, like the hedgehog *Postpalerinaceus vireti* and the mole *Talpa vallesiensis*, were described from this area (Crusafont and Villalta, 1947; Villalta and Crusafont, 1944). These historical records were all based on surface finds. Since then, much more material has been recovered by wet-screening fossiliferous localities in the area. Particularly during the last decade, micromammal finds from the Vallès-Penedès have increased tremendously, as classical sites were re-opened and new localities were discovered (Alba et al., 2006; Casanovas-Vilar et al., 2011, 2014).

Like other works on some of the first fossil insectivores described in Spain (Crusafont, 1957; Villalta and Crusafont, 1943), this paper presents the finds of *Dinosorex*, a large shrew-like taxon. Assemblages of this remarkable insectivore are usually relatively small, but the large record of the Vallès-Penedès basin encompasses hundreds of teeth from various localities (Table 1). The area also records one of the last European occurrences of the genus and the family. The Heterosoricidae originated as early as the middle Eocene of North America (Harris, 1998; Repenning, 1967) and shows a complex evolutionary pattern (Ziegler, 2009), which holds certainly also true for the fossil history of the genus *Dinosorex*. Hitherto *Dinosorex* was considered to have originated in the early Miocene of Anatolia (Van den Hoek Ostende, 1995). The description of a species from the Late Oligocene in Germany seems shift the origin to Europe (Engesser and Storch, 2008), but Ziegler (2009) pointed out that, in the absence of the diagnostic lower incisor, this *D. pusillus* may just as well belong to the genus *Quercysorex*. It is clear, however, that *Dinosorex* was absent during the earlier part of the Miocene and (re-)entered central Europe at the end of the Early Miocene. From the Middle Miocene, three species have been defined, namely *Dinosorex sansaniensis* (Lartet, 1851) (type locality Sansan, France; MN 6), *D. zapfei* Engesser, 1975 (type locality Devínská Nová Ves (fissure), Slovak Republic; MN 6) and *D. pachygnathus* Engesser, 1972 (type locality Anwil, Switzerland; MN 7/8). In addition, two more species were described from the early

Late Miocene, *D. engesseri* Rabeder, 1998 and *D. grycivensis* Rzebik-Kowalska and Topachevsky, 1997. This classification suggests a radiation of different forms at the end of the temporal range of the genus. However, the taxonomy of *Dinosorex* is far from settled, with finds from many localities described in open nomenclature, often with an “aff.” assignment. Therefore, we are currently undertaking a revision of central European forms. As a first step, we here focus on the Iberian finds of the “terror-shrew” *Dinosorex* (named after the lethal-looking anterior dentition of the fossils), and compare our results with the published late Middle Miocene and Late Miocene record.

2. Material and methods

The basic description is based on the material of the locality ACM/C4-A1, which yielded the largest available assemblage of *Dinosorex* from the Vallès-Penedès basin. The consequent exceptions to the standard morphology, as well as particular cases with material not represented in ACM/C4-A1, have been highlighted at the end of the description. Measurements taken as detailed in Fig. 1 were carried out using a Nikon Meascope. SEM photographs were taken at the Servei de Microscopia Electrònica from Universitat Autònoma de Barcelona. We follow Klieemann et al. (2014) in assigning a family rank rather than subfamily rank to the Heterosoricidae, but agree with these authors that the ranking of the group is rather a subjective matter.

Acronyms in alphabetical order: **ACM** (Abocador de Can Mata, several localities: **C1-A1**; **C1-E7**; **C1-D1**; **C2-B3**; **C3-A5**; **C3-B2**; **C4-A1**; **C4-A3**; **C4-C1**; **C5-A4**; **C5-C2**; **C5-C3**; **C5-D1**; **C5-D2**; **C5-D4**; **C5-D7**; **C6-A2**; **C6-A2+C4-A3**; **C6-C1**; **C8-A1**; **C8-B1**; **C8-By**; **C9-A1**); **BCV1** (Barranc de Can Vila 1); **CdB** (Castell de Barberà); **CF** (Can Feliu); **CLL** (Can Llobateres 1/Clàssic); **CM** (Can Missert); **CP** (Can Poncic); **CPL** (Can Pallars de Llobateres); **CFEU** (Can Feu); **EDAR** (Estació Depuradora d'Aiguës, several localities); **HS** (Hostalets Superior); **RT11** (Autopista Rubi-Terrassa 11); **S** (Santiga); **SQ** (Sant Quirze Clàssic); **SQA** (Sant Quirze A); **TCLLO** (Trinxera de Can Llobateres 0); **TCLL1** (Trinxera de Can Llobateres 1). See also Table 1.

3. Systematic palaeontology

Family HETEROSORICIDAE Viret and Zapfe, 1952
Genus *Dinosorex* Engesser, 1972

Table 1

List of localities from the Vallès-Penedès Basin that yielded fossils of *Dinosorex*. The number of fossil specimens of this genus in each locality is indicated in the last column. Age in Myr is indicated as a constrained range between minimum and maximum, as provided by work in progress by Casanovas-Vilar et al.

Tableau 1

Liste des localités du bassin Vallès-Penedès dans lesquelles *Dinosorex* a été trouvé. Le nombre de spécimens fossiles du genre pour chaque localité est indiqué dans la dernière colonne. L'âge en Ma est indiqué comme une datation médiane entre les valeurs minimales et maximales, suivant les données fournies par des travaux en cours par Casanovas-Vilar et al.

Age	Locality	Acronym	Elements (N)
9.5–9.7	Trinxera de Can Llobateres 1	TCLL1	2
9.5–9.7	Trinxera de Can Llobateres 0	TCLL0	6
9.5–9.7	Autopista Rubí-Terrassa 11	RT11	2
9.5–9.7	Can Llobateres 1	CLL	70
9.5–9.9	Can Pallars	CPL	7
9.5–9.9	Can Feu	CFEU	1
9.9–10.4	Estació Depuradora d'Aigües Residuals 22	EDAR22	1
9.9–10.4	Estació Depuradora d'Aigües Residuals 2	EDAR2	1
9.9–10.4	Estació Depuradora d'Aigües Residuals 13	EDAR13	1
9.9–10.4	Estació Depuradora d'Aigües Residuals 1	EDAR1	1
9.9–10.4	Estació Depuradora d'Aigües Residuals 3	EDAR3	2
9.9–10.4	Santiga	S	1
9.9–10.4	Can Ponsic	CP	2
10.5–10.7	Hostalets de Pierola	HS	8
10.4–11.1	Can Missert	CM	4
10.4–11.1	Castell de Barbera	CdB	84
10.4–11.1	Can Feliu	CF	3
11.1–11.5	San Quirze A	SQA	14
11.1–11.5	San Quirze	SQ	6
11.2–11.6	Abocador de Can Mata C8-B1	ACM/C8-B1	7
11.6	Abocador de Can Mata C6-C1	ACM/C6-C1	12
11.6	Abocador de Can Mata C8-By	ACM/C8-By	2
11.6	Abocador de Can Mata C6-A2	ACM/C6-A2	6
11.6	Abocador de Can Mata C5-D1	ACM/C5-D1	70
11.6	Abocador de Can Mata C5-D2	ACM/C5-D2	1
11.6	Abocador de Can Mata C8-A1	ACM/C8-A1	1
11.6	Abocador de Can Mata C5-D3	ACM/C5-D3	1
11.6	Abocador de Can Mata C5-D4	ACM/C5-D4	1
11.6–12.0	Abocador de Can Mata C5-A4	ACM/C5-A4	1
11.6–12.0	Abocador de Can Mata C5-D7	ACM/C5-D7	1
11.6–12.0	Abocador de Can Mata C4-A1	ACM/C4-A1	141
11.6–12.0	Abocador de Can Mata C4-A3	ACM/C4-A3	2
11.6–12.0	Abocador de Can Mata C5-C2	ACM/C5-C2	4
11.6–12.0	Abocador de Can Mata C4-C1	ACM/C4-C1	2
11.6–12.0	Abocador de Can Mata C5-C3	ACM/C5-C3	3
11.6–12.0	Abocador de Can Mata C3-A5	ACM/C3-A5	4
11.6–12.0	Barranc de Can Vila 1	BCV1	37
12.0–12.1	Abocador de Can Mata C3-B2	ACM/C3-B2	2
12.0–12.1	Abocador de Can Mata C1-A1	ACM/C1-A1	4
12.0–12.1	Abocador de Can Mata C2-B3	ACM/C2-B3	1
12.2–12.4	Abocador de Can Mata C1-E7	ACM/C1-E7	5
12.2–12.4	Abocador de Can Mata C1-D1	ACM/C1-D1	1
12.2–12.4	Abocador de Can Mata C9-A1	ACM/C9-A1	1

