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An unusual insectivore assemblage from the early Miocene of southwestern Europe: The talpids and dimylids from the Ribesalbes–Alcora Basin (Spain)



Un assemblage inhabituel d'insectivores au Miocène inférieur du Sud-Ouest de l'Europe : les talpidés et les dimylidés du bassin de Ribesalbes–Alcora (Espagne)

Vicente D. Crespo^{a,b,*}, Rafael Marquina-Blasco^{b,c},
Francisco Javier Ruiz-Sánchez^{b,c,d}, Plini Montoya^c

^a Museo Paleontológico de Alpuente, Av. San Blas 17, 46178 Alpuente, Valencia, Spain

^b Museu Valencià d'Història Natural, L'Hort de Feliu, P.O. Box 8460, 46018 Algínet, Valencia, Spain

^c Departament de Geologia, Universitat de València, Dr. Moliner 50, 46100 Burjassot, Valencia, Spain

^d INCYT-UPSE, Universidad Estatal Península de Santa Elena, 7047 Santa Elena, Ecuador

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ABSTRACT

The Miocene record of talpids and dimylids in south-western Europe is very scarce. In the present work, we study for the first time the talpids and complete the description of the dimylids, already started with a new species of the genus *Plesiodimylus* from the Ribesalbes–Alcora Basin (MN4, lower Aragonian, early Miocene) by Crespo et al. (2018). The talpids recovered in Ribesalbes–Alcora comprise the most common *Desmanodon daamsi* and *Desmanella fejfari*, for which the last known occurrence is recorded here. The dimylids comprise the species *Plesiodimylus ilercavonicus*, which expands the biostratigraphic record of the genus and species and has been found in a new site. On the other hand, we discuss the palaeoecological significance of this assemblage.

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R É S U M É

L'enregistrement miocène de talpidés et dimylidés dans le Sud-Ouest de l'Europe est très rare. Dans le présent travail, nous étudions pour la première fois les talpidés et complétons la description des dimylidés, déjà entamée par Crespo et al. (2018), avec une nouvelle espèce du genre *Plesiodimylus* du bassin de Ribesalbes–Alcora (MN4, Aragonien inférieur, Miocène précoce). Les talpidés récoltés dans ce bassin constituent les plus communs *Desmanodon daamsi* et *Desmanella fejfari*, pour lesquels la dernière occurrence connue

* Corresponding author. Museo Paleontológico de Alpuente, Av. San Blas 17, 46178 Alpuente, Valencia, Spain.

E-mail addresses: vidacres@gmail.com (V.D. Crespo), rafael.marquina@uv.es (R. Marquina-Blasco), francisco.ruiz@uv.es (F.J. Ruiz-Sánchez), plinio.montoya@uv.es (P. Montoya).

est enregistrée là. Les dimylidés présentent l'espèce *Plesiodimylus ilercavonicus*, qui élargit l'enregistrement biostratigraphique du genre et de l'espèce et a été trouvée dans un nouveau site. Par ailleurs, nous discutons la signification paléocécologique de cet assemblage.

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1. Introduction

Although the mammalian record of the Spanish Miocene is well known, the publications focussed on the systematic palaeontology of the insectivores are poor. Moreover, insectivores are more abundant and better represented in the palaeontological record in the North of Europe than in the South, indicating a latitudinal humidity gradient (Furió et al., 2011; Van den Hoek Ostende et al., 2016).

The record of the family Talpidae in the early Miocene from the Iberian Peninsula is very poor and generally limited to the genus *Desmanodon* (Jovells-Vaqué et al., 2018; Van den Hoek Ostende, 1997, 2003; Van den Hoek Ostende et al., 2016). This genus is an immigrant from Turkey that reached Europe around the MN2/3 transition and became extinct at the beginning of the MN5 (Van den Hoek Ostende et al., 2016). The rest of genera are very scarce and considered as transient. *Desmanella* has only been reported in the MN3 of the Rubielos de Mora Basin and in the site of Montalvos 2 and *Myxomygale* occurs in only three sites throughout the whole Spanish early Miocene (Van den Hoek Ostende, 2003; Van den Hoek Ostende et al., 2016). The family is apparently absent in the interval MN5–MN7 + 8, during most of the middle Miocene (Furió et al., 2011).

The family Dimylidae reaches its maximum diversity during the early Miocene, in central Europe (Ziegler, 1999), but in the South of Europe it is represented by only two genera: *Chainodus* and *Plesiodimylus*. The first genus only occurs in the Rubielos de Mora Basin (Van den Hoek Ostende et al., 2016) and in the site of Turó de les Forques from the Vallès–Penedès Basin (unpublished material) (Casanovas-Vilar et al., 2016; Furió et al., 2011), both dated as MN3, whereas the second is only known as a recently described species: *Plesiodimylus ilercavonicus* Crespo, Furió, Ruiz-Sánchez and Montoya, 2018, from Mas d'Antolino B 5 in the Ribesalbes–Alcora Basin (Crespo et al., 2018).

The two families, Talpidae and Dimylidae, rarely co-occur in the same site in southwestern Europe during the early Miocene, by the scarcity in the finds of the second family. This has only been documented in Alto de Ballester 1, where the talpids *Desmanella fejfari* Gibert, 1974, *Myxomygale minor* Ziegler, 1990 and *Desmanodon daamsi* Van den Hoek Ostende, 1997 coexist with the dimylid *Chainodus* cf. *sulcatus* Stephan-Hartl, 1972, and in Rubielos de Mora 2 (Van den Hoek Ostende et al., 2017), where *D. fejfari* and *D. daamsi* have been found with *Chainodus intercedens* (Müller, 1967). This association is only recorded again at the end of the middle Miocene in some sites of the Vallès–Penedès Basin (Van den Hoek Ostende and Furió, 2005).

