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Enters the shrew, some considerations on the Miocene palaeobiogeography of Iberian insectivores



« Opération musaraigne », quelques considérations sur la paléobiogéographie des insectivores ibériques

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ABSTRACT

The fossil record of the Iberian insectivores forms a subset of those found in central Europe. Comparison of the late early to early late Miocene record of the two areas shows that, particularly during the late Early Miocene, central European taxa have transient occurrences in Spain. Most taxa appear earlier and survive longer in central Europe. A notable exception is the gymnure *Galerix*, which extirpates earlier in central Europe, except for a transient occurrence in Germany just prior to its extinction. The main period of insectivore migrations is the late middle Miocene, although some of the taxa that enter remain restricted to the coastal areas. Overall, the pattern of distribution in time and space is best explained by the preference of insectivores for humid environments, as were found during the early Miocene and re-appeared at the end of the middle Miocene.

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R É S U M É

L'enregistrement fossile des insectivores ibériques forme un sous-ensemble de ceux que l'on trouve en Europe centrale. La comparaison de ces enregistrements du Miocène montre que, en particulier à la fin du Miocène inférieur, des taxons d'Europe centrale migrent en Espagne. La plupart des taxons apparaissent plus tôt et survivent plus longtemps en Europe centrale. Une exception notable est le cas du galericiné *Galerix*, qui disparaît plus tôt en Europe centrale, exception faite d'une courte apparition transitoire en Allemagne juste avant son extinction définitive. La principale période où se jouent les migrations d'insectivores est la fin du Miocène moyen, bien que certains taxons restent restreints aux zones côtières. Dans l'ensemble, le modèle de distribution dans le temps et l'espace s'explique par la préférence des insectivores pour les environnements humides, comme ceux observés au Miocène inférieur et à la fin du Miocène moyen.

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1. Introduction

Long-term records of micromammals, in combination with magnetostratigraphy and/or radiometric datings, enable us to date with great precision events such as faunal turnovers, or first and last occurrences of specific taxa. Comparison between overlapping records of different basins allows us to find similarities in the dating of events, which may have a common cause in changes in the global system. At least equally interesting are differences between basins. Differences in the first and last occurrences of taxa make it possible to reconstruct migration patterns at a fine chronostratigraphic scale.

A good example of such a comparison between two long-term records is the work done by Van der Meulen et al. (2011, 2012). They compared the datings of rodent events in the middle Miocene of the North Alpine Foreland Basin (NAFB) of southern Germany and Switzerland with those from the Aragonian type section and adjacent sections in central Spain. These are, at present, two of the most extensively studied Miocene basins for which correlations based on mammal biostratigraphy, magnetostratigraphy and radiometric dating are available (e.g., Abdul Aziz et al., 2008, 2010; Daams et al., 1999; Kálin and Kempf, 2009; Reichenbacher et al., 2013; Van Dam et al., 2006; Van der Meulen et al., 2011, 2012). Van der Meulen et al. (2012) concluded that, although the order of rodent events was virtually the same in both basins, there was a significant diachrony for some of these events, with taxa occurring earlier in central Europe than in the Iberian Peninsula. As the events formed the basis of the biochronological MN-system these results had consequences for the biochronology of the European Miocene. While Van der Meulen et al. (2012) show the limitations of long distance correlations solely based on small mammals, they open new possibilities for palaeobiogeography: differences in times of migrations may reflect the waxing and waning of ecosystems.

In this paper, we focus on the distribution of the insectivores from the late early-early late Miocene, comparing the central European and Spanish record. In contrast to rodents, insectivores are generally seen as poorly suitable for stratigraphic purposes, given the mostly conservative nature of the group. What might be a disadvantage in fine and local biostratigraphy, is in contrast useful for long distance comparisons because, in contrast to rodents, issues relating to the recognition of chronospecies versus geographic variants can be excluded in most of the cases. Moreover, insectivores are considered as good palaeoenvironmental indicators, and particularly indicative of humid environments. Furió et al. (2011a), for instance, showed that throughout the Miocene insectivore diversity is higher in the northern parts of Europe, indicating a latitudinal gradient in humidity. Therefore, this group is expected to show a different pattern of distributional changes than the rodents, which, based on Van der Meulen et al. (2012), often shows stepwise migration into the Iberian Peninsula. Our aim is to explore these differences, and thus provide a basis for understanding the processes behind mammal migrations on a geological time scale.

2. Material and methods

The Spanish eulipotyphlans can be considered as a nested subset of those occurring at higher latitudes (Furió et al., 2011a). In other words, many of the central European taxa never reached the Iberian Peninsula. Thus, for the following discussion, we focus on the most common insectivore taxa for the Spanish middle Miocene. Taxa with only a few occurrences will be briefly discussed in the general paragraph per family, after which the Iberian and central European fossil record of the more common taxa will be discussed.

As we compare our data with the studies of Van der Meulen et al. (2011, 2012), we follow their correlation with the records of the NAFB for both the Swiss and German parts of the basin, taking into account new correlations made by Reichenbacher et al. (2013). Abdul Aziz et al. (2008, 2010) suggested considerably older ages for the late Early/early Middle Miocene German localities in the basin. We are aware that correlations are partly still in flux and that many problems exist.

We do not restrict ourselves in our comparison to the NAFB and the sections of Daroca alone. The Aragonian type section has a very low diversity of eulipotyphlans, and, although a number of papers have appeared (De Jong, 1988; Van Dam et al., 2011; Van den Hoek Ostende and Doukas, 2003; Van den Hoek Ostende et al., 2009, 2012), the taxonomy of the Darocan insectivores has not yet been fully elaborated. Large differences may occur between Iberian basins (e.g., Van den Hoek Ostende et al., in press), particularly in insectivores, but as we are interested in large scale biogeographical patterns, this problematic does not need further exploring here. By the same reasoning, data from other Central/East European basins are included whenever pertinent to the discussion, although here clear differences can be found in the insectivore composition as well (e.g., Ziegler, 2006a).