Dinosorex grycivensis Rzebik-Kowalska and Topachevsky, 1997 (Figs. 2–4; Table 2)

Synonymy

Sorex sp., in: Bataller, 1924: p. 4 (SQ)

Sorex sp., in: Bataller, 1938: p. 19 (SQ)

Trimylus Schlosseri, in: Bataller, 1938: p. 19 (SQ)

Crociodura (Trimylus) schlosseri, in: Villalta and Crusafont, 1943: p. 185 (SQ, HS)

Heterosorex sansaniensis Lartet, in: Villalta and Crusafont, 1944: p. 4 (SQ, HS)

Heterosorex sansaniensis (Lartet), in: Crusafont, 1957: p. 77 (CP, HS)

Dinosorex aff. *sansaniensis*, in: Engesser, 1972: p. 94 (CLL)

Heterosorex sansaniensis, in: Gibert, 1974: 10 (CB, CLL, HS, SQ)

Dinosorex sansaniensis, in: Agustí and Gibert, 1982: p. 30 (HS, SQ, CdB, CP, CLL)

Dinosorex sp., in: Van den Hoek Ostende and Furió, 2005: p. 215 (S)

Dinosorex sansaniensis (Lartet, 1851), in: Alba et al., 2006: p. 303 (ACM)

Dinosorex sansaniensis, in: Casanovas-Vilar et al., 2008: p. 591 (BCV1)

Dinosorex zapfei Engesser, 1975, in: Furió et al., 2011: p. 207 (BCV1)

Dinosorex sp., in: Casanovas-Vilar et al., 2012: p. 225 (CFEU)

Dinosorex grycivensis Rzebik-Kowalska and Topachevsky, 1997, in: this work (all localities)

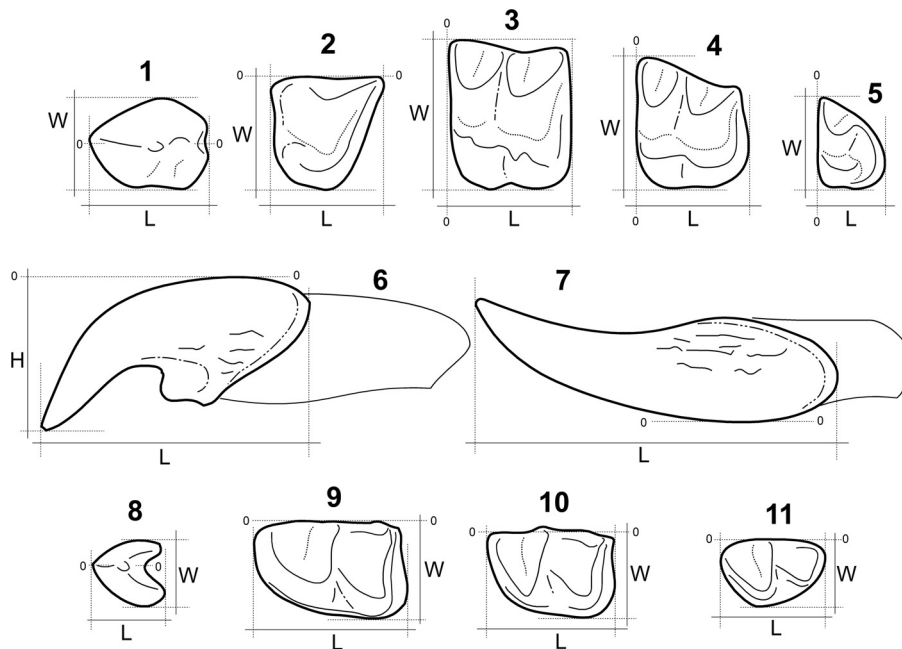


Fig. 1. Measurements taken on dental elements of *Dinosorex*. 1 – First upper antemolar; 2 – fourth upper premolar; 3 – first upper molar; 4 – second upper molar; 5 – third upper molar; 6 – upper incisor; 7 – lower incisor; 8 – lower antemolars; 9 – first lower molar; 10 – second lower molar; 11 – third lower molar. H = Height; L = Length; W = Width. Reference lines are indicated with dotted lines with “0” at their extremes.

Fig. 1. Mesures effectuées sur les éléments dentaires de *Dinosorex*. 1 – Première prémolaire supérieure; 2 – quatrième prémolaire supérieure; 3 – première molaire supérieure; 4 – deuxième molaire supérieure; 5 – troisième molaire supérieure; 6 – incisive supérieure; 7 – incisive inférieure; 8 – prémolaires inférieures; 9 – première molaire inférieure; 10 – seconde molaire inférieure; 11 – troisième molaire inférieure. H = Hauteur; L = longueur; W = largeur. Les spécimens ont été alignés conformément aux lignes pointillées délimitées par des «0».

Description

Nearly all teeth show discolouration near the tips, consistent with original pigmentation.

I1- (Fig. 4.2, 4.4, 4.6) The first upper incisor is a massive tooth, forming a strong hook with a bifid tip. On the mesial side, the enamel-dentine boundary slopes towards the front halfway down the tooth. At the labial side, this boundary is bordered by a cingulum. The enamel on the only mildly protruding talon is wrinkled, and these wrinkles extend somewhat onto the labial side.

A1- (Fig. 2.5, 2.14) The outline of the occlusal surface is subrectangular; the labial side is slightly longer than the lingual side. The tip of the only cusp lies far to the labial side, in the front part of the antemolar. A sharp centrocrista runs over the tip, ending at the front at the anteriormost corner of the antemolar, at the back just labially of the middle at a posterior emargination. Perpendicular to the centrocrista, a more or less well defined ridge runs from the tip to the lingual side of the tooth, where it ends in a slight thickening. The back of the tooth is bordered by a thick cingulum. On the posterolingual side, just next to this cingulum, there is an elevation, which in some specimens (e.g., IPS-58485) forms a true cusp. The cingulums on the labial, lingual and anterolingual sides are much less pronounced than the posterior one.

P4- (Fig. 2.4, 2.9, 2.13) The outline of the occlusal surface is nearly trapezoidal, the labial side being clearly longer than the lingual side. The latter is oriented more or less posterolingually. The labial part of the tooth consists of the high and large paracone. This cusp bears a sharp posterocrista,

which bends labially close behind the tip. A thick ridge runs along the anterior, lingual and labial side of the P4, starting in front of the paracone and connecting to the posterior end of the posterocrista. The small protocone forms part of this ridge, with its tip lingually of that of the paracone. The ridge is thickest at the posterolingual side of the tooth. The posterior basin is very deep.