Agustí et al. (1988) describe an indeterminate species of the genus *Paratalpa* from the classical locality of Mas de Antolino 2. Since the common mole in Spanish MN4 localities is *Desmanodon*, whose dentition is similar to that of *Paratalpa* (Van den Hoek Ostende, 1989; Van den Hoek Ostende and Furió, 2005), in our opinion the Mas de Antolino specimen(s) should be assigned to *Desmanodon*.

2. Geographic and geologic setting

The Ribesalbes–Alcora Basin is located in an intramontane basin in eastern Spain (Fig. 1; Agustí et al., 1988). The studied section is about 100 metres thick; it is composed by grey and yellow mudstones, limestones, and sandstones (Crespo et al., 2019) and belongs to “Unit Three” *sensu* Anadón (1983).

Mammalian fossils in the Ribesalbes–Alcora Basin were first reported by Agustí et al. (1988). Crespo et al. (2019) have recently described up to 45 fossiliferous sites in seven sections and their mammalian assemblages. Particularly relevant are the southernmost record of the herpetotheriid *Amphiperaterium frequens* (von Meyer 1846) and the description of the new species *Plesiodimylus ilercavonicus* (Crespo et al., 2018; Furió et al., 2012).

The studied sections can be correlated with the local biozone C, in the upper part of MN4 (lower Aragonian, early Miocene) of the Calatayud–Montalban Basin (Spain), and corresponds to the chronologic interval 16.5–16 Ma (Crespo et al., 2019; Van der Meulen et al., 2012).

3. Material, methods, and abbreviations

The photographic images of the specimens were taken with a SEM HITACHI 4800 at the “Servei Central de Suport a la Investigació Experimental” (SCSIE) of the “Universitat de València Estudi General” (UVEG). The fossil material is stored at the “Museu de la Universitat de València d'Història Natural” (MUVHN), Burjassot, Spain.

For the talpids, we have used the nomenclature of Van den Hoek Ostende (1989) and the measurements of Hutchison (1974) and Van den Hoek Ostende (1989). In the case of the dimylids, we have followed the nomenclature and measurements used by Müller (1967) updated by Klietmann et al. (2014a). Measurements (length × width) are given in millimetres and were taken using a Leica MZ75 binocular microscope, by means of the displacement of a mechanical stage, connected to a Sony Magnescale measuring equipment. Lower teeth are designated with lower-case letters (lower molars: m1, m2 and m3; lower premolars: p1, p2, p3 and p4; lower canine: c; lower incisor: i) and upper teeth are written in upper-case letters

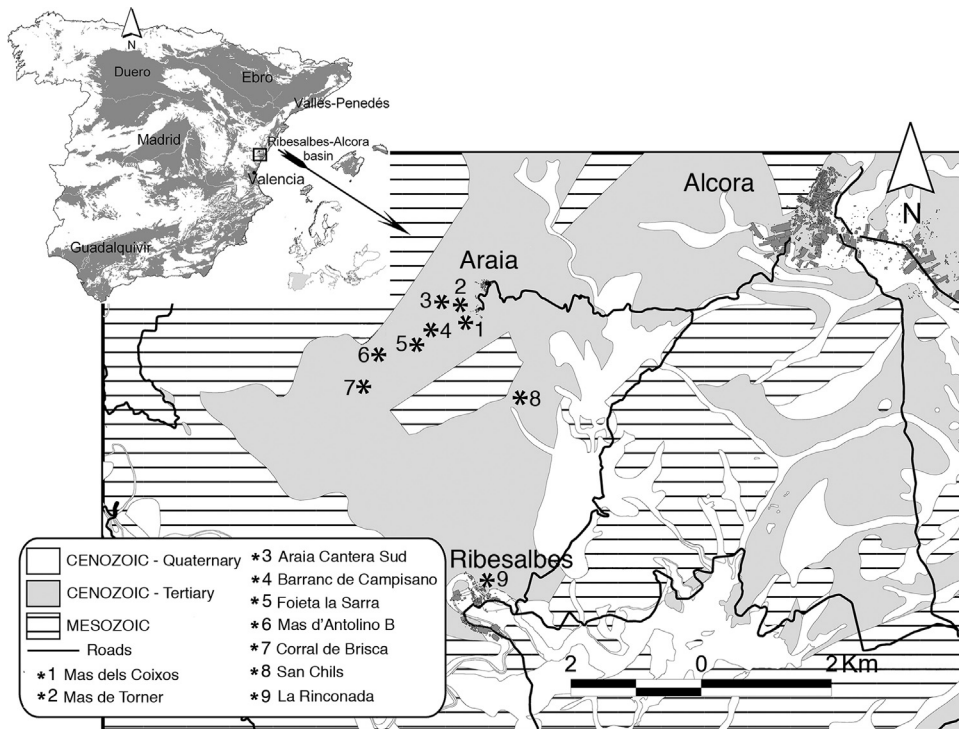


Fig. 1. Spanish Cenozoic basins, with location of the Ribesalbes–Alcorta Basin and the schematic distribution of sediments. La Rinconada and San Chils are the classical Fossil-Lagerstätte sites with remains of insects, plants and amphibians. Modified from Crespo et al. (2018).