3. The fossil record of the Iberian middle Miocene Eulipotyphla

3.1. Erinaceidae

In the Neogene of Europe, the hedgehog family (Erinaceidae) is represented by two subfamilies, the Erinaceinae and the Galericinae. The record of the Erinaceinae is poor. Moreover, there are many taxonomical problems, to the point that even genera may not be distinguished on the basis of isolated molars (Ziegler, 2006b). By contrast, the Galericinae are extremely common, particularly during the Miocene. The vast majority of these finds belong to the Galericini, the only other genus, *Lantanothereium*, being restricted to a limited number of localities only.

The Galericini encompass six Miocene genera, of which the insular forms *Deinogalerix* (Butler, 1980; Villier et al., 2013) and *Apulogalerix* (Masini and Fanfani, 2013), and the Iberian Early Miocene endemic *Riddleria* (Van den Hoek Ostende, 2006) are not considered here. The other three genera, *Galerix*, *Parasorex* and *Schizogalerix*, were at one point all lumped under the genus *Galerix*. Engesser (1980) erected the genus *Schizogalerix* for forms from the middle

Miocene of Turkey and the late Miocene of Europe, and Van den Hoek Ostende (2001a) reinstated the genus *Parasorex*. As a result, some of the older records are in need of revision. Occurrences listed as *Galerix* sp. for the Swiss part of the NAFB by Kälén and Kempf (2009) could pertain either to *Galerix* or to *Parasorex*. In addition, there is a taxonomic issue about the early late Miocene Galericiini. Van den Hoek Ostende (2001a) had postulated a convergence between *Parasorex* and *Schizogalerix*. Yet, central European species like *Schizogalerix voesendorfensis* are morphologically very similar to the Spanish *Parasorex socialis*, and the true relationship between these forms – and the proper classification – still needs to be elaborated. For the moment, the traditional view of classifying the Spanish forms as *Parasorex* is maintained, but we are aware that a review of these forms will influence any biogeographical conclusions.

3.1.1. *Galerix*

The gymnure *Galerix* represents a very common element in the late Early and Middle Miocene faunas of Europe, where it is represented by multiple species. The genus appears to have originated in Anatolia, the oldest finds coming from uppermost Oligocene deposits (De Bruijn et al., 1992). In that area, it is found throughout the Early Miocene. It migrated into Europe around the MN 2/MN 3 transition (Van den Hoek Ostende, 1992, 2001a, 2001b).

The first occurrence of the genus in Spain, with the species *Galerix remmertii* is dated to the latest most MN 2 (Ramblar 1); in the lower part of local zone Z. *Galerix remmertii* continues to be present throughout the Ramblian (Van den Hoek Ostende, 2003). The species is quite abruptly replaced by *G. symeonidisi* at the beginning of the Aragonian (beginning MN 4, \approx 17.0 Ma, Van den Hoek Ostende and Doukas, 2003). *Galerix symeonidisi* is in its turn replaced by *G. exilis*. Van den Hoek Ostende and Doukas (2003) showed that the variation of some assemblages in the Daroca–Calamocha Basin was too large to be attributed to a single species. Based on this, and a change in both size and morphology, they suggested that the mixed assemblages resulted from a gradual replacement, taking place in local zones C-Db (\approx 16.5–15.8 Ma). Still, many elements from the mixed assemblages cannot be identified with certainty to one or the other species, which makes it impossible to precisely pinpoint the time of entrance of *G. exilis* and extirpation of *G. symeonidisi*. In the Daroca–Calamocha Basin, *G. exilis* has its last occurrence in the Uppermost Aragonian locality of Carrilanga (Zone G3, \approx 11.3 Ma; Van Dam et al., 2014b), where it is found together with *Parasorex* (De Jong, 1988).

The oldest *Galerix* remains in southern Germany are found in MN 3 fissures (Klietmann et al., 2014a; Ziegler, 1990a, 1994). Here, *G. aurelianensis* is found, a close relative to *G. remmertii* and mainly differing from the Spanish species by its slightly larger size. Presumably, the two species stem from the same migration from Turkey. As in Spain, this first *Galerix* is replaced by *G. symeonidisi*. By contrast, this replacement seems to have been more gradual in Germany, as the two species are found together in fissure fillings correlated to early MN 4 (Ziegler, 1990a). The oldest occurrence of the species is in its type locality

Aliveri (Greece), which is considered to be older than the central and western European MN 4 localities (Van den Hoek Ostende et al., 2015). Thus, *G. symeonidisi* seems to be part of the MN 4 migration wave that also brought modern type cricetid rodents (*Democricetodon*, *Megacricetodon*) into Europe (Van den Hoek Ostende et al., 2015).

Also the replacement of *Galerix symeonidisi* by *G. exilis* appears to occur in Germany as it did in Spain. Here too, assemblages are found with mixed characters, which initially were interpreted as intermediate stages in a *symeonidisi-exilis* lineage (Ziegler and Fahlbusch, 1986). The localities of Rembach, Forsthart and Rauscheröd, in which these mixed assemblages were found, are placed in zone OSMA, the upper boundary of which was placed by Van der Meulen et al. (2012) at around 16.5 Ma. This implies that the *G. symeonidisi* appears in Spain at about the same time it extirpates in the NAFB. Reichenbacher et al. (2013) place the upper boundary of the zone even higher, but their figure 13 suggests an age for the localities of Forsthart, Rembach and Rauscheröd between 16.8 and 17.0 Ma, which would indicate even an extirpation of the species in Germany before its entrance in Spain. A similar problem occurs with the distribution of *Heterosorex* (see below). As such a sudden shift in the distribution of two taxa seems unlikely, this discrepancy could result from a problem in the correlations. Alternatively, the pattern could result from a gap in our knowledge, with the taxa persisting longer in central Europe than the present record recognizes. In that case, a revision of the Swiss record of *Galerix* may provide part of the solution.

