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Distribution and evolutionary history of the Early Miocene erinaceid *Galerix symeonidisi* Doukas, 1986

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The distribution of the Early Miocene galericine *Galerix symeonidisi*, with records from Greece, Germany, Spain and Austria is discussed. The identification of *G.* cf. *symeonidisi* from the Anatolian Çankiri basin is changed into *G.* cf. *uenayae* on the basis of additional material. *Galerix symeonidisi* enters Europe at the MN 3/ MN 4 transition. Differences in the pattern of replacement of the preceding *Galerix* species in Germany and Spain suggest that ecological factors played a role in that replacement. *Galerix symeonidisi* is succeeded by *G. exilis* in Western and Central Europe. A *G. symeonidisi - G. exilis lineage*, as has been proposed in literature, is rejected. The record from the Daroca-Calamocha area (Spain) is instead interpreted as a case of gradual replacement. The replacement is considered the result of an opening of the landscape when conditions became dryer. In Greece, *G. symeondisi* is not replaced by *G. exilis*. In Karidia, a galericine has been found which shows features intermediate between *G. symeondisi* and the oldest representatives of *Schizogalerix*, suggesting that *symeonidisi* might be ancestral to that genus.

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INTRODUCTION

One of the major faunal events in the European Neogene is the change in smaller mammal faunas near the MN 3/MN 4 transition at the beginning of the Aragonian (Fahlbush 1989). During this faunal turnover the glirid/eomyid faunas of Europe are replaced by muroid dominated faunas. This faunal turnover is well documented, particularly in Spain (Daams *et al*. 1999). The focus of the research on this micromammal event lies, however, on rodents. Little is known about the change in the European insectivore faunas at the MN 3/ MN 4 transition. Ziegler (1989, 1990) recognised a number of immigrants in the MN 4 insectivore faunas of southern Germany, but also some new arrivals in MN 3, and thus concluded that in the Early Miocene insectivores entered Europe in two migration waves. Van den Hoek Ostende (2001a) also discussed the insectivore migrations in the late Early Miocene and came to the same conclusion.

In this paper we discuss the distribution of one of the insectivores that appears in the European faunas in MN 4, *Galerix symeonidisi*. The choice for this small erinaceid is prompted by two reasons: it has a large distribution as it is known from Greece (Doukas 1986), Germany (Ziegler & Fahlbush 1986, Ziegler 1990), Austria (Ziegler 1998), Anatolia (Sen *et al*. 1998) and Spain (this paper), and it has a remarkable short life span for an insectivore species, as it is known from MN 4 and the lowermost part of MN 5 only. In order to be able to explain the distribution of *G. symeonidisi* we will also discuss the *Galerix* species that preceded and followed this erinaceid in the various regions.

HISTORY OF RESEARCH

Galerix symeonidisi was described by Doukas (1986) from a lignite mine near Aliveri (Greece; MN 4). The species was considered peculiar in that it possessed many characteristics of the so-called *exilis*-group of *Galerix*, but also possessed a hypocone on the P3, a character found in the *socialis*-group. This is even more notable, since we now believe that the *exilis*-group and *socialis*-group should be assigned to different genera (*Galerix* and *Parasorex* respectively, Van den Hoek Ostende 2001b). Thus, *G. symeonidisi* is the only *Galerix* s.s. species that invariably possesses a hypocone on the P3, although such a hypocone is rarely also found in other species (Ziegler 1983; Van den Hoek Ostende 1992).

The first *Galerix symeonidisi* finds from Germany were described by Ziegler & Fahlbush (1986). They presented material from the fissure fillings of Petersbuch 2 and Erkertshofen 1 and 2, and from the limnic deposits of Rembach, Rauscheröd and Forsthart (all MN 4). On the basis of the German assemblages Ziegler & Fahlbush (1986) suggested that *Galerix symeonidisi* is a direct ancestor of *G. exilis*, which occurs in the same area from MN 5 onwards. They observed a gradual increase in size in their assemblages. The Rembach assemblage was considered to belong to an intermediate form, *G.* aff. *symeonidisi*, since it contains one P3 with a hypocone (*symeonidisi* like), one in which the hypocone is absent (*exilis* like) and a third, worn P3, in which the hypocone is present but small. Schötz (1988) classified the *Galerix* from the German locality of Niederaichbach also as *G.* aff. *symeonidisi*. This assemblage too contains P3 with (N=2) and without (N=4) a hypocone. The faunule from Niederaichbach is placed in MN 5, which makes it the youngest published occurrence of *G. symeonidisi*.

Ziegler (1990) described *G. aurelianensis*, also from southern Germany. This large species appears in MN 3 and thus preceded *G. symeonidisi* in that region. The two species co-occur in the oldest MN 4 localities, viz. the fissure fillings Petersbuch 2 and Erkertshofen 1 + 2. Ziegler suggested in his paper an extra character to distinguish between *Galerix* species. Provided one has suitably large assemblages, the ratio of the connections between protocone, metaconule and hypocone on the M1 and M2 could be used taxonomically. Ziegler based this suggestion on the observation that the protocone-metaconule connection is rare in *G. symeonidisi*, whereas it is almost invariably present in *G. aurelianensis*. In *G. exilis* it is present in c. 35 % of the M1 and c. 75 % of the M2 (Ziegler 1983). *Galerix aurelianensis* and *G. symeonidisi* are also known from the Austrian MN 4 localities of Obersdorf 3 and 4. They are, however, surprisingly rare, and the identification of the species was mainly based on the size of the elements (Ziegler 1998). Equally surprising is the apparent total absence of the genus *Galerix* in the MN 4 lignites of the Polish locality Belchatów C (Rzebik-Kowalska pers. comm.).