Fig. 1. Bassins cénozoïques espagnols, avec la localisation du bassin de Ribesalbes–Alcorta et la distribution schématique des sédiments. La Rinconada et San Chils sont les sites classiques de Lagerstätte à conservation de restes d’insectes, de plantes et d’amphibiens fossiles. Modifié selon Crespo et al. (2018).

(upper molars: M1, M2 and M3; upper premolars: P1, P2, P3 and P4; upper canine: C; upper incise: I).

Throughout the text, the names of the localities often appear abbreviated as follows: MCX: Mas dels Coixos. MTR: Mas de Torner. BC: Barranc de Campisano. FS: Foieta la Sarra. MAB: Mas d’Antolino B. CBR: Corral de Brisca.

4. Systematic palaeontology

4.1. *Desmanodon daamsi*

Family Talpidae Fischer, 1814.

Subfamily Talpidae *incertae sedis*.

Genus *Desmanodon* Engesser, 1980.

Desmanodon daamsi Van den Hoek Ostende, 1997.

Localities: Mas dels Coixos 6 (MCX6); Barranc de Campisano 1 (BC1); Mas d’Antolino B 0A, 0B, 3, 5 y 11 (MAB0A, MAB0B, MAB3, MAB5 and MAB11).

Material: MCX6: 1 M2; BC1: 4 i/l, 1 i1, 1 i3, 1 P3, 1 M3; MAB0A: 1 P4, MAB0B: 1 i1, 1 i2, 1 p2, 1 I3, 1 M2, 2 M3; MAB3: 7 i/l, 1 p?, 2 p1, 1 p2, 2 m1, 1 m2, 1 I, 2 P2, 1 P4, 2 M1, 1 M2, 2 M3; MAB5: 11 i/l, 1 p1, 2 c, 2 p4, 4 m1, 1 I, 2 P2, 2 M1, 3 M2, 2 M3; MAB9: 1 p4; MAB11: 2 i/l, 1 p3, 1p4, 2 m3, 1 P1, 2 P3, 1 M2; MAB13: 1 m3.

Measurements: See Table 1.

4.1.1. Description

c (Fig. 2A): one root; the main cusp is conical and the tooth has a sub-elliptical shape; the tip is curved towards

the posterior side and a small cuspule is present at the posterior base of the tooth.

p1 (Fig. 2B): tooth with one large root and a sub-elliptical shape. The protoconid is well developed. The anterior crest is shorter than the posterior one. The posterolingual side has a rounded protrusion and connects to a small cuspule. No cingulid is present; the p1 from MAB5 shows a small cingulid.

p2: similar to p1 but larger and with a posterolingual side showing a rounded protrusion and a connection to a small cuspule. The posterior crest is longer than the anterior one, which is very short. A posterior small cingulid is present.

p3 (Fig. 2C): tooth with two roots and a sub-elliptical shape. The protoconid is well developed. The anterior side is wider than the posterior one, while the posterolingual side is more developed. The centrocristid end in two small cuspules characterized by an anterolingual and posterolabial corner.

p4 (Fig. 2D): tooth with two roots and a sub-triangular shape. The labial flank is enlarged. Two ridges are present in the protoconid; the anterior one is short and connected to a paraconid, whereas the posterior one is directed in a posterior and somewhat lingual direction. The metacristid is present in the posterior side of the tooth. A poorly developed cingulum is present around the tooth.

m1 (Fig. 2E): the tooth has two roots. The paraconid is only an enlargement of the paracristid. This crest is curved between the paraconid and the protoconid. The

Table 1
Measurements of the teeth of talpids and dimylids.

Tableau 1
Mesures des dents de talpidés et dimylidés.

<i>Desmanodon daamsi</i>									
Element	Site	Length				Width			
		n	Min.	Med.	Max.	n	Min.	Med.	Max.
c	MAB5	2	0.88	0.90	0.92	2	0.56	0.57	0.58
p1	MAB3	2	0.71	0.75	0.79	2	0.44	0.48	0.52
	MAB5	1		0.71		1		0.55	
p2	MABOB	0		–		1		0.64	
	MAB3	1		0.82		1		0.59	
p3	MAB11	1		0.87		1		0.61	
p4	MAB5	1		1.25		1		0.93	
	MAB9	1		1.23		1		0.81	
m1	MAB5	2	1.96	1.98	1.99	3	1.38	1.41	1.45
m3	MAB13	0		–		1		1.13	
P1	MAB11	1		0.66		1		0.54	
P2	MAB3	0		–		1		0.57	
	MAB5	2	0.79	0.80	0.80	2	0.59	0.59	0.59
P3	BC1	1		0.92		1		0.61	
	MAB11	2	0.87	0.92	0.96	2	0.60	0.61	0.61
M1	MAB3	1		2.29		1		1.85	
	MAB5	1		2.72		1		1.81	
M2	MABOB	1		1.73		1		2.06	
	MAB5	1		1.73		1		1.92	
M3	MABOB	1		1.10		1		1.50	
	MAB3	1		1.28		1		1.74	
	MAB5	1		1.18		1		1.68	
<i>Desmanella fejfari</i>									
p1	MTR2	1		0.65		1		0.53	
p2,3	MTR2	1		0.77		1		0.56	
P1	MTR2	1		0.69		1		0.54	
P4	MTR2	1		1.37		1		1.70	
M1	MTR2	1		1.51		1		1.48	
M2	MTR2	1		1.37		1		1.70	