In Germany, the last occurrences are seen in fissure fillings such as Goldberg, Steinberg and Petersbuch 68 upper (Prieto and Rummel, 2009; Ziegler et al., 2005). The latter is particularly of interest, since a large species of *Galerix* is found next to *Parasorex*, a genus that abruptly replaces *Galerix* in the course of the middle Miocene in central Europe (see below). With the migration of its counterparts *Parasorex* and/or *Schizogalerix* after the Miocene Climatic Optimum, *Galerix* retreated to the south. The most significant exception is its re-occurrence in Hammerschmiede (Prieto et al., 2011), which can be interpreted as a micro-pulse contrary to the general trend, in which the genus expanded northwards. Notably, one locality ascribed to the middle-late Miocene transition from the Vallès-Penedès (Ecoparc de Can Mata VCE-Bc C5n.2n, 10.7 Ma) has also provided fossil elements of this genus, whereas the immediately older and younger localities are strictly dominated by *Parasorex*, and could therefore be part of the same trend. Other than that, the genus is only documented in the Vallès-Penedès Basin in the late Aragonian localities ACM/C9-A1 (C5An.2n = 12.46 Ma) and probably in ACM-BCV1 (11.97 Ma) (Furió et al., 2011b; dates following Casanovas-Vilar et al., 2016), suggesting that by that time *Galerix* was mostly restricted to the Spanish inland basins.

3.1.2. *Parasorex*

The genus *Parasorex* seems to have originated in south-eastern Europe. Doukas and Van den Hoek Ostende (2006) postulated a descent of the Austrian *Parasorex pristinus* (MN 5; Ziegler, 2003a, there as *Schizogalerix pristinus*) via “*Galerix*” *kostakii* from *G. symeonidisi*. Prieto et al. (2012)

suggested that the species *kostakii* was better placed in *Parasorex*, shifting the first occurrence of the genus to MN 4 in Greece. The genus is restricted to eastern Europe during the first part of the Middle Miocene, where it is found in the Early and Middle Badenian localities from Austria (Grund, Mühlbach; Ziegler, 2003a, 2006a) and Hungary (Sámsonháza 3, Hasznos, Litke; Hír et al., 2016; Prieto et al., 2012, 2015). From there, the genus expanded eastwards.

In the Vallès-Penedès, *Parasorex* appears throughout the Late Aragonian. Thus, it appears here earlier than in the Daroca-Calamocha area, where its first occurrence is at the very end of the Aragonian, in the locality of Nombrevilla 2 (11.9 Ma; Van Dam et al., 2014b). Here, and in the younger locality of Carrilanga (11.3 Ma), it co-occurs with *Galerix*, which on two occasions also makes a reappearance in the Vallès-Penedès. After the extinction of the latter genus, *Parasorex* continues as the only Galericipini, and survives in Spain well into the Pliocene.

In the NAFB, *Parasorex socialis* is a good biostratigraphic marker as its first occurrence is definitively the result of an abrupt migration. Prieto and Rummel (2009) propose that the species first occurs in Germany in the fissure filling Petersbuch 68. Based on part of the cricetid rodents of this assemblage, they correlate the fauna to the Swiss locality Zeglingen (local zone Oeschgraben, beginning at around 14.2 Ma). The same first occurrence is recognized in the NAFB by the presence of the species in Rutzentobel 550 m. Shortly after, during MN 7 and onward (ca 13.9 Ma; Steinheim, Helsinghausen? Bois de Raube 3; Bolliger, 1994; Kálin, 1997; Kálin and Kempf, 2009; Ziegler, 2006a). *Parasorex socialis* becomes the only Galericipini in the wide majority of the localities (e.g., Anwil; Engesser, 1972). Younger deposits are scarce in the NAFB, but *Parasorex* seems to be replaced by *Schizogalerix*, which is recognized around the middle to late Miocene transition (e.g., Nebelbergweg, Kálin and Engesser, 2001).

3.1.3. *Lantanothereum*

The genus *Lantanothereum* is quite rare, but can be numerous in some localities if environmental conditions are favourable (e.g., Hambach 6C; Ziegler and Mörs, 2000). Apparently, this gymnure thrived in humid environments. A large number of species has been described (*L. sanmigueli*, *L. piveteaui*, *L. lactorensis*, *L. longirostre*, *L. tobieni*, *L. sansaniense*, *L. robustum*, and *L. sabinae*) but many of these are based on limited material only, and a revision is needed to clarify the taxonomical problems obviously surrounding this genus.

The presence of *Lantanothereum* in the Iberian Peninsula is restricted to the Vallès-Penedès area. Crusafont et al. (1955) described *Lantanothereum piveteaui* from early Miocene deposits of the basin. However, based on their description of the holotype and only specimen, this is probably a misidentification of a Galericipini species. Unfortunately, this specimen is lost. A recent survey of new early Miocene collections from the area by MF and LHO yielded no *Lantanothereum* remains.

By contrast, *Lantanothereum sanmigueli*, the smallest representative of the genus, is very well documented in the Vallès-Penedès. It has its first occurrence in Castell de Barberà, which is traditionally placed in the late middle

Miocene. However, there are significant doubts about the real age of this site, being alternatively attributable to the early Vallesian (Casanovas-Vilar et al., 2016; Rotgers and Alba, 2011). Otherwise, it is known from a series of Vallesian localities in the basin, such as Can Llobateres and Can Poncic (Gibert, 1974), Can Feu (Casanovas-Vilar et al., 2012) or Ronda Oest Sabadell D6 (Furió and Alba, work in progress), and was also found in the Turolian site of Ronda Oest Sabadell A-1.