M1- (Fig. 2.3, 2.8, 2.12) The outline of the occlusal surface is sub-square, the molar being only somewhat wider than long. The metacone is larger than the paracone; whereas the base of the paracone reaches to midway the molar, the base of the metacone extends somewhat more lingually. The mesostyle is undivided or only superficially divided. The protocone is well developed. Its anterior arm ends against the paracone, just in front of its base. The posterior arm runs in the direction of the metacone, but bends sharply to connect to the pronounced hypocone. The hypocone forms the starting point for the thick posterior ridge, which ends against the flank of the posterior arm of the metacone. There is a small batch of cingulum between the bases of the protocone and hypocone.

M2- (Fig. 2.2, 2.7, 2.11) The M2 is clearly wider at the front than at the back. The paracone and metacone are sub-equal in size; the arms of the metacone stand at a somewhat larger angle than those of the paracone. The protocone and particularly the hypocone are less pronounced than in the M1. The posterior ridge is wider than in the M1, with a clearly backwards slanted surface.

M3- (Fig. 2.1, 2.6, 2.10) The outline of the occlusal surface forms half a circle, with a straight anterior side. The

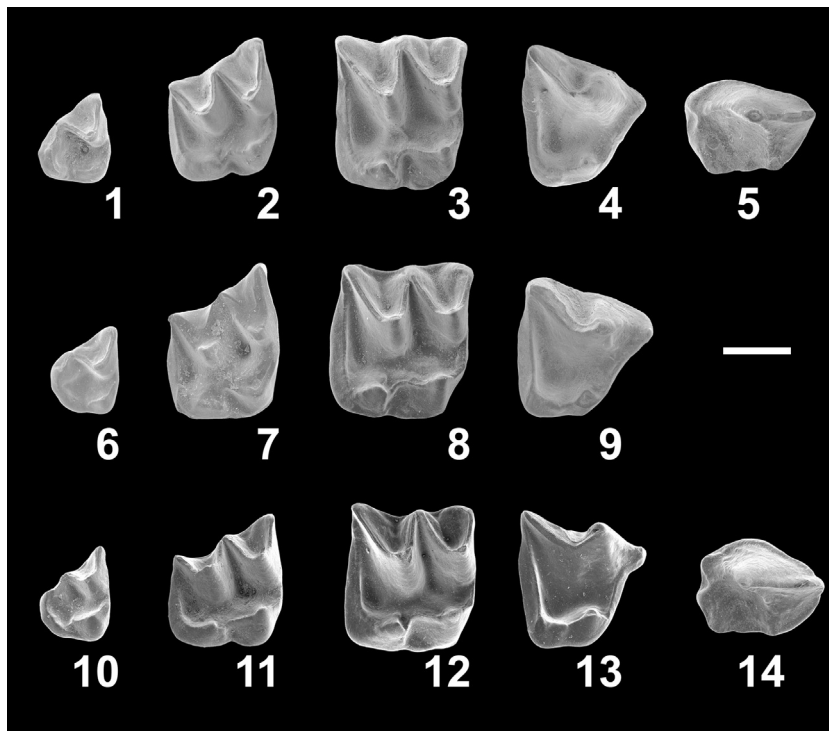


Fig. 2. Upper dentition of *Dinosorex grycivensis* from three localities in the Vallès-Penedès Basin. (1–5) Abocador de Can Mata (ACM) C4–A1: 1–right M3 (IPS-58528); 2–right M2 (IPS-58515); 3–right M1 (IPS-58504); 4–right P4 (IPS-58495); 5–right A1 (IPS-58481). (6–9) Can Llobateres (CLL): 6–left M3 (reversed) (IPS-42915); 7–left M2 (reversed) (IPS-65299); 8–right M1 (IPS-42914); 9–right P4 (IPS-62445). (10–14) Barranc de Can Vila 1 (BCV1): 10–right M3 (IPS-23476); 11–left M2 (reversed) (IPS-23469); 12–left M1 (reversed) (IPS-23472); 13–left P4 (reversed) (IPS-23461); 14–left A1 (reversed) (IPS-23493). All teeth in occlusal view. Scale bar equals 1 mm.

Fig. 2. Dentition supérieure de *Dinosorex grycivensis* de trois localités du bassin Vallès-Penedès. (1–5) Abocador de Can Mata (ACM) C4–A1 : 1 – M3 droite (IPS-58528); 2 – M2 droite (IPS-58515); 3 – M1 droite (IPS-58504); 4 – P4 droite (IPS-58495); 5 – A1 droite (IPS-58481). (6–9) Can Llobateres (CLL) : 6 – M3 gauche (retournée) (IPS-42915); 7 – M2 gauche (retournée) (IPS-65299); 8 – M1 droite (IPS-42914); 9 – P4 droite (IPS-62445). (10–14) Barranc de Can Vila 1 (BCV1) : 10 – M3 droite (IPS-23476); 11 – M2 gauche (retournée) (IPS-23469); 12 – M1 gauche (retournée) (IPS-23472); 13 – P4 gauche (retournée) (IPS-23461); 14 – A1 gauche (retournée) (IPS-23493). Toutes les dents sont présentées en vue occlusale. Échelle : 1 mm.

larger part of the molar consists of the paracone and the clearly lower protocone. The back is bordered by a ridge, consisting of the metacone and its anterior arm, and the hypocone. The latter is only faintly recognisable in one specimen (IPS 58525); in the others, it is fully merged with the metacone. The posterior arm of the protocone ends freely in the trigon basin.

i1- (Fig. 4.1, 4.3, 4.5, 4.7) Various fragments of the large lower incisor have been found, but only two specimens were complete. The i1 is acusulate. The tip of the incisor is strongly curved upwards. The posterolabial surface shows wrinkled enamel. Labially, the tooth is bordered by a well-developed cingulid. On the lingual side, the enamel-dentine boundary slopes sharply to the front and back again.

a1- The occlusal surface is heart-shaped. The tip of the main cuspid lies in the anterior part of the antemolar. It has a pronounced anterior ridge, and very faint posterior arms on both the labial and lingual sides. The tooth has no distinct cingulids. It is the largest tooth of the lower antemolar row.

a2/3- Like in the a1, the occlusal surface of the unicuspid is heart-shaped, but the posterior emargination is much less pronounced. The labial and lingual sides are convex; the labial side extends slightly further to the rear than the

lingual side. The tip of the antemolar lies centrally. It displays a faint ridge towards the anterior most side, and an equally faint second ridge at an angle of 45° to the first moving to the anterolingual side. The back of the antemolar is bordered by an extremely thick cingulid, which tapers out along the lingual and labial sides, ending almost at the front of the tooth. The isolated elements are difficult to identify as a2 or a3, because they have a very similar morphology. Only when stacked in their original position in the mandible, can they be confidently identified as such.

m1- (Fig. 3.3, 3.6, 3.9) The trigonid is narrower but longer than the talonid, with a long paralophid and wide trigonid basin. The oblique cristid ends against the centre of the protolophid. The metacristid is poorly developed. The hypolophid connects to the posterolabial flank of the entoconid without any sign of separation. The posterior cingulid is very wide. There is a strong cingulid on the labial side, tapering out against the flank of the paralophid. The development of the lingual cingulid is quite variable. In some specimens, the hypolophid runs behind the entoconid without a clear separation. This condition can be sometimes combined with the presence of a ridge sloping sharply down to connect to the posterolingual corner of the molar.