protoconid is the highest cusp, while the metaconid is slightly lower. The protocristid is high and straight. The metacristid is short, meeting the entocristid at a very low level. The trigonid basin is an open, deep and narrow valley. The talonid is longer and much wider than the trigonid; both are wider than long. The entoconid is lower than the metaconid. The entocristid is longer than the metacristid. Both are bent downwards and connected. In two specimens, the entostylid is an enlargement that appears at the base of the entoconid, whereas in others it is a cuspule; it is slightly curved in a posterolabial direction. The hypoconid is connected to the entoconid with a straight postcristid. In two specimens, the oblique cristid runs downward anterolabially and is connected to the base of the protocristid, but in the others it is not connected to the protocristid. The hypoflexid is long and wide in the lingual side, the trigonid basin is small and deep. In one specimen it is closed by a small cingulid. The cingulid starts near the base of the paraconid and ends next to the entostylid, its anterior side is wider than the posterior one.

m3 (Fig. 2F): the tooth is broken. The trigonid is closed and narrower than the talonid. In occlusal view, the metaconid is more protruding than the entoconid. The protoconid is slightly higher than the metaconid. The protocristid is angular. The talonid is closed. The entocristid is not present. The hypoconulid is poorly developed, and it is

only a small cuspule near the entoconid. The oblique cristid has a low connection with the trigonid, under the middle of the protocristid. The lingual basin is small and closed by a cingulid.

P1 (Fig. 2G): the tooth has one root and is rounded in occlusal view. It has only a big paracone and a poorly developed cingulum. A small crest thickens the cingulum on both the anterior and the posterior sides.

P2 (Fig. 2H): the tooth has one root and a sub-triangular shape. The paracone is well developed. A small cingulum is present in the posterior and the lingual sides of the tooth; it is more pronounced in the posterolingual part.

P3 (Fig. 2I and J): the tooth has two roots. The paracone is well developed and it has a posterior ridge that runs in a slightly S-shaped curve and connects to the posterior cingulum. The anterior cingulum is small, whereas the posterior cingulum is well developed and borders a narrow valley.

M1 (Fig. 2K and L): the tooth has one lingual and two labial roots. The paracone is lower than the metacone. The parastyle is a small cusp at the base of the preparacrista. The mesostyle is divided, but its two cusps are joined, the anterior mesostyle is smaller. The postmetacrista is long; the anterior cingulum starts in the metastyle; the anterior labial side of the postmetacrista shows a small cingulum at the base of the metacone valley; this cingulum ends next

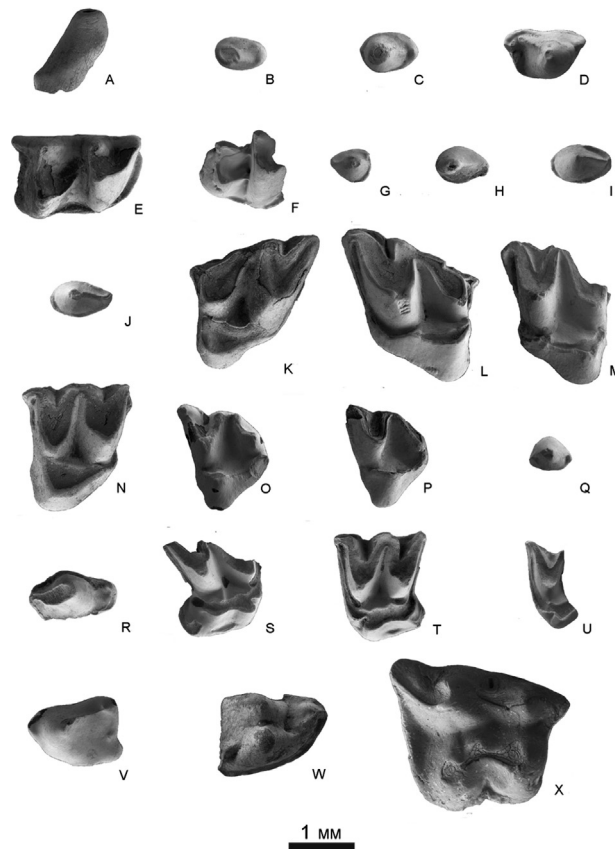


Fig. 2. Teeth of talpids and dimylids from the Ribesalbes–Alcora Basin. *Desmanodon daamsi*: A, right c (lateral view, MAB5-440); B, left p1 (MAB3-806); C, left p3 (MAB11-123); D, right p4 (MAB9-4); E, left m1 (MAB5-370); F, left m3 (MAB13-3); G, right P1 (MAB11-139); H, left P2 (MAB5-767); I, left P3 (BC1-162); J, left P3 (MAB11-141); K, left M1 (MAB3-703); L, right M1 (MAB5-726); M, left M2 (MAB0B-38); N, right M2 (MAB11-97); O, left M3 (MAB3-697); P, left M3 (MAB5-398). *Desmanella fejfari*: Q, right P1 (MTR2-189); R, right P4 (MTR2-198); S, right M1 (MTR2-200); T, left M2 (MTR2-194); U, left M3 (MTR2-184); *Plesiodymylus ilercavonicus*: V, left dp4 (MAB11-133); W, right m1 (MAB11-114); X, right M1 (BC1-200).