Sen *et al*. (1998) classified a mandible from the Anatolian MN 4 locality Semsettin as *Galerix* cf. *symeonidisi*. They did not have the upper molars of the Semsettin *Galerix*, which are necessary to make a more definite species identification. Unlike in Germany, *G. symeonidisi* is in Anatolia preceded by small species of *Galerix*, viz. *G. saratji* and *G. uenayae* (Van den Hoek Ostende 1992; de

Bruijn *et al*. 1992). The *Galerix* assemblages from the uppermost Oligocene/Lower Miocene of Anatolia show that the genus was present in Anatolia at a time that it, or any other galericine, was absent from Europe. On the basis of these finds Van den Hoek Ostende (1992, 2001) concluded that *Galerix* immigrated into Europe near the MN 2/ MN 3 transition. He tentatively suggested that *G. symeonidisi* might also be of Anatolian origin, migrating into Europe near the MN 3/ MN 4 transition (Van den Hoek Ostende 1992).

From literature it is already clear that *Galerix symeonidisi* had a wide geographical distribution. In the following section we present new material from Greece and Spain. We also discuss the *Galerix* cf. *symeonidisi* from the Anatolian MN 4 locality of Semsettin (Sen *et al*. 1998). New material from this locality, as well as from the coeval locality of Hisarçik was graciously put at our disposal for study by Dr. Sevket Sen (Paris), and is used to clarify the taxonomical position of this Anatolian *Galerix* species.

SPAIN

Galerix P3 bearing a hypocone, a tell-tale sign for the possible presence of *G. symeonidisi*, have also been found in the Daroca-Calamocha area of the Teruel Basin (Spain). This area has yielded one of the finest fossil records for smaller mammals in the world. Apart from the type section of the Aragonian and adjacent Aragonian sections, a number of Ramblian sites are found in the vicinity as well. In over thirty years of fieldwork a enormous amount of smaller mammal molars have been found, among which over a thousand elements of *Galerix*. Nevertheless, the fossil record of *Galerix* from the area is not as ideal as one might think. Although there is a lot of material, it is dispersed over more than 150 localities, ranging a period of over 10 million years. Insectivores are relatively rare in the area, and except for a few exceptions *Galerix* constitutes less than 5 % of the fauna, and often even less than 1 %. Thus, most *Galerix* assemblages consist of a few molars only, which makes comparison between assemblages very difficult. Fortunately, there are exceptions. Most Late Aragonian localities studied by De Jong (1988) give a relatively complete picture of the *Galerix* dentition. In the Lower and Middle Aragonian there are only three assemblages with nearly a complete dentition, viz. Artesilla, La Col C and La Col D. Also, the Ramblian localities of Valhondo 1 and Ramblar 7 yielded most of the various elements of *Galerix*.

Figure 1 shows the distribution of P3 with and without a hypocone for *Galerix* in the Daroca-Calamocha area. P3 with a hypocone are found in zones B - Da. In addition two specimens in zone A (Ramblar 1 and 3) and two in zone Dd (Valdemoros 3E) posses a hypocone. P3 without a hypocone are found throughout the sections, also when P3 with a hypocone occur. As we noted earlier, a protocone-metaconule connection is rare in *G. symeonidisi*. Figure 2 shows an increase in the number of M1 and M2 lacking the protocone-metaconule connection in the same range in which P3 with a hypocone occur, viz. zone B - Da.

Another characteristic of *Galerix symeonidisi* is its small size. Figures 3-4 give the ranges for the lengths of the m2 and M2, respectively. These elements were chosen since they are far more often preserved completely than the m1 and M1. In these figures the assemblages of *Galerix* are scored as if they were homogeneous, i.e. contain one species only. The figures show that there is a large *Galerix* in zone A, which is succeeded by a smaller one in zone B. In zones C and Da the average sizes increase, until they reach the level of zone A. In size the *Galerix* assemblage of zones Dc-Dd and E agree with those from the Upper Aragonian, which were identified as *Galerix exilis* by De Jong (1988). The m1 and M1 show a similar, though far more incomplete picture.

Thus, we find a small-sized *Galerix* at the same time that we find P3 with a hypocone