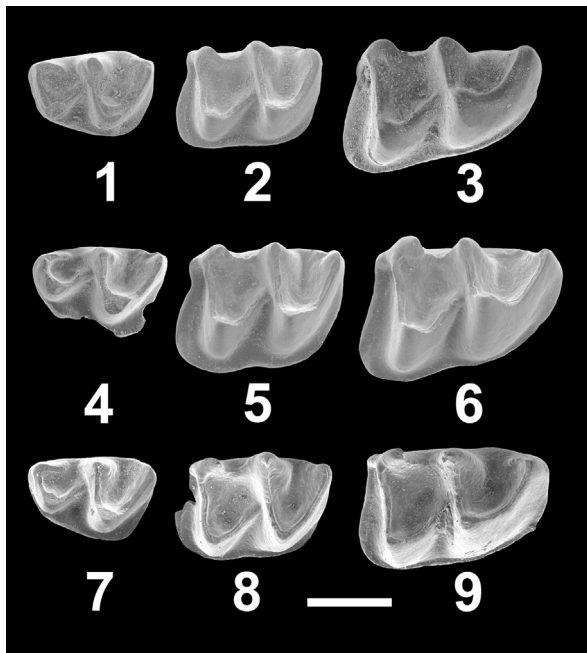


Fig. 3. Lower dentition of *Dinorex grycivensis* from three localities in the Vallès-Penedès Basin. (1–3) Abocador de Can Mata (ACM) C4-A1: 1 – left m3 (reversed) (IPS-58550); 2 – right m2 (IPS-58547); 3 – right m1 (IPS-58539). (4–6) Can Llobateres (CLL): 4 – right m3 (IPS-42924); 5 – right m2 (IPS-42909); 6 – right m1 (IPS-42922). (7–9) Barranc de Can Vila 1 (BCV1): 7 – right m3 (IPS-23481); 8 – left m2 (reversed) (IPS-23482); 9 – left m1 (reversed) (IPS-23478). All teeth in occlusal view. Scale bar equals 1 mm.

Fig. 3. Dentition inférieure de *Dinorex grycivensis* de trois localités du bassin Vallès-Penedès. (1–3) Abocador de Can Mata (ACM) C4-A1 : 1 – m3 gauche (retournée) (IPS-58550); 2 – m2 droite (IPS-58547); 3 – m1 droite (IPS-58539). (4–6) Can Llobateres (CLL) : 4 – m3 droite (IPS-42924); 5 – m2 droite (IPS-42909); 6 – m1 droite (IPS-42922). (7–9) Barranc de Can Vila 1 (BCV1) : 7 – m3 droite (IPS-23481); 8 – m2 gauche (retournée) (IPS-23482); 9 – m1 gauche (retournée) (IPS-23478). Toutes les dents sont présentées en vue occlusale. Échelle : 1 mm.

m2- (Fig. 3.2, 3.5, 3.8) In contrast to the m1, the trigonid and talonid are of similar length and width. The metaacristid is better developed than in the m1. In all other characters, the m2 resembles the first molar.

m3- (Fig. 3.1, 3.4, 3.7) The talonid is reduced, but its separate structures are still discernable. The oblique cristid ends close to the metaconid. Only one of the m3 has a posterior cingulid. The labial cingulid widens to the front into a very strong anterolabial part.

3.1. Specimens from other localities from the Vallès-Penedès Basin

3.1.1. Castell de Barberà (CdB)

There are three lower antemolars, as depicted by the complete dental series of IPS-65883. The small a2 and a3 are stacked tightly between the relatively large a1 and the m1. The mandibular condyle is completely preserved in specimen IPS-65884. In dorsal view, the condyle bends medially and the major axes of the facets make an angle of about 70° with respect to the lingual margin of the tooth row. The condyle has two separated facets, but there is a

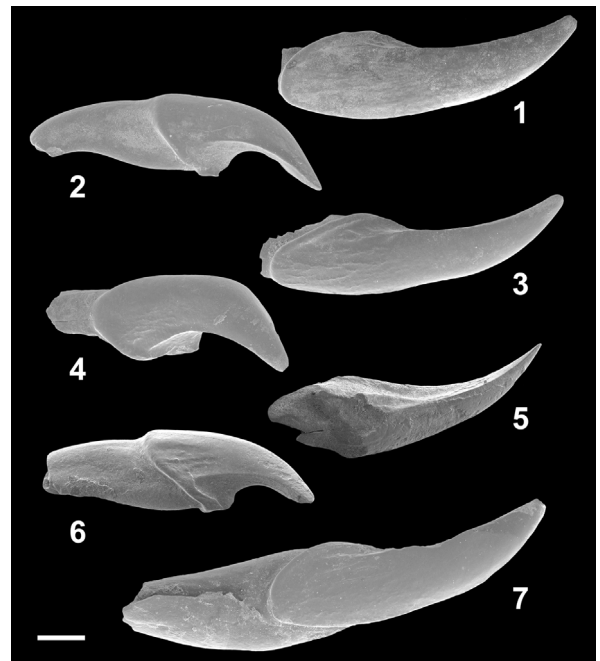


Fig. 4. Upper and lower incisors of *Dinorex grycivensis* from four localities in the Vallès-Penedès Basin. (1–2) Abocador de Can Mata (ACM) C4-A1: 1 – right i1 (IPS-58467); 2 – right I1 (IPS-58540). (3–4) Can Llobateres (CLL): 3 – right i1 (IPS-42919); 4 – right I1 (IPS-42916). (5–6) Barranc de Can Vila 1 (BCV1): 5 – left i1 (reversed) (IPS-23487); 6 – left I1 (reversed) (IPS23490). (7) Castell de Barberà (CdB): 7 – left i1 (reversed) (IPS-65900). All teeth in lateral labial view. Scale bar equals 1 mm.

Fig. 4. Incisives supérieures et inférieures de *Dinorex grycivensis* de quatre localités du bassin Vallès-Penedès. (1–2) Abocador de Can Mata (ACM) C4-A1 : 1 – i1 droite (IPS-58467); 2 – I1 droite (IPS-58540). (3–4) Can Llobateres (CLL) : 3 – i1 droite (IPS-42919); 4 – I1 droite (IPS-42916). (5–6) Barranc de Can Vila 1 (BCV1) : 5 – i1 gauche (retournée) (IPS-23487); 6 – I1 gauche (retournée) (IPS23490). (7) Castell de Barberà (CdB) : 7 – i1 gauche (retournée) (IPS-65900).

vertical ridge in the interarticular area likely a relict of a former connection between both. This vertical ridge runs from the ventrolingual edge of the upper facet to the dorsolabial corner of the lower one. Thus, the interarticular area is divided into two zones, a bigger labial surface with the concavity downwards, and a smaller one at the medial side with the concavity oriented posterodorsally. The upper condylar facet is rather cylindrical, but the posterolabial extreme is somewhat narrower than the anterolingual one. The lower condylar facet is a smooth surface regularly curved posteroventrally. The lower incisors have slightly undulating edges as seen in IPS-65900 (Fig. 4.7). In this locality, there is a m2 (IPS-65962) with a hypolophid which runs behind the entoconid, without, however, any furrow to separate the two.

4. Discussion

4.1. Taxonomic assignment of the Vallès-Penedès *Dinorex*

The first thorough descriptions of a heterosoricid from the Vallès-Penedès stems from Villalta and Crusafont

Table 2

Range of the measurements of the dental elements of *Dinosorex grycovivensis* found in the localities from the Vallès-Penedès Basin. Acronyms of the localities are listed in Table 1. Measures have been taken as detailed in Fig. 1.