Fig. 2. Dents de talpidés et de dimylidés du Bassin de Ribesalbes–Alcora. *Desmanodon daamsi* : A, c droite (vue latérale, MAB5-440) ; B, p1 gauche (MAR3-806) ; C, p3 gauche (MAB11-123) ; D, p4 droite (MAB9-4) ; E, m1 gauche (MAB5-370) ; F, m3 gauche (MAB13-3) ; G, P1 droite (MAB11-139) ; H, P2 gauche (MARS5-767) ; I, P3 gauche (BC1-162) ; J, P3 gauche (MAB11-141) ; K, M1 gauche (MAB3-703) ; L, M1 droite (MA5-726) ; M, M2 gauche (MAB0B-38) ; N, M2 droite (MA11-97) ; O, M3 gauche (MAB3-697) ; P, M3 gauche (MAB5-398). *Desmanella fejfari* : Q, P1 droite (MTR2-189) ; R, P4 droite (MTR2-198) ; S, M1 droite (MTR2-200) ; T, M2 gauche (MTR2-194) ; U, M3 gauche (MTR2-184). *Plesiodymylus ilercavonicus* : V, dp4 gauche (MAB11-133) ; W, m1 droite (MAB11-114) ; X, M1 droite (BC1-200).

to the metacone. The metacone is large and V-shaped, the labial groove is narrow. The protocone has two small cinguli in anterolingual and posterolingual positions in MAB5. The preprotocrista is short and ends at the anterolabial corner of the paracone. The postprotocrista is short and wide, the hypocone is an enlargement of the crest, the posthypoconista is directed downward and connects to the wide posterior cingulum, which is narrower and ends at the metastyle in the MAB3 material.

M2 (Fig. 2M and N): the tooth has one lingual and two labial roots. The paracone is higher than the metacone, in MAB5 it is slightly smaller. The parastyle is a small enlargement and is bent forwards. The anterior cingulum is poorly developed. The mesostyle is divided and with a larger anterior part. The metastyle is a small enlargement, which connects to the small posterior cingulum. The trigon basin is narrow and deep, wider in MAB5. The preprotocrista is short and high and connects to the lingual base of the paracone; the protoconule is absent. The postprotocrista is long

and connects to the hypocone, which appears as a ridge enlargement. The posthypoconista connects to the posterior cingulum. The large and wide cingulum starts at the posthypoconista and ends at the mesostyle.

M3 (Fig. 2O and P): the tooth has three roots. The preparacrasta connects to the parastyle, an enlargement of the ridge. The mesostyle is double; the postparacrasta mesostyle is larger. The metacone is an enlargement of a ridge, and it is fused to the base of the metacone. The protoconule is absent. The preprotocrista connects to the anterolingual side of the paracone; the postprotocrista connects to the metacone. No cingula are present.

4.1.2. Remarks

The most frequent talpid in the early and early–middle Miocene in Spain is the genus *Desmanodon*, which has been found in several localities of the Spanish basins as Calatayud–Montalbán, Teruel, Rubielos de Mora and

Vallès–Penedès (Hordijk et al., 2015; Van den Hoek Ostende, 1997; Van den Hoek Ostende et al., 2016, 2017).

The distinction between early Miocene *Desmanodon* and *Paratalpa* requires the observation of the humeri, since the dental morphology of the two genera is very much alike (Van den Hoek Ostende, 1989, 1997; Ziegler, 1990). Unfortunately, no humerus of either genus have been found in the studied sites. Nevertheless, the last record of *Paratalpa* is older than the MN4, whereas *Desmanodon* has been recorded in the MN3–4 of Europe, replacing the first genus before the MN4 (Van den Hoek Ostende, 1997; other refs from MN3–4). This genus was probably an immigrant at the MN2–MN3 transition, together with the genus *Galerix* (Van den Hoek Ostende, 2003).

The material from the Ribesalbes–Alcora Basin is characterized by a preprotocrista connected to the base of the paracone in the upper molars and the oblique cristid connected to the central point of the posterior face of the trigonid. For these reasons, the material is ascribed to the genus *Desmanodon* (Ruiz-Sánchez et al., 2013).

Desmanodon daamsi is the species with the least divided metastyle and the most inflated cusps within this genus, which is in agreement with our studied material. The specimen size in the Ribesalbes–Alcora Basin is typical of a small-medium sized species, similar to the population of *D. daamsi* from the Calatayud–Montalbán Basin, albeit with a smaller M1.

4.2. *Desmanella fejfari*

Subfamily Urosilinae Dobson, 1883

Genus *Desmanella* Engesser, 1972

Desmanella fejfari Gibert, 1974

Localities: Mas de Torner 2 (MTR2), Mas d'Antolino B 3 (MAB3).

Material: MTR2: 1 p1; 1 p2,3, 1 P1, 1 P4, 1 M1, 2 M2, 1 M3; MAB3: 1 M1,2.

Measurements: Table 1

4.2.1. Description

p1: the tooth is small and has one root. It shows a small labial cingulid and a narrow valley.

p2/p3: small, laterally flattened tooth with one root. The protoconid is well developed and has a wide cingulid.

P1 (Fig. 2Q): small tooth, with a sub-triangular shape in occlusal view. The paracone is well developed and has a small lingual cingulum.

P4 (Fig. 2R): a broken tooth without protocone. The postprotocrista becomes weaker in the last part and connects to the cingulum. The parastyle is very large and consists of two small cuspules formed by the cingulum; between the parastyle and the paracone, there is a wide valley. Two cingula, a narrow labial and a small posterolingual one, are present.