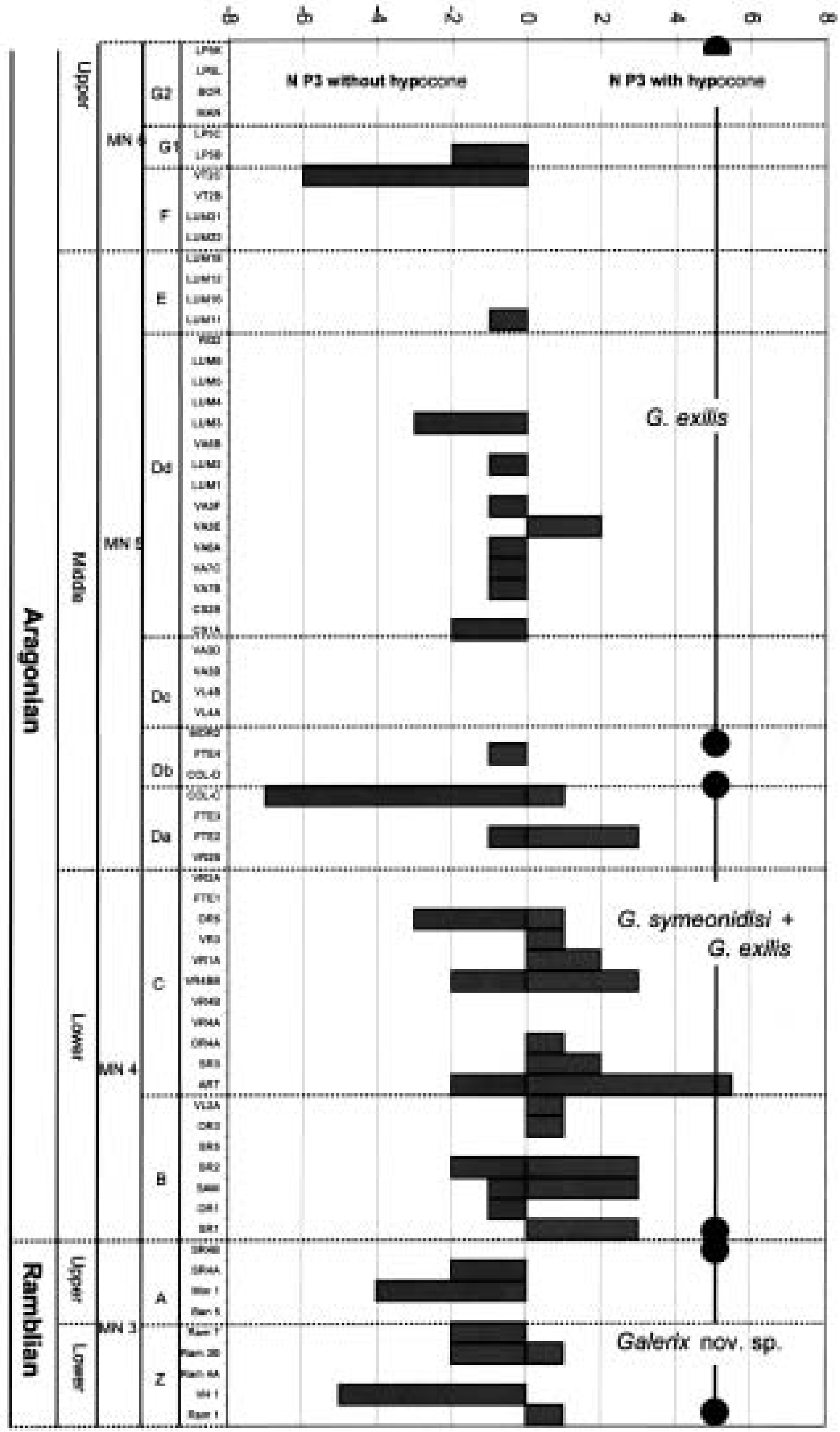

Figure 1 Distribution of the P3 of *Galerix* with and without hypocone in the Daroca-Calamocha area.