Whereas the genus does not occur in Spain until the beginning of the late Miocene, it has sparse but regular occurrences in central Europe from the late early Miocene onwards. Pending a comprehensive taxonomic revision of the genus, however, little can be said. It is noteworthy that the migration into Spain seems to be part of an overall southward shift of the distribution. *Lantanothereum* was found in the Greek MN9 locality of Plakias (De Bruijn et al., 2012) and possibly in the Vallesian of Bulgaria (J. Prieto pers. obs.). Notably, the Spanish species *L. sanmigueli* appears in Austria around the same time, near to the base of the Pannonian (Ziegler, 2006a, 2006b).

3.2. *Talpidae*

Today, a family with a rather modest diversity, the moles (*Talpidae*) were far more numerous in the Miocene. Finding four or more species in one locality is no exception. However, only five genera reached Spain. Presumably low humidity, and the absence of favourable soil conditions, are limiting factors for the group (Furió et al., 2011a).

3.2.1. *Desmanodon*

The history of the talpid *Desmanodon* resembles that of the gymnure *Galerix*. It too has its origins in Anatolia and presumably migrated into Europe around the MN 2/MN 3 transition (Van den Hoek Ostende, 1997), where closely related species occurred in Spain (*D. daamsi*) and central Europe (*D. antiquus*). An important difference between the two taxa is that *Galerix* became extinct in Turkey already during the early Miocene, whereas *Desmanodon* continued into the middle Miocene (Engesser, 1980) and recently, even a new species from the late Miocene was described (Furió et al., 2014).

The first occurrence of *Desmanodon* in the Iberian Peninsula is in the locality of Naverrete del Rio (latest MN 2; Van den Hoek Ostende, 1997, 2003). From then on, it is a common occurrence in the faunas of the Daroca-Calamocha area until its last occurrence in the locality of Fuente Sierra 4 (zone Db, 15.82 Ma). *Desmanodon* has also been recognised in the localities of the Rubielos de Mora Basin (Van den Hoek Ostende, 1997; Van den Hoek Ostende et al., in press), in the locality of Montalvos 2 in the Teruel Basin (Hordijk et al., 2015), as well as in the Early Miocene deposits of the Vallès-Penedès (MF and LHO, pers. obs.).

The oldest occurrence of *Desmanodon* in central Europe is in the MN 3 fissure filling Stubersheim 3 (Ziegler, 1990b). Apparently, the environment for this talpid was less favourable in this region during MN 3 and early MN 4, for it is rare in Stubersheim 3 and missing in well-studied insectivore assemblages such as Ahnikov 1 ("Mercur-Nord", Van den Hoek Ostende and Fejfar, 2006), Wintershof-West (Ziegler,

1994), Petersbuch 2, Erkertshofen 1 + 2 (Ziegler, 1985) and Petersbuch 28 (Klietmann et al., 2015). It is present in the stratified localities of Rembach, Rauscheröd and Forsthart (Ziegler and Fahlbusch, 1986). The species *D. antiquus* has its last occurrence at Puttenhausen (OSM C+D; Ziegler, 1985, 2006b; Klietmann et al., 2015). Considering that Reichenbacher et al. (2013) place the zone OSM C+D between 16.0 and 15.0 Ma, the last occurrence in central Europe could be coeval with the one in Spain, but possibly a bit younger.

At the end of the middle Miocene, *Desmanodon* reappears in central Europe, this time with the species *D. crocheti* (Prieto, 2010). Outside the NAFB, a closely related form is found in the Hungarian MN6 localities of Sámsonháza 3 and Hasznos (Hír et al., 2016; Prieto et al., 2012, 2015) and also in the older locality of Litke (JP pers. obs.). The genus is still present in the early late Sarmatian of Gratkorn (*D. fluegeli*, Prieto et al., 2010, 2014). Based on morphological similarities with Anatolian forms, this younger appearance of *Desmanodon* is considered a new immigration of the taxon into Europe, which this time did not reach the Iberian Peninsula.

3.2.2. *Desmanella*

Desmanella is a uropiline mole genus (García-Alix et al., 2011), of which the stratigraphic range covers most of the Neogene. Although most of its 14 species have been described from Europe and Asia Minor, the genus ranged as far eastwards as China (Qiu, 1996).

In the early Miocene of Spain, *Desmanella* only knows two transient occurrences. It is found in the MN3 localities of the Rubielos de Mora Basin (Gibert, 1975; Van den Hoek Ostende et al., in press), and is also known from Montalvos 2 (zone C, MN4, Hordijk et al., 2015). At the end of the middle Miocene and during the Vallesian, the genus becomes more common, although its presence in the Vallès-Penedès is rather anecdotic (e.g., Agustí et al., 2005). One of the best assemblages is that of the Late Aragonian site of ACM C4/A1 (11.72 Ma). In the Daroca-Calamocha area, *Desmanella* is first found in the Vallesian of the Cañada section (Van den Hoek Ostende et al., 2012) and in the locality of Pedregueras 2A (De Jong, 1988). After the Vallesian, the genus becomes a regular presence in the faunas of the Teruel Basin (Mein et al., 1990; Van Dam, 1997) and transient in the Granada Basin (García-Alix et al., 2011).

The oldest occurrence of *Desmanella* is in the uppermost Oligocene of Germany (Eggingen-Mittelhart, MP 30, Van den Hoek Ostende, 1989). The genus is continuously present in central Europe up to and including MN4 (Van den Hoek Ostende and Fejfar, 2006; Ziegler, 1985, 1990b), with the species *D. engesseri* having its last occurrence in the locality of Forsthart (OSM A). There is only one German record from the MN units 5 and 6, *Desmanella* sp., from Viehhausen (Ziegler et al., 2005). Apart from that, the genus has been reported from the MN6 fissure of Devínská Nová Ves (Fejfar and Sabol, 2005). Thus, the absence of the genus in Spain coincides with a much poorer record in central Europe, but this may also reflect the lower number of localities present for that period. From MN 7 + 8 on, the record is again more abundant, with *D. stehlini* being recorded from various Petersbuch fissures (Ziegler, 2003b)

and from its type locality Anwil (Engesser, 1972). The genus is represented by *D. aff. rietscheli* in the early late Miocene localities of Austria (Ziegler, 2006b), a form closely related to the species found in the German MN 11 locality of Dorn-Dürkheim (Storch, 1978). The genus survives well into the Pliocene, given its presence at the MN 15 locality of Wölferstheim (Dahlmann, 2001).