M1 (Fig. 2S): the tooth has a sub-quadrate shape and it has large curve in the posterior margin. The paracone is conical and enlarged in the lingual side. The postparacrista is broken. The mesostyle is clearly divided. The preprotocrista connects the protoconule, which is a small elongated cone, with the protocone. The postprotocrista connects to the hypocone, a strong enlargement of the

ridge; the posthypocrista ends at the base of the hypocone. The protoconule, the hypocone, and the protocone project low, very rounded ridges to the large and deep trigon basin. Between these cusps, the lingual margin shows large and wide grooves. The anterior and wide cingulum connects the protoconule to the parastyle; a small lingual cingulum is present and connects the protocone with the hypocone; the posterior cingulum starts at the base of the hypocone, forms a deep emargination, a tiny accessory cuspule and ends at the metastyle.

M2 (Fig. 2T): tooth subrectangular shape; paracone slightly smaller than the metacone, both clearly V-shaped and with pronounced lingual grooves. The parastyle is a small enlargement of the ridge connecting to the anterior cingulum; this wide cingulum connects to the protoconule. The mesostyle is slightly divided, with its anterior part larger than the posterior one. The metastyle is connected to the posterior cingulum. The preprotoconule is small and connects to the protoconule; the preprotoconule crista connects to the anterior cingulum. A small lingual cingulum is present between the protocone and the hypocone. The postprotocrista connects to the hypocone; the posthypocrista connects to the posterior cingulum; this narrow cingulum connects with the metastyle. A well-developed cingulum is present on the hypoconical flange.

M3 (Fig. 2U): only the anterior half of the tooth is preserved. The paracone is V-shaped. The preparacrista connects to the parastyle, an enlargement of the ridge. The protoconule is only an enlargement of the wide anterior cingulum, which connects to the parastyle. The preprotocrista is very short.

4.2.2. Remarks

This genus is very common in the late Miocene assemblages from the Iberian Peninsula (De Jong, 1988; Rümke, 1974; Van den Hoek Ostende et al., 2012; the listings in Van Dam and Rubio, 2003), but it is extremely rare in the faunas from the early Miocene (Van den Hoek Ostende et al., 2017). The early Miocene species of *Desmanella* show a greater resemblance to the genus *Asthenoscaptor* than the younger species do. However, the differences in molar morphology are still very clear. Although the separation between the lingual cusps of the M1 and M2 is not as pronounced in *Desmanella*, the cusps are still separated by folds from the lingual side (Van den Hoek Ostende and Fejfar, 2006). Another similar talpid is *Myxomygale*, but this genus is characterized by less inflated lingual cusps (Ruiz-Sánchez et al., 2013) and a posterior emargination of the M1 and M2 less developed (Van den Hoek Ostende, 2001) than in our material; for these reasons, we ascribe the material to the latter genus.

The genus *Desmanella* is very diverse and comprises thirteen species, but *D. fejfari* shows the most divided mesostyle in M1,2, as in our material (Klietmann et al., 2014b; Van den Hoek Ostende and Fejfar, 2006), which therefore has been assigned to this species.

The Spanish species *D. fejfari* is poorly known and has only been found in MTR2, MAB3, Alto de Ballester 1 and 2 and Rubielos de Mora 2 (this paper; Van den Hoek Ostende et al., 2017). The material from the Ribesalbes–Alcora Basin is similar to the one from Rubielos de Mora 2, with a strong

lingual ridge of the lingual conuli on the M1, 2 (Gibert, 1974). Nevertheless, additional material of this species is required to make an accurate comparison (Van den Hoek Ostende and Fejfar, 2006).

In the MN4 from the Iberian Peninsula, this genus is absent from the Daroca–Calamocha area, and only occurs in Montalvos 2 (Teruel Basin) as cf. *Desmanella* sp. (Hordijk et al., 2015).

4.3. Indeterminate remains of talpids

Localities: Mas dels Coixos 2 and 3 (MCX2 and MCX3), Mas de Torner 1 (MTR1), Foietta la Sarra 1 (FS1), Mas d'Antolino B 7 (MAB7), Corral de Brisca 0B and 1 (CBROB and CBR1).

Material: MCX2: 1 p1/p2; MCX3: 1 i/l; MTR1 1 i/l; FS1: 2 i/l; MAB7: 1 i/l; CBROB: 2 i, 3 p; CBR1: 1 i/l.

4.3.1. Remarks

We include here very scarce non-diagnostic remains found in these sites that have been ascribed to an indeterminate form of talpidae. The small premolars similar to this tooth that were found in other sites and incisors with spade-shape allow us to classify this material as being from talpid origin. But this remains are non-diagnostic, and we cannot classify as *Desmanodon* or *Desmanella*.

4.4. *Plesiodimylus ilercavonicus*

Family Dimylidae Schlosser, 1887

Genus *Plesiodimylus* Gaillard, 1897

Plesiodimylus ilercavonicus Crespo, Furió, Ruiz-Sánchez y Montoya, 2018

Localities: Barranc de Campisano 1 (BC1), Mas d'Antolino B 11 (MAB11).

Material: BC1: 1 m1, 1 M1 (2.91 × 2.22); MAB11: 1dp4 (1.46 × 1.07), 1 m1(trigonid only).