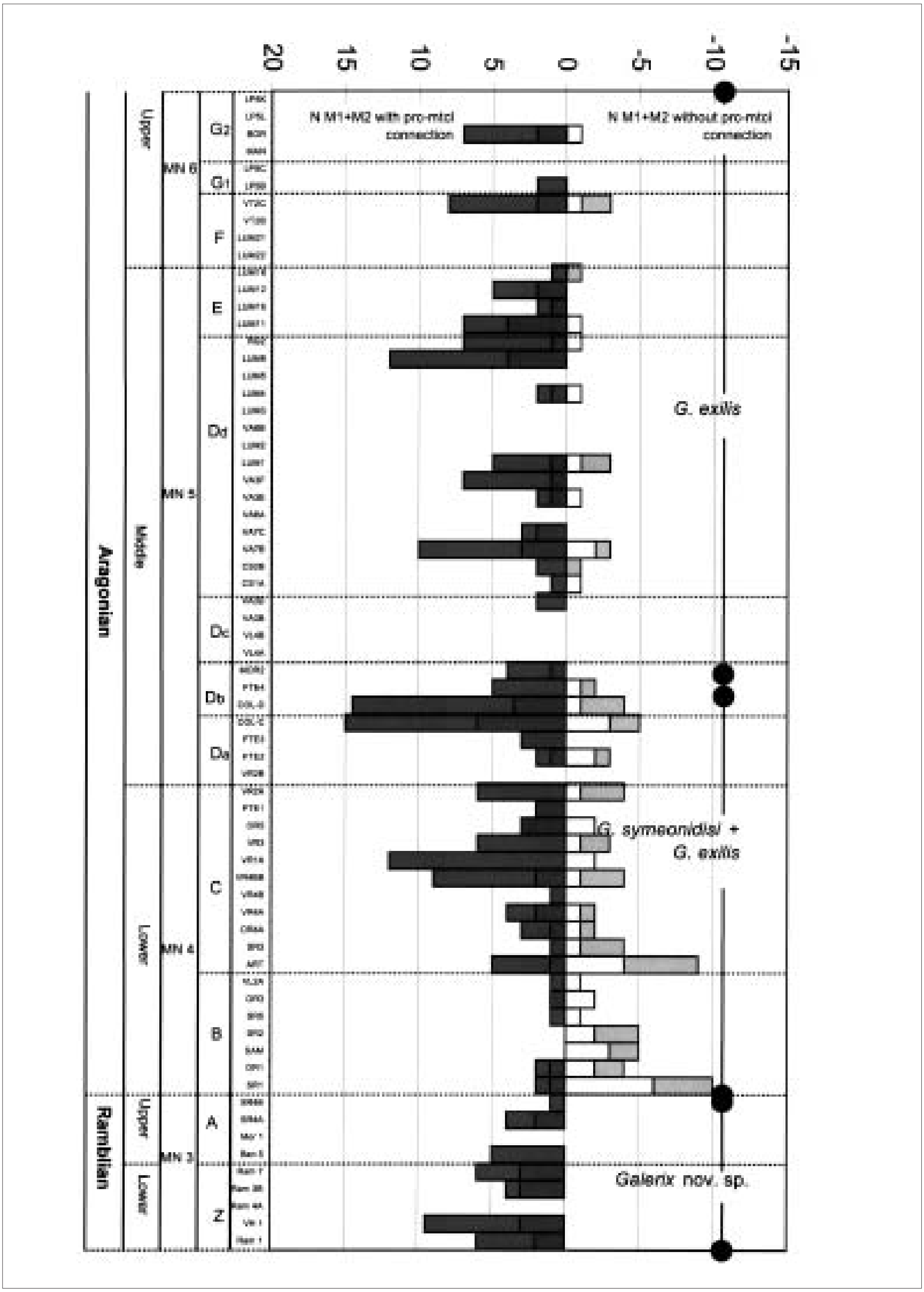

Figure 2 Distribution of the presence/absence of the protocone-metaconule connection on the M1 and M2 of *Galerix* in the Daroca-Calamocha area..

and at which the protocone-metaconule connection of the M1 and M2 is frequently absent. Since this species shows the two main characteristics of *G. symeonidisi*, and since it agrees well in size with the Greek and German assemblages, we assume that it is *G. symeonidisi*. However, not all of the P3 in the ranges in which this species occurs bear a hypocone. This could be explained by the evolutionary trend proposed by Ziegler & Fahlbush (1986), who suggested that *G. symeonidisi* evolves into *G. exilis* by losing the hypocone on the P3 and by an increase in size. At first sight this explanation seems plausible, since the average size increases at the same time the number of P3 with a hypocone decreases (Figs. 3-4).

There is, however, another possible interpretation of the data set. The same pattern would be obtained if we have a small and a large species with and without a hypocone on the P3 respectively, of *Galerix* co-existing in zone B, after which the smaller one dwindles in number and disappears near the Da/Db zone boundary. Demonstrating a bimodal distribution of sizes would of course be the best method for showing the presence of two species in an assemblage. Unfortunately, none of the assemblages contains a sufficient number of one element to make a useful histogram. Nevertheless, there are a number of reasons why we prefer the interpretation of gradual replacement: (1) Although the average values increase gradually in the M2, the maxima suddenly increase halfway zone C, whereas the minima suddenly increase in Db. (2) In some cases, the average lies close to the maximum, indicating an uneven distribution of sizes. This is apparent in the m2 of La Col C and La Col D (uppermost Da and lowermost Db, respectively). (3) The ranges are often very large. Although a deviation of 10 % above and below the median is not uncommon in smaller mammals, it is highly unlikely that such a wide range is encountered several times in our small samples. Large variation is particularly found in the upper part of zone C-Db, the range in which the protocone-metaconule connection and the P3 without a hypocone become more numerous.

Our model contradicts the model proposed by Ziegler & Fahlbush (1986). They made quite a convincing argument that *Galerix symeonidisi* evolves into *G. exilis*. Their assemblages seem to indicate an increase in size and the only assemblage in which both P3 with and without a hypocone were found, Rembach, does not show the large variation in size found in the Spanish assemblages. An important argument in favour of a *symeonidisi-exilis* lineage was the presence in Rembach of a P3 with a hypocone which was "worn, but certainly already reduced", and thus of intermediate from. However, the illustration of this P3 (Ziegler & Fahlbush 1986, plate 1, fig. 27) shows that the circumference at the base of the worn hypocone is similar in size to that of the hypocone of the unworn P3 from the same locality. Based on this photograph, we do not concur that the hypocone was "certainly already reduced". Ziegler & Fahlbush (1986) classified the *Galerix* from Rembach as *G.* aff. *symeonidisi*. Later, the *Galerix* from Niederaichbach was also classified as *G.* aff. *symeonidisi* (Schötz 1988), also on the basis of the presence of both types of P3. This assemblage, however, does show a large variation in size. Whereas some elements fall in the size range of the German *symeonidisi* assemblages, other fall in the upper part of the size range of *G. exilis* (Schötz 1988, figs 7, 8). Our model seems therefore also applicable to the German assemblages.

Since we are dealing with very small and mixed assemblages, giving a description of the Spanish *Galerix symeonidisi* is not straightforward. The size ranges of *G. symeonidisi* and the larger species overlap and, given the similarity in morphology, most individual elements cannot be identified. The characteristics of *G. symeonidisi* can, however, be deduced from our data set: (1) The hypocone of the P3 is not as well developed as in the Greek or German assemblages, where it is sub-equal in volume to the proto-