3.2.3. *Myxomygale*

The urotrichine talpid *Myxomygale* is quite infrequent in Spain. So far, it has been only recorded in Ramblar 1 (Zone Z, uppermost MN2 Van den Hoek Ostende, 2003) and Alto de Ballester 1 and 2 (MN 3; Van den Hoek Ostende and Furió, 2005) and in Pico del Fraile 2 (MN 5; Zone Dc; C5Br.; 15.5 Ma.; Ruiz-Sánchez et al., 2013) in the Tudela Fm. (Ebro Basin). Though more common, the genus is still rare in central Europe (e.g., Van den Hoek Ostende and Fejfar, 2006; Ziegler, 1985, 1990b). Its range covers the whole early Miocene, but the younger records are scarce, only reported from the rich localities of Sandelzhausen and Petersbuch 10. Therefore, biogeographical conclusions would be tentative. Although the interrupted record suggests that *Myxomygale* appears in Iberian Peninsula as a transient taxon, the limited number of finds may also reflect the overall rarity of the genus.

3.2.4. *Proscapanus*

According to the data compiled by Van den Hoek Ostende and Furió (2005), *Proscapanus* seems to be a transient taxon in the middle Miocene of Moratilla. In the Vallès-Penedès, "*Alloscapanus lehmani*" was reported from Castell de Barberà by Gibert (1975). As "*Alloscapanus*" is to be considered a junior synonym of *Proscapanus*, this is apparently the only published record of the latter genus in the Vallès-Penedès Basin. However, the presence of *Proscapanus* in other localities cannot be discarded (e.g., Furió et al., 2011a), but most await a taxonomic revision of the talpids of the basin. This genus is far more frequent in central Europe than in Spain, with a number fossil occurrences in the middle Miocene from Germany (Ziegler, 2006a).

3.2.5. *Talpa*

Talpa rates among the living mammals with the longest fossil record. Its oldest record is from the early Miocene of Germany (Ulm-Westtangente, MN 2, Ziegler, 1990b). Whereas there are many records from the middle Miocene of central Europe, the genus appears in Spain only at the end of that period, in upper Aragonian sediments from the Hostalets de Pierola area (most of them Abocador de Can Mata sections, ACM), usually as a minor component of the insectivore assemblages and at that time restricted to the Vallès-Penedès (Van den Hoek Ostende and Furió, 2005). It is a quite common element in the Vallesian series of the basin, where it is represented by two species, *T. vallesiensis* and *T. minuta*. After that, the genus is also found in the inland, such as the Teruel Basin (Mein et al., 1990; Van Dam, 1997), but is notably absent in the southern basins as the Granada Basin (García-Alix et al., 2008).

3.3. Dimylidae

3.3.1. Plesiodimylus

Within the Dimylidae, *Plesiodimylus* has the largest temporal and geographical distribution. It has its first appearance in early MN3 faunas as Frankfurt Nord Bassin (Stephan-Hartl, 1972) and Ahnikov 1 (Van den Hoek Ostende and Fejfar, 2015) and is found various German fissure fillings (Klietmann et al., 2014b; Müller, 1967; Ziegler and Fahlbusch, 1986; Ziegler, 1990a, 2005, 2006a, 2006b). It survives well into the Late Miocene, the youngest record being from the Late Miocene locality of Dorn-Dürkheim (Storch, 1978). Finds have been reported ranging from Spain to Greece (Doukas, 1986) and Turkey (Engesser, 1980). A large number of species has been proposed, but the taxonomy of the genus still seems to be somewhat in a state of flux. This is mainly because the first species described, *P. chantrei*, has long been used as a taxonomic waste basket, with many occurrences either having been attributed to it directly, or with an aff. designation.

As yet, there are no published records of Iberian *Plesiodimylus* prior to the late Aragonian. Nevertheless, it has been recently found both in the Ribesalbes-Alcora Basin, associated with MN4 faunas (Crespo-Roures et al., work in progress), and in lower Miocene deposits of the Vallès-Penedès Basin (MF and LHO, pers. obs.). However, the largest collection of *Plesiodimylus* in Spain stems from the late Aragonian and the Vallesian of the latter basin, in which it is invariably present. The oldest records in there are found in ACM/BDL1 and ACM/C9-A1 (12.46 Ma). The youngest records in the basin are from the Torrent de Febulines sites, with an interpolated age of 9.08 Ma (Casasnovas-Vilar et al., 2016).

3.3.2. Chainodus/Metacordylodon

In contrast to the relatively primitive *Plesiodimylus*, *Chainodus* has a highly specialised dentition. The genus is often considered to be ancestral to the middle Miocene *Metacordylodon* (e.g., Ziegler, 1990a), which is one of the most advanced forms of the family. However, a review of particularly the Middle Miocene material assigned to these genera is necessary to ascertain their phylogenetic relationship. Here, we consider them under one heading, awaiting such a review.

Chainodus is only known from some Early Miocene transient occurrences in Spain. It has been found in the Ramblian localities of the Rubielos de Mora Basin (Gibert, 1975; Van den Hoek Ostende et al., in press), which stand out for their atypical composition indicating an environment that differs from that of coeval localities on the Iberian Peninsula. A recent survey of the Early Miocene of the Vallès-Penedès showed the genus had an occurrence in this basin. In the same basin, *Metacordylodon* is found in two much younger localities. This genus is known from the late Aragonian/early Vallesian from San Quirze A and Castell de Barberà.