Tableau 2

Amplitude des mesures des éléments dentaires de *Dinosorex grycovivensis* du bassin Vallès-Penedès. Les acronymes des localités sont présentés dans le Tableau 1. Les méthodes de mesure sont détaillées dans la Fig. 1.

Tooth	Measurement	Locality	Min	Mean	Max	Sd	N		
I1	L	CLL	4.00	4.45	4.85	0.28	8		
		EDAR 13		4.14			1		
		CdB	3.59	3.99	4.48	0.32	6		
		ACM/C8-B1	4.04	4.13	4.23	0.13	2		
		ACM/C6-C1	4.21	4.39	4.58	0.26	2		
		ACM/C5-D1	4.07	4.24	4.42	0.13	6		
		ACM/C3-A5		4.63			1		
		ACM/C4-A1	3.87	4.30	4.60	0.23	13		
		ACM/C5-C3		4.74			1		
		BCV1	4.31	4.40	4.55	0.13	3		
		CLL	1.97	2.33	2.72	0.26	8		
		EDAR 13		1.80			1		
		CdB	1.85	2.16	2.54	0.28	7		
	ACM/C8-B1	2.04	2.04	2.05	0.01	2			
	ACM/C6-C1	2.47	2.54	2.62	0.10	2			
	ACM/C5-D1	1.89	2.07	2.41	0.19	6			
	ACM/C5-D3		1.99			1			
	ACM/C3-A5		2.43			1			
	ACM/C4-A1	1.82	2.19	2.55	0.21	13			
	ACM/C5-C3		2.92			1			
	BCV1	1.78	1.86	1.99	0.09	4			
	A1	L	CPL		2.19			1	
			EDAR 2		2.23			1	
			CdB	2.16	2.23	2.31	0.10	2	
			ACM/C6-C1	2.18	2.24	2.34	0.08	3	
			ACM/C5-D1	2.13	2.24	2.31	0.09	3	
ACM/C4-A1			2.12	2.21	2.24	0.04	11		
ACM/C3-A5				2.16			1		
BCV1			2.06	2.17	2.27	0.08	5		
W			CPL		1.61			1	
			EDAR 2		1.56			1	
		CdB		1.44			1		
		ACM/C6-C1	1.52	1.54	1.59	0.04	3		
		ACM/C5-D1	1.50	1.55	1.60	0.05	3		
		ACM/C4-A1	1.43	1.51	1.58	0.05	11		
		ACM/C3-A5		1.45			1		
		BCV1	1.39	1.53	1.60	0.08	5		
		P4	L	TCLL1	2.06	2.12	2.18	0.08	2
				TCLL0	2.04	2.05	2.07	0.02	2
CLL				2.11	2.27	2.5	0.17	4	
CPL					2.13			1	
CFEU				2.12			1		
EDAR 1				2.25			1		
S				2.08			1		
CdB	2.06			2.18	2.24	0.06	10		
SQA				2.30			1		
ACM/C8-B1	2.10			2.14	2.19	0.06	2		
ACM/C6-A2				2.34			1		
ACM/C5-D1	2.10			2.18	2.34	0.08	7		
ACM/C5-A4			2.07			1			
ACM/C4-A1	1.98		2.12	2.22	0.10	6			
BCV1	2.04		2.09	2.16	0.05	5			
W	TCLL1			2.10			1		
	TCLL0		1.95	2.02	2.10	0.10	2		
	CLL		2.10	2.19	2.32	0.09	4		
	CPL			2.13			1		
	CFEU			1.85			1		
	EDAR 1			2.22			1		
	S			1.87			1		
	CdB	2.02	2.12	2.25	0.07	10			
	SQA		2.06			1			
	ACM/C8-B1	2.32	2.33	2.35	0.02	2			
ACM/C6-A2		2.06			1				
ACM/C5-D1	2.01	2.08	2.14	0.04	7				
ACM/C4-A1	1.98	2.11	2.25	0.09	6				
BCV1	1.89	2.07	2.17	0.11	5				

Table 2 (Continued)

Tooth	Measurement	Locality	Min	Mean	Max	Sd	N	
M1	L	TCLL0	2.10	2.12	2.15	0.03	2	
		CLL	2.15	2.25	2.34	0.06	9	
		EDAR 22		2.25			1	
		CM		2.07			1	
		CdB	2.05	2.22	2.39	0.10	9	
		SQA	1.98	2.11	2.18	0.07	6	
		ACM/C8-B1	2.12	2.14	2.16	0.03	2	
		ACM/C6-C1	2.09	2.10	2.12	0.02	2	
		ACM/C5-D1	2.14	2.21	2.34	0.06	13	
		ACM/C5-D7		2.19			1	
		ACM/C4-A1	2.12	2.23	2.36	0.07	7	
		ACM/C4-A3	2.18	2.21	2.25	0.05	2	
		ACM/C4-C1		2.20			1	
		BCV1	2.13	2.17	2.23	0.03	6	
		TCLL0	2.45	2.50	2.56	0.08	2	
		CLL	2.44	2.53	2.70	0.08	8	
	EDAR 22		2.29					
	CM		2.45					
	CdB	2.33	2.50	2.62	0.09	9		
	SQA	2.33	2.39	2.49	0.06	5		
	ACM/C8-B1	2.47	2.50	2.54	0.05	2		
	ACM/C6-C1	2.26	2.34	2.43	0.12	2		
	ACM/C5-D1	2.44	2.52	2.62	0.06	13		
	ACM/C5-D7		2.40			1		
	ACM/C4-A1	2.36	2.50	2.63	0.09	7		
	ACM/C4-A3	2.56	2.59	2.62	0.04	2		
	BCV1	2.38	2.42	2.50	0.06	3		
	M2	L	TCLL0		2.00		0.00	2
			RT11		2.03			1
			CLL	1.96	2.05	2.14	0.13	2
			EDAR 3		2.02			1
			CM		2.02			1
CdB			1.87	1.98	2.08	0.09	6	
SQA				1.99			1	
ACM/C8-B1			1.79	1.86	1.93	0.10	2	
ACM/C6-C1				2.02			1	
ACM/C5-D1			1.95	1.99	2.09	0.05	5	
ACM/C5-D2				1.98			1	
ACM/C5-D4				1.95			1	
ACM/C4-A1			1.95	1.99	2.09	0.04	16	
ACM/C4-A3				2.14			1	
ACM/C5-C3				2.11			1	
ACM/C3-A5				2.01			1	
BCV1		1.89	1.95	2.01	0.05	4		
ACM/C1-A1		1.97	2.01	2.06	0.06	2		
W		TCLL0	2.23	2.25	2.27	0.03	2	
		RT11		2.03			1	
		CLL	2.32	2.37	2.42	0.07	2	
		CM		2.22			1	
		CdB	2.14	2.29	2.38	0.08	6	
		SQA		2.24			1	
		ACM/C8-B1	2.30	2.32	2.34	0.03	2	
		ACM/C6-C1		2.17			1	
		ACM/C5-D1	2.29	2.37	2.50	0.08	5	
		ACM/C5-D2		2.19			1	
		ACM/C4-A1	2.13	2.27	2.43	0.06	15	
		ACM/C4-A3		2.32			1	
		ACM/C5-C3		2.35			1	
		ACM/C3-A5		2.30			1	
	BCV1	2.03	2.11	2.20	0.09	4		
	M3	L	CLL		1.03			1
ACM/C5-D1				1.22			1	
ACM/C4-A1			1.06	1.11	1.15	0.04	4	
BCV1				1.14			1	
W		CLL		1.37			1	
		ACM/C5-D1		1.63			1	
		ACM/C4-A1	1.46	1.50	1.55	0.04	3	
		BCV1		1.50			1	