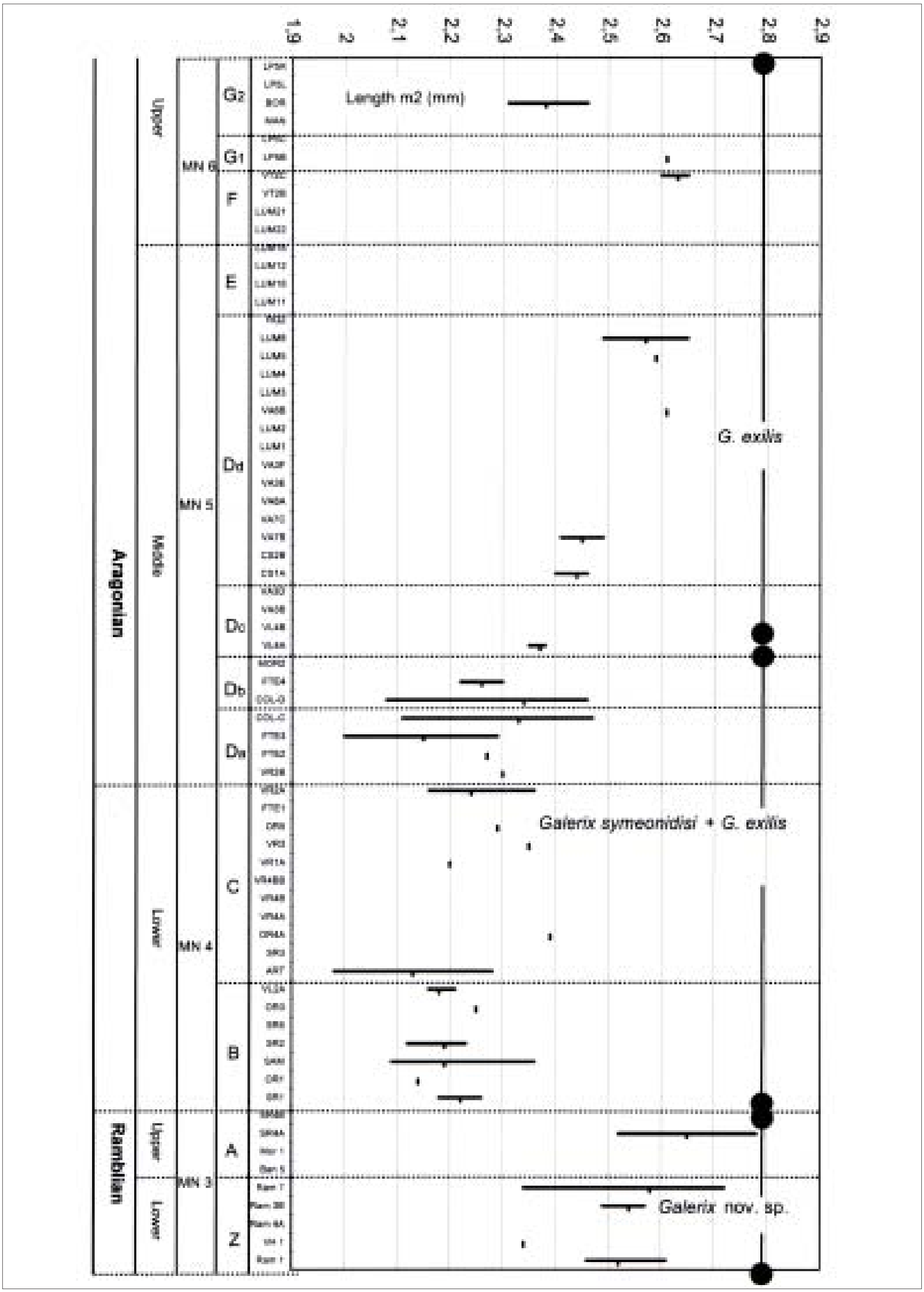

Figure 3 Distribution of the lengths of m2 in the Daroca-Calamocha area. Data have been presented per assemblage, also if the presence of two species is suspected.