In central Europe, *Chainodus* is known from the earliest Miocene onwards (Ziegler, 1990a, 2006a) and survives into the Middle Miocene with occurrences in Hambach 6C (Ziegler and Mörs, 2000) and Belchatów B (Rzebik-Kowalska, 1996). However, as mentioned above, there may

be some confusion with *Metacordylodon*. Rzebik-Kowalska, for instance, reported *Chainodus* from Belchatów A, a level at the Middle to Late Miocene transition, whereas Ziegler (2000) listed *Metacordylodon* already for the locality of Sandelzhausen (MN5). It is clear that these advanced dimylids are rare on the Iberian Peninsula, but persisted at higher latitudes up to the Late Miocene.

3.4. Heterosoricidae

3.4.1. Heterosorex

Heterosorex, the type genus of its family, is mostly an early Miocene taxon. There are some finds from the upper Oligocene (Brunet et al., 1981; Ziegler, 1989), and a peculiar Lazarus occurrence in the French late middle Miocene locality La Grive-Saint-Alban. The genus is also mostly restricted to central Europe, the easternmost occurrence of *Heterosorex* being in the Greek locality of Aliveri (Doukas, 1986).

In Spain, *Heterosorex* appears as a transient at the very end of MN2 (Ramblar 1, which similarly holds transient occurrences of the mole *Myxomygale* and the shrew *Soricella* (Van den Hoek Ostende, 2003)), Cetina de Aragon (Van den Hoek Ostende and Furió, 2005) and Navarrette de Rio (Adrover, 1972, 1975). In the MN3 locality of Alto de Ballester 1, it appears again as a transient and once more in combination with *Myxomygale* (Van den Hoek Ostende et al., in press). *Heterosorex* makes a somewhat longer appearance in the Daroca Calamocha area during local zone C (upper MN4). Its first occurrence is at the locality of Artesilla (16.49 Ma), the last at Vargas 2B (15.92 Ma). Apart from the localities in the sections near Daroca, *Heterosorex* has also been found in O'Donell (Van den Hoek Ostende and Furió, 2005), Buñol (Robles et al., 1991), Mas Antolino (Agustí et al., 1988), Montalvos 2 (Hordijk et al., 2015) and has recently been discovered in Lower Miocene deposits from the Vallès-Penedès (MF and LHO, pers. obs.).

In central Europe, the record seems to be quite continuous throughout the early Miocene (Doben-Florin, 1964; Ziegler, 1989; Ziegler and Fahlbusch, 1986). The last occurrence in the NAFB is in the locality of Forsthart, but the genus appears later in the Middle Miocene locality of Hambach 6 (Ziegler and Mörs, 2000). The distribution in time and space of *Heterosorex* is somewhat peculiar. The localities of Rembach, Forsthart and Rauscheröd are placed in zone OSMA, the upper boundary of which was placed by Van der Meulen et al. (2012) at around 16.5 Ma. This implies that the genus appears in Spain at about the same time it extirpates in the NAFB. Reichenbacher et al. (2013) place the upper boundary of the zone even higher, but their figure 13 suggests an age for the localities of Forsthart, Rembach and Rauscheröd between 16.8 and 17.0 Ma. These data suggest that *Heterosorex* had already disappeared from central Europe before it entered Spain, which does not seem very plausible. Therefore, there is either a problem with the correlation, or the record is incomplete with the actual extirpation of *Heterosorex* occurring later than the current finds indicate.

3.4.2. Dinosorex

The origin of the genus *Dinosorex* is somewhat unclear. Engesser and Storch (2008) reported the oldest species of

the genus from the Oligocene of Germany, but as Ziegler (2009) pointed out, this species could also be referred to *Quercysorex*. The next oldest find is from the early Miocene of Anatolia (Van den Hoek Ostende, 1995), which would imply an Anatolian origin, just as for the gymnure *Galerix* and the mole *Desmanodon*. *Dinosorex* migrated into Europe at the end of the early Miocene, well after the other two Anatolian genera.

In Spain, the genus has only been found in the Vallès-Penedès Basin, where it is one of the most frequent elements of the eulipotyphlan assemblages. The oldest record in this basin corresponds to ACM/C9-A1 (C5An.2n = 12.46 Ma). However, as noted by Furió et al. (2015), the presence of *Dinosorex* before the onset of the basin infill cannot be ruled out. Most of the late Aragonian and Early Vallesian localities from the Vallès-Penedès Basin have delivered fossil remains of *D. grycivensis*. The last occurrences of *Dinosorex* in this basin are recorded in sites associated to the early-late Vallesian transition (MN 9–MN 10; 9.6 Ma) (Trinxera de Can Llobateres 0, Can Llobateres 1 and Autopista Rubí-Terrassa 11). Therefore, *Dinosorex* can be considered a real victim of the so-called “Vallesian Crisis”, which in turn was not as much dramatic as stated in its original concept (Casanovas-Vilar et al., 2014, 2016; Daxner-Höck et al., 2015).

Dinosorex has its first occurrence in Germany in the fissure Petersbuch 2 and in Austria in Obersdorf 3 (Ziegler, 1989, 1998, 2006a). From then on, it occurs regularly in central European faunas. An interesting phenomenon occurs at the end of its record, during the Vallesian. Furió et al. (2015) noted that the species not only persisted in the Vallès-Penedès for a very long time, but that the species itself, *D. grycivensis* also had a wide distribution, as it was originally described from the Ukraine. The Austrian *D. engesseri*, described by Ziegler (2006b), is very similar to this species. By contrast, multiple forms seem to develop in the NAFB, such as *D. cf. pachygnathus* from Nebelbergweg, which according to Kälén and Engesser (2001) could represent a new species. Hammerschmiede, close in age, also yielded a *Dinosorex*, but this form has smaller lower incisors than the Swiss form (JP, pers. obs.). The case of *Dinosorex* shows that besides differences in terms of distributions and migrations, basins in fact may also differ in evolutionary dynamics.