4.4.1. Description

dp4 (Fig. 2V): the tooth has two roots; its overall outline resembles a wide triangle. The protoconid is relatively low crowned; it is positioned in the anterior half of the tooth; it is conical and bending posteriorly and slightly lingually. The labial flank is enlarged. The only ridge runs down in the tip of the protoconid to the posterior and lingual direction, connecting to the postero lingual and small metaconid. A wide parastyle is present, this cusp is a pretrude of protoconid. A tiny posterior cingulid is present, and previously the tooth has a wide platform in posterolabial side; a tiny cingulid is present in labial side of the protocone.

m1: The tooth from BC1 is fragmented and only presents a well-developed labial cingulum, with a protruding protoconid and a larger metaconid. A fragment of talonid is present. The m1 of MAB11 (Fig. 2W) is broken and only the trigonid is preserved; the paraconid is small. There is a short paracristid connecting the paraconid to the anterior base of the protoconid. There is a small cingulid connecting the bases of the paraconid and the metaconid. The protoconid and the metaconid are close to each other and similar in size, and the protocristid is not present, both cusps are joined by the rounded lateral edge. The labial cingulid is

well developed. The oblique cristid is connected to the base of the protoconid.

M1 (Fig. 2X): The tooth has a small parastyle and a compressed paracone. The mesostyle is connected to the metacone. The metastyle is not represented as a cusp, but as a worn ridge. The posterior margin is straight in occlusal view and it bears a marked cingulum that closes the posterior valley. The anterior base of the protocone is connected to the parastyle by a tiny and short ridge. The postprotocrista runs from the protocone to the anterior base of the hypocone. There is a slight 'central' well-developed elevation on the labial side of the rearmost extreme of the postprotocrista. The lingual cingulum is V-shaped between the protocone and the hypocone.

4.4.2. Remarks

Outside the type locality of *Plesiodimylus ilercavonicus* located in this basin (MAB5), only scarced and poorly preserved remains have been recovered of this species. These material have the same characteristics as in the type locality, regarding the size (although the M1 is slightly smaller), or the lingual cuspid of m1 (Crespo et al., 2018).

5. Discussion

Desmanodon is the most abundant mole in Ribesalbes–Alcora and is present in almost all sites in this basin, with the sole exception of MTR2, in which *Desmanella* occurs instead. As stated by Van den Hoek Ostende and Fejfar (2006), *Desmanodon* “was capable to deal with relatively dry environments”. This was partly based on the absence of the genus in Merkur-Nord, a locality that is also rich in Dimylidae. From the morphology of the humeri it can be deduced that *Desmanodon* was a fossorial animal, although less specialized than *Talpa* or *Proscapanus* (Klietmann et al., 2014b; Prieto, 2010), as already suggested by previous works (Van den Hoek Ostende, 1989). In central Europe, *Desmanodon* is absent from karstic fissures, but it is a typical dweller of lacustrine sites, included those characterized by dry conditions, although with a close presence of a stable water body, like Forsthard, Rembach, or Rauscheröd (Klietmann et al., 2014b; Ziegler and Fahlbusch, 1986). In addition, whereas in central Europe the superficial fossorial moles usually do not exceed 50% (Klietmann et al., 2014b), they constitute the most abundant moles in the Ribesalbes–Alcora Basin.

The uropsiline *Desmanella* shares with the extant genus *Uropsilus* a slender non-flattened humerus, more typical of a terrestrial quadruped than of a specialized burrower or swimmer (Furió et al., 2011; Van den Hoek Ostende, 2001; Van den Hoek Ostende and Fejfar, 2006), which indicates that it was more or less similar in ecology to the recent shrew moles (García-Alix et al., 2011). Therefore, *Desmanella* was probably a litter burrower, limited to soft lands, with abundant organic material, where it could search for insects and be moderately able to climb (García-Alix et al., 2011; Hooker, 2016). Although Van den Hoek Ostende (2001) comments that the Uropsilinae, or shrew-like moles, were seen as more or less independent of humidity, *Desmanella* is interpreted as requiring rather wet environments by García-Alix et al. (2008); their view was

later explained by the biogeography, which clearly linked *Desmanella* to moist environments in Spain (García-Alix et al., 2011). In contrast, owing to its small size, it probably did not survive cold winters, and needed at least moderate temperatures (Gureev, 1979). An additional characteristic is the high abundance of this genus in MTR2, the site with the highest percentage of ochotonids (pikas) in the Ribesalbes–Alcora Basin. In MN4 of the Iberian Peninsula, the presence of this genus is restricted to Montalvos 2, also with abundant ochotonids (Hordijk et al., 2015), while it has not been found in the nearby site of Buñol or in the basins of Calatayud–Montalbán or Vallès–Penedès (Jovells-Vaqué et al., 2018; Robles et al., 1991; Van den Hoek Ostende and Furió, 2005; Van der Meulen et al., 2012). The pikas, according to Ge et al. (2013), have a preference for plants as included in the families Astaraceae, Rosaceae, and Fabaceae. The first family is dominant in the upper Burdigalian of the Vallès–Penedès Basin, and generally, the grasses in this period of time in Iberian ecosystems (Barrón et al., 2010). This kind of plants was probably dominant in these sites, thus favouring pikas and probably *Desmanella*.