Table 2 (Continued)

Tooth	Measurement	Locality	Min	Mean	Max	Sd	N
i1	L	TCLLO		6.33			1
		CLL	6.03	6.65	7.07	0.26	18
		HS	6.54	6.66	6.79	0.17	2
		CM		6.89			1
		CdB	6.54	6.85	7.14	0.20	7
		ACM/C5-D1	6.28	6.67	6.96	0.25	6
		ACM/C4-A1	6.38	6.63	6.89	0.19	6
		ACM/C5-C2		6.63			1
		ACM/C5-C3		7.30			1
		BCV1		6.46			1
		CdB		1.44			1
		ACM/C5-D1		1.45			1
		a1	L	BCV1		1.20	
ACM/C4-A1	1.36			1.45	1.57	0.10	4
ACM/C6-A2				1.53			1
CdB				1.22			1
ACM/C5-D1				1.10			1
W	BCV1			1.05			1
	ACM/C4-A1		1.06	1.10	1.15	0.04	4
	ACM/C6-A2			1.15			1
	CLL		2.44	2.63	2.78	0.09	13
	CPL			2.64		0.00	2
m1	L	CP	2.59	2.63	2.67	0.05	2
		HS	2.39	2.60	2.76	0.12	6
		CdB	2.51	2.62	2.79	0.08	17
		SQA		2.63			1
		SQ	2.48	2.55	2.63	0.10	2
		ACM/C5-D1	2.41	2.53	2.72	0.10	12
		ACM/C8-A1		2.49			1
		ACM/C4-A1	2.32	2.54	2.68	0.14	8
		ACM/C5-C3		2.73			1
		BCV1	2.48	2.53	2.57	0.05	3
		ACM/C3-B2		2.48			1
		ACM/C1-E7		2.61			1
		ACM/C1-D1		2.43			1
	W	CLL	1.53	1.67	1.77	0.07	11
		CPL	1.70	1.73	1.77	0.05	2
		CP	1.48	1.48	1.49	0.06	2
		HS	1.54	1.76	2.21	0.23	6
		CdB	1.54	1.66	1.89	0.10	17
		SQA		1.75			1
		SQ	1.65	1.72	1.80	0.10	2
		ACM/C5-D1	1.45	1.57	1.78	0.09	12
		ACM/C8-A1		1.66			1
		ACM/C4-A1	1.51	1.64	1.86	0.11	8
		ACM/C5-C3		1.81			1
		BCV1	1.51	1.57	1.69	0.10	3
		ACM/C3-B2		1.60			1
		ACM/C1-E7		1.58			1
ACM/C1-D1		1.50			1		
m2	L	CLL	1.96	2.17	2.24	0.09	9
		CPL	2.08	2.20	2.28	0.10	3
		EDAR 3		2.11			1
		CP	2.15	2.16	2.17	0.01	2
		HS	2.06	2.24	2.37	0.11	6
		CdB	2.10	2.25	2.42	0.09	17
		CF		2.02			1
		SQA	2.07	2.19	2.32	0.17	2
		SQ	1.90	1.97	2.05	0.10	2
		ACM/C8-By		2.00			1
		ACM/C5-D1	2.00	2.18	2.39	0.13	11
		ACM/C8-A1		2.20			1
		ACM/C4-A1	1.96	2.16	2.31	0.10	15
		ACM/C5-C2		2.19			1
		ACM/C5-C3		2.32			1
		BCV1	1.97	2.04	2.09	0.05	5
		ACM/C1-A1	2.07	2.09	2.12	0.03	2
		ACM/C1-E7		2.25			1
		ACM/C9-A1		2.12			1

Table 2 (Continued)

Tooth	Measurement	Locality	Min	Mean	Max	Sd	N		
	W	CLL	1.40	1.50	1.61	0.10	9		
		CPL	1.36	1.44	1.51	0.07	3		
		EDAR 3			1.50			1	
		CP	1.52	1.62	1.73	0.15	2		
		HS	1.32	1.46	1.59	0.10	6		
		CdB	1.31	1.46	1.64	0.09	17		
		CF		1.48				1	
		SQA	1.33	1.39	1.46	0.09	2		
		SQ	1.43	1.53	1.63	0.14	2		
		ACM/C8-By		1.40				1	
		ACM/C5-D1	1.23	1.42	1.56	0.09	11		
		ACM/C8-A1		1.41				1	
		ACM/C4-A1	1.32	1.50	1.64	0.09	14		
		ACM/C5-C3		1.70				1	
		BCV1	1.19	1.31	1.40	0.08	4		
		ACM/C1-A1	1.35	1.42	1.50	0.10	2		
		ACM/C1-E7		1.44				1	
		ACM/C9-A1		1.39				1	
		m3	L	CLL	1.59	1.66	1.71	0.06	3
				HS	1.57	1.60	1.63	0.03	3
CdB	1.40			1.63	1.83	0.12	8		
SQA	1.64			1.66	1.70	0.03	3		
SQ	1.57			1.62	1.68	0.08	2		
ACM/C6-C1	1.63			1.68	1.72	0.05	3		
ACM/C8-By				1.58				1	
ACM/C5-D1	1.50			1.59	1.74	0.10	4		
ACM/C8-A1				1.59				1	
ACM/C4-A1	1.56			1.68	1.88	0.10	9		
ACM/C5-C2				1.67				1	
BCV1	1.59			1.60	1.62	0.02	2		
ACM/C3-B2				1.63				1	
ACM/C1-E7	1.58			1.62	1.67	0.06	2		
CLL	1.01			1.17	1.33	0.16	3		
HS	1.19			1.23	1.28	0.04	3		
CdB	1.06			1.15	1.30	0.07	8		
SQA	1.10			1.13	1.15	0.02	3		
SQ	1.09			1.15	1.22	0.09	2		
ACM/C6-C1	0.98			1.11	1.24	0.13	3		
ACM/C8-By		1.09				1			
ACM/C5-D1	1.06	1.13	1.20	0.07	4				
ACM/C8-A1		1.04				1			
ACM/C4-A1	1.08	1.18	1.29	0.07	9				
ACM/C5-C2		1.09				1			
BCV1	1.00	1.05	1.11	0.08	2				
ACM/C3-B2		1.06				1			
ACM/C1-E7	0.97	1.05	1.13	0.11	2				

(1943) and Crusafont (1957), who identified “*Heterosorex sansaniensis*” from the localities of Sant Quirze and Hostalets de Pierola, one of the few heterosoricid taxa known at the time. While introducing the genus *Dinosorex*, Engesser (1972) already noted differences between the typical form from Sansan, which he transferred to his new genus, and the form from Can Llobateres. He classified the latter as *D. aff. sansaniensis*, considering it intermediate in morphology between the French species and *D. pachygnathus* from Anwil. In his unpublished PhD Thesis, Gibert (1974) considered *Dinosorex* as a junior synonym of *Heterosorex*, as he assumed two characters of Engesser’s generic diagnosis (number of antemolars and hypolophid–entoconid connection) to be of little taxonomic value. Thus, the reference to this form as “*Heterosorex*” persisted. However, as shown in the present work, all lower incisors from the Vallès-Penedès are acusulate, and the inner cusps of M1 and M2 are always

clearly defined, which is in line with the characteristics of *Dinosorex* rather than *Heterosorex*.