3.5. Soricidae

The shrews (Soricidae) are nowadays the dominant group of eulipotyphlans. During the Early and Middle Miocene, Soricidae had not obtained their dominant position yet, and were in diversity at most equal to the Talpidae.

Because of the conservative nature of their molars, the taxonomy of shrews is largely based on the anterior dentition and the morphology of the condyle, characters that are not easily preserved in the fossil record. It is by no means a coincidence that much of the taxonomy was based on finds from fissure fillings (e.g., Doben-Florin, 1964; Ziegler, 1989), where the chances of finding complete mandibles are considerably better. Unfortunately, the Iberian fossil record of the family mostly consists of isolated molars, and its taxonomy is as yet far less elaborated than that of other

Spanish insectivores. Therefore, the discussions here are limited to one genus only. *Paenelimnoecus* is characterized by the strong reduction and even loss of the entoconid, and is as such easily recognizable even if only isolated lower molars are available.

3.5.1. *Paenelimnoecus*

In the Daroca sections, *Paenelimnoecus* appears rather sparsely (Van den Hoek Ostende et al., 2009). It has its first occurrence in the locality of San Marco (zone B, 16.69 Ma), and its last record is in Valdemoros 6B (zone Dd, 14.39 Ma). Van den Hoek Ostende et al. (2009) explained the patchy record of this small shrew by a combination of rarity and the use of a larger mesh size (0.7 mm) in the Middle Miocene localities of the basin. The last appearance date in the basin may therefore lie well before the true extirpation. In the case of the first occurrence, however, the sampling argument does not hold, as all localities containing the tiny elements of eomyids (i.e., up to zone C) have been sampled with a 0.5-mm mesh. Therefore, an appearance in zone B, which is characterized by multiple immigrants, seems highly plausible.

In the Vallès-Penedès Basin, *Paenelimnoecus* appears occasionally in several localities throughout the late Aragonian and Vallesian (MN 7+8 to MN 10). The genus reappears in the central basins in the Turolian (late Miocene), with occurrences in Vivero de Pinos (zone K, MN 11, ~8.1 Ma; Adrover, 1986) and in the southeastern areas (e.g., Van Dam et al., 2014a), and its record continues into the Pliocene (e.g., Minwer-Barakat et al., 2010).

In central Europe, *Paenelimnoecus* is first found in the fissure of Wintershof-West (MN 3), so it occurs earlier than in Spain. It shows a nearly continuous record, but has not – yet – been recorded in MN 6 localities (Ziegler, 2006a). Notably, this gap coincides with the hiatus in the Iberian record.

4. Discussion

As diachronicities between Spain and central Europe are well known from the rodent record (Van der Meulen et al., 2011, 2012), the aim of this paper was to explore whether this holds true for insectivores as well. A number of diachronicities were found (Fig. 1), such as the timing of the extinction of *Galerix* and the entrance of *Parasorex*. Within Spain, both occur earlier in the Vallès-Penedès Basin than in the inland, but *Galerix* shows some temporary extensions of its range, one of them even reaching southern Germany (Prieto et al., 2011).

Other events, such as the extinction of *Desmanodon* at the beginning of the Middle Miocene, seem to occur more or less simultaneously. The lack in overlap in the temporal distribution of *Galerix symeonidisi* and the apparent extinction of *Heterosorex* in central Europe at the time of its entrance in Spain are presumably an artefact of yet insufficiently resolved correlations. Many of the occurrences in Spain, such as those of *Myxomygale* and *Proscapanus*, and the earlier occurrences of *Desmanella*, *Plesiodimylus* and *Chainodus*, can be seen as transient occurrences sensu Van der Meulen et al. (2005).