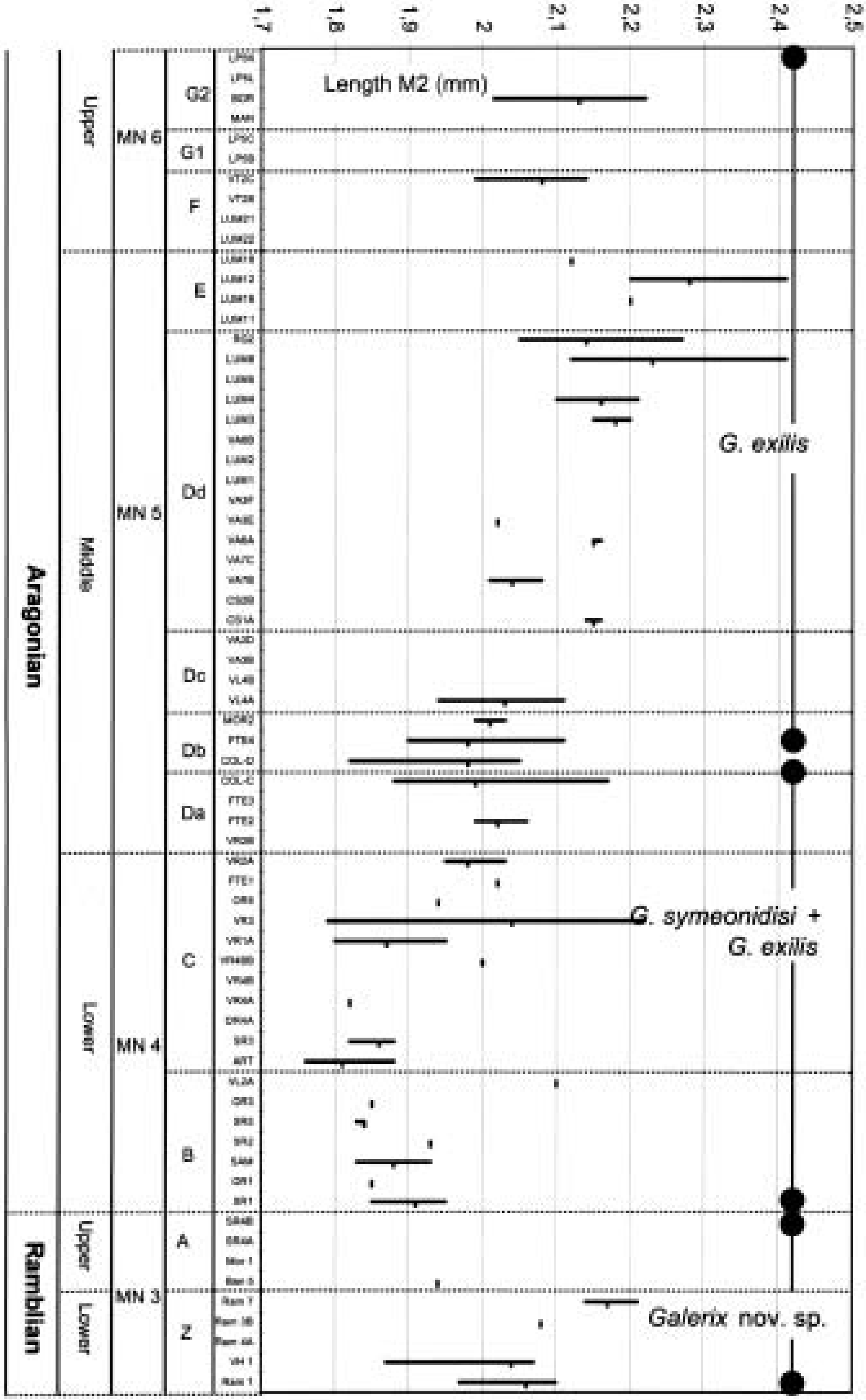

Figure 4 Distribution of the lengths of M2 in the Daroca-Calamocha area. Data have been presented per assemblage, also if the presence of two species is suspected.

cone of the premolar. In the Daroca-Calamocha area the hypocone is usually smaller than the protocone and may even be just a tiny bulge behind that cusp. The P3 with a hypocone in the Ramblian localities Ramblar 1 and Ramblar 3 and the Middle Aragonian locality Va 3E are considered to belong to larger *Galerix* species found in the Ramblian and Middle and Upper Aragonian, respectively. (2) The posterior cingulum of the m1 and m2 is never connected to the entoconid-hypoconid crest. (3) The posterior arm of the metaconule of the M1 and M2 never reaches the posterolabial corner of the molar. (4) The paraconid of the p4 may be cone-shaped or elongated, but is never connected to the protoconid by a paralophid.

The *Galerix* assemblages from the Middle Aragonian are similar to the younger ones described by De Jong (1988), and can also be classified as *G. exilis*. Thus, like in Germany, the Spanish *G. symeonidisi* assemblages are followed by *G. exilis* assemblages. In Germany the *symeonidisi* assemblages are preceded by *G. aurelianensis*. This species is morphologically close to *G. exilis*, but larger. The morphological differences are so small, that Ziegler (1990: 18) remarked on the holotype of the species: "If one knew this specimen only, an identification as *Galerix* aff. *exilis* would be justified, since except for the larger measurements and the position of the foramen mentale there are no differences with *Galerix exilis* from Steinberg and Goldberg."

The Ramblian *Galerix* species in Spain is similar in size to *G. exilis* from the Upper Aragonian, but somewhat larger than assemblages from the Middle Aragonian. It is about 10 % smaller than *G. aurelianensis* from Germany, with which it shares the high frequency of the presence of a protocone-metaconule connection. In the Spanish Ramblian *Galerix* this connection is even invariably present. The species will be described in detail elsewhere (Van den Hoek Ostende in press) and is here designated *Galerix* nov. sp.

The question remains, whether the second *Galerix* in the mixed assemblages with *G. symeonidisi* is a continuation of the Ramblian *Galerix* or an earlier occurrence of *G. exilis*. Figures 3-4 show a drop in size between *Galerix* nov. sp. and the mixed assemblages, whereas the higher part of the ranges in the Lower Aragonian is in line with those from the Middle Aragonian. Therefore we assume that the second species in the mixed assemblages is *G. exilis*.

GREECE

The Spanish and German fossil record of *Galerix symeonidisi* are fairly complete and show both the entry and the disappearance of the species, as well as the species preceding and following *G. symeonidisi*. To date, the Greek record is far more incomplete. For a long time the only Greek MN 4 locality was Aliveri, the type locality of *G. symeonidisi*. A joint Greek-Dutch project, however, has yielded two new localities in Thrace, Karidia and Komotini. Karidia, which is placed in the upper part of MN 4, has yielded a large number of galericine molars. The galericine of this locality, which will be described in full elsewhere, is remarkable in that it has a number of characters in common with *Schizogalerix*, such as a posterior arm of the metaconule that continues to the posterolabial corner of the M1/M2. This character is also known from the genus *Parasorex*, which is found in Central and southwestern Europe in the late Middle Miocene-Pliocene. Further research will be needed to determine in what genus the species should be placed. However, it is clear that it is not *Galerix exilis* and, hence, that the succession of galericines in MN 4/MN 5 in Greece differs from that in Spain and Germany.