As for the specific ascription, the identification of *D. sansaniensis* for the Vallès-Penedès species also persisted in the literature for a long time (e.g., Van den Hoek Ostende and Furió, 2005) due to a lack of detailed studies. However, Furió et al. (2011) recently demonstrated that the *Dinosorex* from the late Middle Miocene locality of Barranc de Can Vila was phenotypically different from *D. sansaniensis*, based both on morphology and size, the Spanish form being clearly smaller. It was thus suggested that the specimens represented *D. zapfei*, a species, which has its type locality in Slovak Republic (Devínská Nová Ves (fissure), MN 6). The assemblages from the Vallès-Penedès, including that of Barranc de Can Vila, are quite consistent in the dimensions of the elements. Measurements are sufficient to discard the ascription to “*D. huerzeleri*” (= *Quercysorex huerzeleri*, according to Ziegler, 1998) and *D. pusillus*, as these species

are clearly smaller (Engesser, 1975; Engesser and Storch, 2008) than the one present in the Vallès-Penedès. The morphology of the Spanish *Dinosorex* is characterized by the hypolophid of the m1 and m2 connecting to the entoconid (Modus A, according to Engesser, 1975) with a few exceptions, the development of entocristids on the lower molars, the absence of a hypoloph on the M1 and M2 and only moderate wrinkling of the incisor enamel. The direction of the hypolophid clearly distinguishes our species from *D. sansaniensis* and *D. pachygnathus*. Moreover, the first is clearly larger and the latter has longer upper and lower incisors. The characters fit well with *D. zapfei*. However, Furió et al. (2011) did not consider the proportion between the dental elements, which is clearly different in the Vallès-Penedès species and falls within the range of the Moldavian material described by Rzebik-Kowalska and Lungu (2009) as *D. grycivensis*. Whereas the length of the m1 of the type mandible of *D. zapfei* falls in the uppermost range of our material, its m3 is smaller than any found in the Vallès-Penedès.

Two species, both described as “zapfei-like” are coeval with the material from the Vallès-Penedès: *D. grycivensis* Rzebik-Kowalska and Topachevsky, 1997 from Grytsiv (Ukraine, MN 9) and *D. engesseri* Rabeder, 1998 from Austria (Götzendorf, MN9). Unfortunately, the differences between these two species are not clearly defined. Rabeder (1998) did not refer to the Ukrainian species, which had only been described a year earlier, when he erected *D. engesseri*, nor did Ziegler (2006) refer to that species in a more comprehensive study of the Austrian material. The most characteristic feature of the latter species is the presence of a strong hypoloph on the M1 and M2 (diagnostic characteristic for Rabeder (1998), and recognized by Ziegler (2006) for instance), a ridge originating from the hypocone moving in the direction of the base of the metacone. We did not observe this feature in our material, although in some worn specimens the enamel from the wear surface of the hypocone seems to form a ridge. Notably, the specimen from Can Llobateres illustrated by Engesser (1972, fig. 22a) clearly shows a hypoloph on the M1, although this character has not been found in any other M1 from our assemblage. A hypoloph was also not observed in *D. grycivensis* (Rzebik-Kowalska and Topachevsky, 1997).

Following the descriptions, the clearest difference between *D. grycivensis* and the Vallès-Penedès material would be the presence of entocristids in the latter. However, the illustrations show that apparently what we consider a weak entocristid was described as absent in *D. grycivensis* by Rzebik-Kowalska and Topachevsky (1997). Ziegler (2006) described this character for *D. engesseri* as “there is no marked entocristid, i.e. the mesial crest of the entoconid is weak and descends steeply”. This seems to hold true for *D. grycivensis* and the Vallès-Penedès material as well.

Another character is the number of lower antemolars. According to Engesser (1975), the number of lower antemolars is variable with the exception of *D. pachygnathus*, which seems to have invariably only two. *Dinosorex pusillus*, purportedly the oldest form of the genus (but note comments on its generic assignment by Ziegler, 2009, has five of them (Engesser and Storch, 2008)). *Dinosorex*

grycivensis has three or four of them (Rzebik-Kowalska and Topachevsky, 1997), and so does *D. zapfei* (Engesser, 1975). The dental formula of *D. sansaniensis* seems to oscillate similarly (Engesser, 2009), and the number of lower antemolars is unknown in *D. anatolicus* and *D. engesseri* (Rabeder, 1998; Van den Hoek Ostende, 1995). In our material, the number of antemolars was observed in Castell de Barberà (one specimen) and Hostalet de Pierola (two specimens). In all these mandibles, there were three antemolars between the lower incisor and the first molar.

Finally, the morphology of the articular condyle is considered of taxonomic value in *Dinosorex*. The general construction of the condyle IPS-65884 from Castell de Barberà is different from that of any of *Dinosorex* depicted in Engesser (1975: fig. 3). In the specimens 1975/1972/2 of *D. zapfei* from Neudorf (Engesser, 1975: fig. 3b) and NHMW1998z0046/0001/53 of *D. engesseri* from Götzendorf (Rabeder, 1998: fig. 5), the two condylar facets are still connected, whereas they are completely isolated from each other in the specimen Ss 887 of *D. sansaniensis* from Sansan (Engesser, 1975: fig. 3c; Engesser, 2009: fig. 3c). The specimen Ss 603 of *D. sansaniensis* from Sansan (Engesser, 1975: fig. 3d) does not preserve the lower facet, but it shows a clearly isolated upper facet. The specimen number 13 of *D. grycivensis* from Grytsiv (Rzebik-Kowalska and Topachevsky, 1997: fig. 3a) seems to display an intermediate state between both extremes, with only a vestigial signal of a former connection. This is also the state most reminiscent of the specimen IPS-65884 from Castell de Barberà, thus, reinforcing our specific attribution. However, it must be noted that all these previously published figures correspond to rather schematic drawings, which may substantially misrepresent (overestimate or underestimate) the connection between both articular facets.

It is remarkable that the material of *Dinosorex* from over forty localities from the Vallès-Penedès Basin included in the present study covers a time-span of about 3 My with no significant differences either in size (Fig. 5) or in morphology between the oldest and the youngest occurrences. Only a few phenotypic outliers have been observed (e.g., hypoloph, hypolophid–entoconid connection), which are clearly due to simple intraspecific variation. More complete specimens showing several diagnostic characters (e.g., articular condyle, complete upper or lower antemolar rows) are, however, few, but in those cases in which there is more than one specimen, these characters appear to be quite constant as well. We consequently assume that there was only one species of *Dinosorex* in the Vallès-Penedès during the time interval ranging from the Late Aragonian to the Late Vallesian, which is here identified as *D. grycivensis*. It is also the only record of this remarkable insectivore on the Iberian Peninsula. As it was present in the basin at the onset of sedimentation, we cannot rule out that *Dinosorex* may have already been present in the area before. Its local extirpation, however, is beyond any doubt, as none of the more than forty localities younger than TCLL1 has provided any *Dinosorex* fossils. In fact, Agustí and Gibert (1982) previously described the extinction of this taxon during the second part of the Vallesian in the Vallès-Penedès area as a significant biostratigraphical event. We can now refine their observation by adding that the extinction of *Dinosorex*