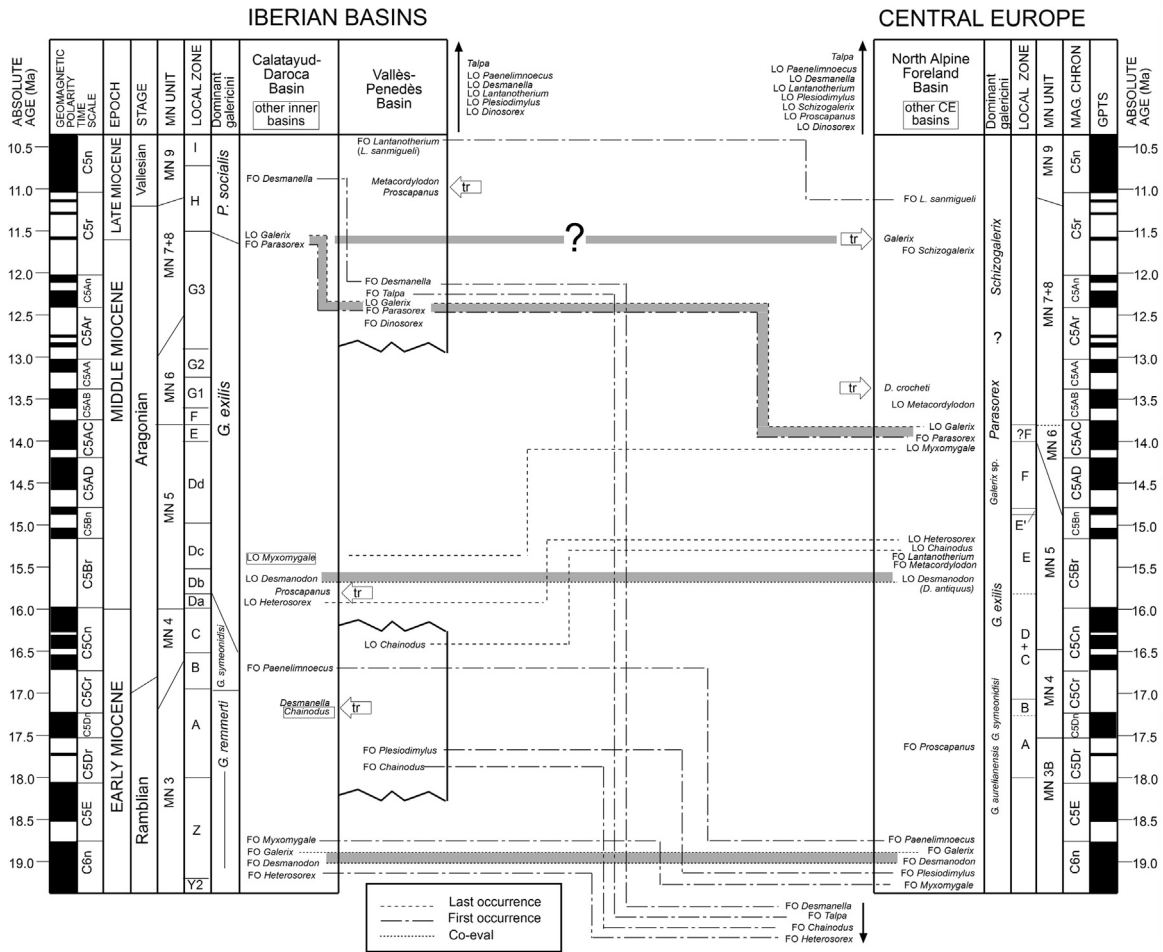


Fig. 1. Selected insectivore events in the Iberian basins Calatayud-Daroca Basin (CDB) and Vallès-Penedès Basin (VPB) compared to the record from the North Alpine Foreland Basin (NAFB). Note that both first and last occurrences of the taxa mostly lie in central Europe. Gray areas indicate notable synchronic and/or associated events in both regions. FO: First occurrence; LO: Last occurrence; tr (in arrow): transient occurrence; generic names included in squares are indicative of occurrences in the nearby areas or basins. Biozonations boundaries follow [Abdul-Aziz et al. \(2008, 2010\)](#) for the NAFB, [Van Dam et al. \(2006\)](#) and [Van der Meulen et al. \(2011, 2012\)](#) for the CDB, and [Casanovas et al. \(2016\)](#) and references therein for the VPB. The Geomagnetic Polarity Time Scale (GPTS) follows [Ogg \(2012\)](#) as figured in [Hilgen et al. \(2012\)](#).

Fig. 1. Sélection des principaux changements fauniques observés chez les insectivores des bassins ibériques Calatayud-Daroca (CDB) et Vallès-Penedès (VPB), comparée à l'enregistrement du bassin d'avant-pays nord-alpin (NAFB). On notera que les premières et les dernières occurrences des taxons se trouvent principalement en Europe centrale. Les zones grisées indiquent les changements fauniques synchrones aux deux régions et/ou leurs événements associés. FO : première occurrence ; LO : dernière occurrence ; tr (flèche) : occurrences transitoires ; les noms de genres encadrés indiquent des occurrences dans des zones ou bassins proches. Les limites des biozones suivent [Abdul-Aziz et al. \(2008, 2010\)](#) pour le NAFB, [Van Dam et al. \(2006\)](#) et [Van der Meulen et al. \(2011, 2012\)](#) pour le CDB et [Casanovas et al. \(2016\)](#) et références incluses pour le VPB. L'échelle temporelle de polarité géomagnétique (GPTS) suit [Ogg \(2012\)](#), comme figuré dans [Hilgen et al. \(2012\)](#).

The largest diachronicities are those involving taxa that enter the Vallès-Penedès in the late Aragonian and early Vallesian, such as *Dinosorex*, *Lantanotherium*, *Talpa*, *Plesiodimylus* (not counting the early transient occurrences) and *Metacordylodon* (Fig. 1). These taxa are restricted to the moist environments of the Vallès-Penedès and seem to be part of a southward extension of humid conditions as proposed by [Madern and Van den Hoek Ostende \(2015\)](#). The heterosoricids and the dimylids become extinct halfway the Vallesian, presumably as a result of increased seasonality. *Talpa*, probably less affected by the climatic change because of its burrowing lifestyle, expands its range to the central basins, and continues to be present in the northern part of Spain until today.

5. Conclusion

Long-term records are an invaluable tool in reconstructing the history of life on earth. If such records are independently dated, comparison between basins allow us to monitor the expansion and retraction of the distribution of taxa. Although many advances have been made, our study suggests that there are still some problems in the correlation between central Europe and the Iberian Peninsula.

Differences between the long-term records of the Spanish Teruel and Vallès-Penedès basins, as well as between the North Alpine Foreland Basin (NAFB) and the nearby Austrian and Hungarian basins, show that significant differences can exist in the fossil record even at relatively

short distances. As such, a detailed understanding of the palaeobiogeography continues to need well-documented localities, both in terms of their stratigraphy and age, as well as the taxonomy.

In many respects, the insectivore record resembles that of the rodents. First occurrences of genera are mostly recorded in central Europe well before these taxa make their appearance in Spain. More so than in rodents, eulipotyphlans have transient occurrences on the Iberian Peninsula. Moreover, some of the diachronicities found are far larger than those in rodents. These phenomena can be linked to the strong preference of insectivores for humidity. Relatively humid environments were either merely temporary available during the late early and middle Miocene, or suitable habitats only appeared during the late middle Miocene or early late Miocene. In the latter case, some taxa (*Plesiodimylus*, *Dinosorex*) remained restricted to the more humid coastal areas. This confirms the strength of Eulipotyphla as palaeoenvironmental indicators. At the same time, our preliminary study shows promise for a far more detailed reconstruction of the distribution of the Miocene ecosystems of Europe in the future.

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