ANATOLIA

Sen *et al*. (1998) described a well-preserved mandible of *Galerix* from the Anatolian MN 4 locality of Semsettin. Unfortunately, the lower dentition of *Galerix* shows few characters that can be used for identifying species and at the time of description no elements from the upper jaw were known. They compared the Semsettin mandible with *G. uenayae*, known from the Anatalian MN 3 locality of Keseköy (Van den Hoek Ostende 1992) and with *G. symeonidisi*. The p4 of the Semsettin mandible has a well-developed metaconid, whereas the metaconid of *G. uenayae* is weak and often absent. The paraconid of this premolar too shows a stronger development than is usual in *G. uenayae*. They also stated that the protoconid-paraconid connection in *G. ueanayae* is broken or weak, and that the p3 is more slender in the Semsettin specimen. Furthermore, *G. uenayae* is smaller than the Semsettin galericine. Sen *et al*. (1998) concluded that their specimen showed the greatest resemblance to *G. symeonidisi* and classified the mandible as *G.* cf. *symeonidisi*.

Since we are interested in the distribution of *Galerix symeonidisi*, the identity of the Semsettin mandible is important to our study. Luckily, Semsettin has yielded additional material since the mandible was described, and *Galerix* has been found in the nearby locality of Hisarçik, so that the preliminary identification can be checked. In Semsettin an additional p4 has been found. In this specimen, the metaconid is reduced to a mere bulge on the postero-lingual flange of the protoconid. The paraconid is voluminous and conical. There is no paralophid. The posterior cingulum is connected to the entoconid-hypoconid crest in one fragment of an m2. This configuration is also known from the molars in the mandible. However, in an isolated m2 the posterior cingulum lies well below the entoconid-hypoconid crest. Two fragmentary upper molars have been found. In both specimens the protocone-metaconid connection is absent. A labial fragment of a P3 has also been found. Unfortunately, the lingual cusps are missing, so that it is not known whether or not the P3 possessed a hypocone.

The nearby and coeval locality of Hisarçik has yielded two complete *Galerix* P3. Both of these lack the hypocone. Apart from the P3, two M2 fragments have been found. In both fragments the protocone-metaconule connection is present. The only *Galerix* p4 from Hisarçik has a well-developed metaconid and an elongated paraconid.

Assuming that the *Galerix* from Semsettin and Hisarçik belong to one and the same species, this species cannot be *G. symeonidisi*. *G. symeonidisi* is characterised by a hypocone on the P3, and the P3 from Hisarçik lack this character. The isolated p4 from Semsettin resembles that of *G. uenayae* in having a very weak metaconid. On the other hand, the metaconid is well developed in the p4 from Hisarçik. The observation of Sen *et al*. (1998) that the paralophid of the m1 and m2 is weak or notched in *G. uenayae* is presumably based on the illustrations of unworn specimens given by van den Hoek Ostende (1992). However, with wear this ridge appears to become stronger and more continuous. We have observed no major differences in the development of this crest between *G. uenayae* and the material from the Anatolian MN 4 localities. It is true that the material from Semsettin and Hisarçik is somewhat larger that *G. uenayae*, but *G. symeonidisi* is even smaller. Thus we believe that the material from Semsettin and Hisarçik is better classified as *Galerix* cf. *uenayae*. Still, one has to bear in mind that this identification is based on scanty material and on the assumption that we are dealing with the same species in both localities.

The locality of Hisarçik is also interesting in another respect. This locality has also yielded, mostly fragmentary, material of *Schizogalerix* next to *Galerix*. This is the first record of a co-occurrence of the two genera and also the oldest record of *Schizogalerix*. The oldest record published thus far is *S. pasalarensis* from the Anatolian MN 5 locality Pasalar (Engesser 1980).

GEOGRAPHICAL VARIATION

Doukas (1986) gave the following diagnosis for *Galerix symeonidisi*: "A small-sized *Galerix* species of which p2 is longer than p3; the P3 bears two lingual cusps and its posterior side is conspicuously emarginated."

According to van den Hoek Ostende (2001b) a p2 longer than a p3 is a diagnostic character for the genus *Galerix*. Following this classification, species previously placed in *Galerix* with a p2 shorter than a p3 should be placed in the genus *Parasorex*. This would leave only the presence of a hypocone on the P3 as a distinctive character, since the strong emargination of the posterior side of the P3 is a direct consequence of the presence of this cusp. However, the presence of a hypocone would be a sufficient for distinguishing *G. symeonidisi* from other species, since it is the only species in *Galerix* s.s. that has this extra cusp.

Apart from the shared presence of the hypocone of the P3, the assemblages from the various regions are very similar in size. There are, however, some remarkable morphological differences between the various assemblages. Although the Spanish assemblages possess a hypocone on the P3, it is by no means as well developed as it is in the Greek or German assemblages. Often it is only a slight elevation on the lingual flange behind the protocone and as such resembles the hypocone that can be found rarely in other species of *Galerix* such as *G. exilis* (Ziegler 1983) or *G. saratji* (van den Hoek Ostende 1992).

In the type locality (Aliveri) the development of the metaconid of the p4 is variable. It may even be absent. In the German and Spanish assemblages the metaconid is well developed. According to Ziegler & Fahlbusch (1986) the paraconid of the p4 is individualised and conical or connected to the protoconid by a paralophid. A similar variation is found in Greece and Spain, where the paraconid may be conical or blade-like, but a true paralophid is never formed. Dr. Ziegler kindly informed us that the term paralophid used for the German material is the same as a blade-like paraconid in our terminology. Thus the development of the paraconid of the p4 is the same for the various regions.