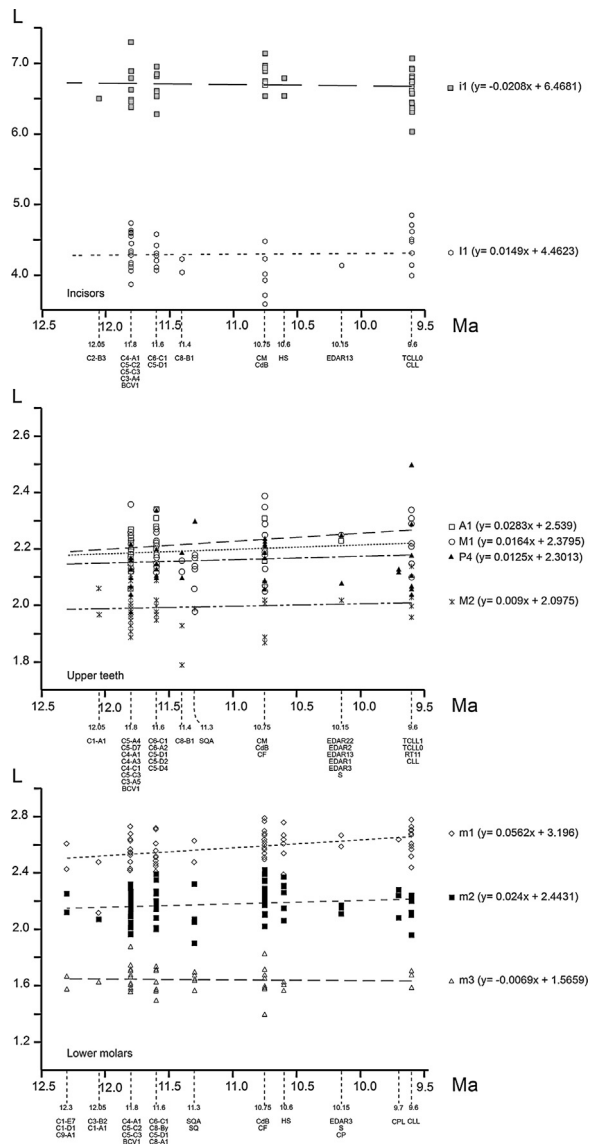


Fig. 5. Scatter diagrams of the lengths of different dental elements of *Dinosorex* from the Vallès-Penedès basin in relation with their estimated age. The age of the sites has been approached as the intermediate age of their ranges. The slopes of the regression lines indicate the general trend to change the length of each tooth through time. Although most of the teeth show a slight lengthening with time (positive slope), the i1 and m3 show the opposite trend. However, none of the trend lines depicted shows a much pronounced slope, which is indicative of the relative stability of the measurements for the period considered.

Fig. 5. Diagrammes de dispersion des longueurs de différents éléments dentaires de *Dinosorex* du bassin Vallès-Penedès, en relation avec l'âge estimé des localités. L'âge médian des sites a été retenu comme approximation de leur datation. Les pentes des courbes de régression indiquent les tendances générales dans le changement des longueurs de chaque dent en fonction du temps. Bien que la majorité des dents montrent une légère augmentation au cours du temps (inclination positive), les i1 et m3 sont caractérisées par une tendance inverse. En définitive, aucune ligne n'est vraiment fortement inclinée, ce qui confirme une stabilité relative des mesures pour la période considérée.

coincides with the first occurrences of the murid genus *Progonomys*, which are confidently constrained in the time interval 9.7–9.5 Ma in the Vallès-Penedès basin as provided by the work in progress by Casanovas-Vilar et al.

4.2. Evolution of *Dinosorex* in the Vallès-Penedès basin, and its relationship with European forms in time and space

The Iberian assemblages are remarkably constant in both size and morphology over a period of three million years. Moreover, as the type locality *D. grycivensis* lies in the Ukraine, it also appears to have had a large geographical distribution. *Dinosorex engesseri* is reported from Austrian localities ranging from the Pannonian F (Götzendorf) to the Pannonian G (Schernham; Ziegler, 2006), and from the Hungarian locality of Rudabánya (Ziegler, 2005), thus, covering a time ranging from ca. 10 Ma to ca. 9 Ma, i.e. the uppermost stratigraphical range of our Spanish sample. There can be little doubt that the species *D. engesseri* from Austria is closely related to our species, and may represent a local variety at this time, evolving morphological characteristics, while the genus remained more conservative in the Vallès-Penedès. Grytsiv is correlated to near the early to middle Bessarabian transition (early Vallesian), and roughly dated to 11–12 Myr (see details in Vasilyan et al., 2013: 301–302). Between Grytsiv and the Pannonian Austrian/Hungarian record, *Dinosorex*–data are scarce, and therefore, we cannot clearly document the first occurrence of *D. engesseri*. *Dinosorex grycivensis* is reported by Rzebik-Kowalska and Lungu (2009) in the Bužor 1 (late middle Bessarabian), a locality which is only slightly younger than Grytsiv.

More precise data are available for the slightly older deposits that correlate to the late Sarmatian s. str. or the middle to late Miocene transition. We can herein refer to the stratigraphically close localities of (see Prieto et al., 2014) Bełchatów (*Dinosorex* sp.; Poland; Rzebik-Kowalska, 1994), Nebelbergweg (*Dinosorex* aff. *pachygnathus*; Switzerland; Kälin and Engesser, 2001), and Hammerschmiede (Germany; *Dinosorex?* n. sp., J.P. pers. obs.). All these fossiliferous localities might include a single heterosoricid species. Kälin and Engesser (2001) did not assign the Swiss species a new name, but provided a detailed comparison. They noticed that the species differs from *D. grycivensis* in its larger size, the absence of an entoconid crest and the modus B-like structure of the hypolophid. In addition, we notice herein that a small hypolophid is present in some of these samples, as can be seen in Fig. 2.12. On the other hand, Rzebik-Kowalska and Lungu (2009) considered the *Dinosorex* from Bełchatów A to belong to *D. grycivensis*, but they did not justify their choice. Closer to the first record of *Dinosorex* in the Vallès-Penedès, the remains from Gratkorn (Austria, early Late Sarmatian s.str. (ca. 12–12.2 My; Gross et al., 2011; Harzhauser et al., 2008)), although well-preserved, cannot be at present assigned confidently to the species level (Prieto et al., 2010, 2014), but an assignment to *D. grycivensis* can be excluded. This underlines the urgent need for a detailed comparison of these forms in order to clearly evaluate the

Iberian *Dinosorex* record in terms of paleobiogeography and palaeoenvironmental influences.

5. Conclusion

The three million years record of *Dinosorex* in the Vallès-Penedès is not only remarkable because it is the only record of this insectivore on the Iberian Peninsula, but also because of its phenotypic stability. This is also quite consistent with the environmental interpretation of the basin, as no major change in the conditions during the time interval ranging from 12.5 to 9.5 Ma has been documented. The differences in the small mammal assemblages in this basin are rather interpreted as complementary zones within the same ecosystem, i.e. open or wooded areas, swampy or dry lands, etc. (Casanovas-Vilar et al., 2011).

Fossils assigned to *D. grycivensis*, a species known from the eastern part of Europe, provide a new insight in the stratigraphical and geographical distribution of this taxon. The last occurrences of the genus *Dinosorex* correspond to MN 10 localities temporary close to the Mid-Vallesian faunal turnover. Although the so-called Vallesian Crisis has been recently challenged as a simple matter of unequally sampling of the area (Casanovas-Vilar et al., 2014), *Dinosorex* seems to have extirpated around the transition between early and late Vallesian.

Having a long-lived and widely distributed species seems to be in sharp contrast with our current knowledge of the evolution of the genus in central Europe, where different species occur. The taxonomy of these forms is still unresolved. Engesser (2009: 14), for instance, openly doubted whether all finds attributed to *D. sansaniensis* really belong to this species, also given its remarkably long range (MN4–MN9). The present paper is therefore a first step in understanding the evolution of the “terror-shrews”. Once the status of the Middle and Late Miocene representatives of central Europe is resolved, we can start drawing conclusions about faunal interchange and the shifting of ecosystems across Europe. This peculiar insectivore, with presumably a quite specific ecological preference, seems an important candidate to monitor environmental changes during that period.

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