In sites with abundant *Desmanella*, *Desmanodon* is not present, probably due to different ecological preferences of the two taxa (Ziegler, 2006). In Spain, the co-occurrence of both taxa has only been recorded in Alto de Ballester 1 and 2, Rubielos de Mora 2 (Van den Hoek Ostende et al., 2017), and MAB3. In the Calatayud–Montalbán Basin, *Desmanella* is not present in the early Miocene, while *Desmanodon* is the unique talpid in this basin. Overall, talpid diversity in Iberian faunas is low throughout the Miocene when compared with the German, Austrian, or Swiss localities. The family even appears to be completely absent for most of the middle Miocene (MN 5–MN7 + 8) in the central basins of Spain (Furió et al., 2011), to only appear again in the early Vallesian (De Jong, 1988; Van den Hoek Ostende et al., 2012). In our studied sites the diversity is higher than in other Iberian basins, but lower than in central Europe. The coexistence of ochotonids and *Desmanella* in MN4 and the higher frequency of this genus in the Iberian Peninsula in the late Miocene, when open lands were common (Barrón et al., 2010), suggest the preference of *Desmanella* for humid open habitats, whereas *Desmanodon* probably preferred more wooded habitats, which would explain the exclusion between both genera in the Iberian Peninsula.

The bizarre dentition of the dimylids indicates that they mainly fed on snails (Crespo et al., 2018; Müller, 1967). During the early Miocene, there was an important diversification of the family Dimylidae in the Molasse Basins of Germany. Only two genera of dimylids, *Chainodus* and *Plesiodimylus*, reached the Iberian Peninsula (Van den Hoek Ostende and Furió, 2005), but they were always quite rare, except in the site MAB5 (Crespo et al., 2018), MAB11 and BC1 from the Ribesalbes–Alcora Basin, some undetermined sites from the Vallès–Penedès Basin (Van den Hoek Ostende et al., 2016) or Alto de Ballester 1 and 2 from the Rubielos de Mora Basin in the case of *Chainodus* (Van den Hoek Ostende et al., 2017). This latter genus was more specialized in durophagy, and its restricted geographical range may reflect the range and abundance of its preys, presumably some kind of terrestrial snails (Furió et al., 2011). Dimylids are considered to be characteristic of

moist environments on the basis of functional morphology. After all, a year-round supply of snails is needed to support the populations, and such a resource can only be expected in humid climates. The pattern found, in which most genera are endemic to the northern areas, thus supports the notion of the humidity gradient, which was already present in the early Miocene, when the Dimylidae were most abundant/diversified (Furió et al., 2011).

The genus *Plesiodimylus* is considered a more insectivorous form by some authors, like the erinaceids or some talpids, due to the fact that it is less specialized genus of the family (Ziegler, 2005). However, Crespo et al. (2018) have shown evidences that at least *P. ilercavonicus* was more adapted to a durophagous diet than erinaceids, talpids and the species of the genus *Plesiodimylus* less amblyodont.

The spatial distribution of this family is commonly correlated with the presence of humid conditions; this fact explains why this family is a resident form in central Europe but a transient group in southern Europe (Van den Hoek Ostende et al., 2016). On the other hand, the relative low temperatures could favour this migration in Spain too, since the only two basins where this family has been detected are Rubielos de Mora and Ribesalbes–Alcora. For Rubielos de Mora, Barrón et al. (2010) estimated a temperature interval of 12.9–16.1 °C, while Ríos (2013), based on isotopic analysis, gave an estimation of 13.31 °C for MAB5, the coolest site and the one with most remains of this family in the Ribesalbes–Alcora Basin. Low temperatures are explained in Rubielos de Mora by the altitudinal location of this basin: about 900 m above sea level (Barrón et al., 2010). On the other hand, site MAB5 is chronologically close to the Mi-2 cold event (Crespo, 2017; García-Paredes et al., 2016). Probably, in first place, the humid conditions and, in second place, the fall of the temperatures (increasing the humidity conditions and thus forest growth) favoured the migration of this family.

6. Conclusions

Talpids and dimylids are relatively abundant in the small mammal assemblages in the Ribesalbes–Alcora Basin, the talpids reach near to 10% in MAB0A and dimylids near to 15% in MAB5 (see Crespo et al., 2019). *Desmanodon daamsi* is described for the first time in this basin in the sites MCX6, BC1, MAB0A, MAB0B, MAB3, MAB5, and MAB11, *Desmanella fejfari* in sites MTR2 and MAB3 and an indeterminate remains of talpid (that we cannot classify as *Desmanodon* or *Desmanella*) in sites MCX2, MCX3, MTR1, FS1, MAB7, CBR0B and CBR1. In addition to MAB5, the record of *Plesiodimylus ilercavonicus* is extended to sites BC1 and MAB11.

The remains of *Desmanodon daamsi* constitute one of the best collections of this species from MN4 of Europe. We have recorded the first remains of *Desmanella fejfari* outside the Rubielos de Mora Basin and the last known occurrence of this species in the early Miocene of the Iberian Peninsula. *Desmanella* only “reappears” again in the MN7 + 8. Due to the fact that *Desmanodon* preferred wooded habitats whereas *Desmanella* lived in rather open habitats during the MN4, both genera rarely co-occur in the same site.

On the other hand, the material of *Plesiodymylus* from the Ribesalbes–Alcora Basin constitutes the first record of this genus in the early Miocene in the Iberian Peninsula and increases both the biostratigraphic range and the number of sites of *P. ilercavonicus*. The migration of the family Dimylidae is favoured by humid conditions.

The occurrence of both Talpidae and Dimylidae indicates an unusual humid habitat in the Ribesalbes–Alcora Basin that has not been found anywhere else in the Iberian Peninsula during MN4.

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