The posterior cingulum of the m1 and m2 may be connected to the hypoconid-entoconid ridge in the Aliveri assemblage. This configuration is also found in most of the m1 and m2 from the Erkertshofen 2 assemblage and rarely in Petersbuch 2, but never in the other German assemblages, nor in Spain.

Thus, the Spanish material differs in various details from that from the type locality Aliveri. Since the German assemblages are intermediate in morphology between the Greek and Spanish ones and since there is no difference in size, we believe it is best to place all assemblages in one species. Furthermore, the observed variation is not uncommon in *Galerix* species. The most remarkable variation is the presence of a connection between the posterior cingulum and the hypoconid-metaconid connection in the Greek and German assemblages. This character is known from *Schizogalerix* (Engesser 1980) but not, with the exception of *G. symeonidisi*, found in any species of *Galerix*.

THE PATTERN

Galerix appears in Europe in MN 3 (Ziegler 1990; van den Hoek Ostende 1992, 2001a), presumably as an immigrant from Anatolia. The species, *G. aurelianensis* in Germany and *Galerix* nov. sp. in Spain, can readily be derived from the Anatolian *G. saratji* which is morphologically similar, but smaller.

The Spanish record shows that *Galerix symeonidisi* enters near the MN 3/MN 4 transition. In Germany too the species is found in the oldest MN 4 locality in the region, Petersbuch 2. A conspicuous difference between the German and the Spanish record is that in Spain *Galerix* nov. sp. disappears at the time *G. symeonidisi* enters, whereas in Germany *G. aurelianensis* continues into MN 4. In Petersbuch 2 it is even the predominant *Galerix* (60 %), becoming more rare in the younger fissure fillings of Erkertshofen 2 and 1 (*c*. 20 % and 3 %, respectively; Ziegler 1990).

Galerix symeonidisi is present in Europe throughout MN 4. The rarity of the species in the Austrian MN 4 localities of Obersdorf 3 and 4 (Ziegler 1998) and its absence in the Polish MN 4 locality of Belchatów C

(Rzebik-Kowalska pers. comm.) suggest that the northeastern limit of the range of the species lay somewhere in the eastern part of Central Europe. The increasing number of P3 without a hypocone and the increasing averages in Figures 3-4 show that the species was already becoming rarer in the later part of MN 4 in the Daroca-Calamocha area. The presence of *Galerix symeonidisi* in the Da-assemblages in the Daroca-Calamocha area as well as in the German locality of Niederaichbach shows that the species survived into the lowermost part of MN 5. After that, it became extinct and is no longer found after Db, nor in German MN 5 localities such as Puttenhausen (Ziegler & Fahlbush 1986) and Maßendorf (Schötz 1988). *G. exilis* takes over completely and is the predominant galericine in western Europe throughout MN 5-MN 7/8. Engesser & Ziegler (1996) listed *G.* cf. *symeonidisi* from the Swiss MN 6 localities of Rümikon and Schwamendingen, but Dr Engesser kindly informed us that this is a preliminary identification based on scanty material (pers. comm. 1999).

A different pattern unfolds in the eastern Mediterranean. In the absence of Greek MN 3 localities, we do not know which galericine preceded *Galerix symeonidisi* in that area. We have one MN 3 record of Galericinae from Anatolia, *Galerix uenayae* from Keseköy (van den Hoek Ostende 1992). In Greece *G. symeonidisi* is not, as in western Europe, succeeded by *G. exilis*, but by a *Schizogalerix* -like galericine. Unfortunately, in the absence of localities we do not know which Galericinae lived here in the Middle Miocene. In Anatolia *Galerix* is succeeded by *Schizogalerix*. The small assemblage from Hisarçik shows that the two genera co-occurred in MN 4.

The pattern is summarised in Figure 5. Note that the allocation of Anatolian Early Miocene localities to the MN-zonation is open to discussion and should be regarded as preliminary at best.

ECOLOGY

The distribution of a species is primarily determined by two factors. Physical barriers may limit the distribution. The disappearance of such barriers, for instance when land bridges are formed, may give rise to migrations. The second main factor in the distribution of a species is its ecology. It must find suitable habitats. Changes in the paleoenvironment may lead to extinction or give rise to evolutionary changes.

In order to comprehend the distribution of *Galerix symeonidisi* in time and space, it is necessary to have some ideas about the environments that it preferred. The ecology of a species can be inferred from the sedimentary facies of the localities in which it is found and from species in the same fauna of which the ecology is known. The ecology can also be inferred from the habitat of extant relatives. However, this is of little use for the Galericinae, since they had a far wider distribution in the past and probably inhabited more ecological niches than they do nowadays (Ziegler 1983, Van den Hoek Ostende 2001a). All extant Galericinae live in forested environments, and *Echinosorex* is even semi-aquatic. However, fossils of *Galerix* were found in Somosaguas (Spain), a locality that is thought to represent a very dry palaeoenvironment (Luis & Hernandez 2000).

Galerix symeonidisi was first described from a lignite quarry (Aliveri, Greece). The material from Komotini/Karidia described above is also derived from lignite beds. In Germany the species was found in fissure fillings (Petersbuch 2, Erkertshofen 1 + 2) as well as in limnic sediments (Forsthart, Rembach and Rauscheröd). The Rauscheröd fauna was collected directly below a lignite bed (Ziegler & Fahlbush 1986). The faunas from the Daroca-Calatayud area in Spain were collected from mudstones, indicative for a shallow lake environment (Daams *et al.* 1999). The fact that *Galerix symeonidisi* was found in lignitic beds is a first indication that this species preferred a rather humid environment. Jung & Mayr (1980) discussed the

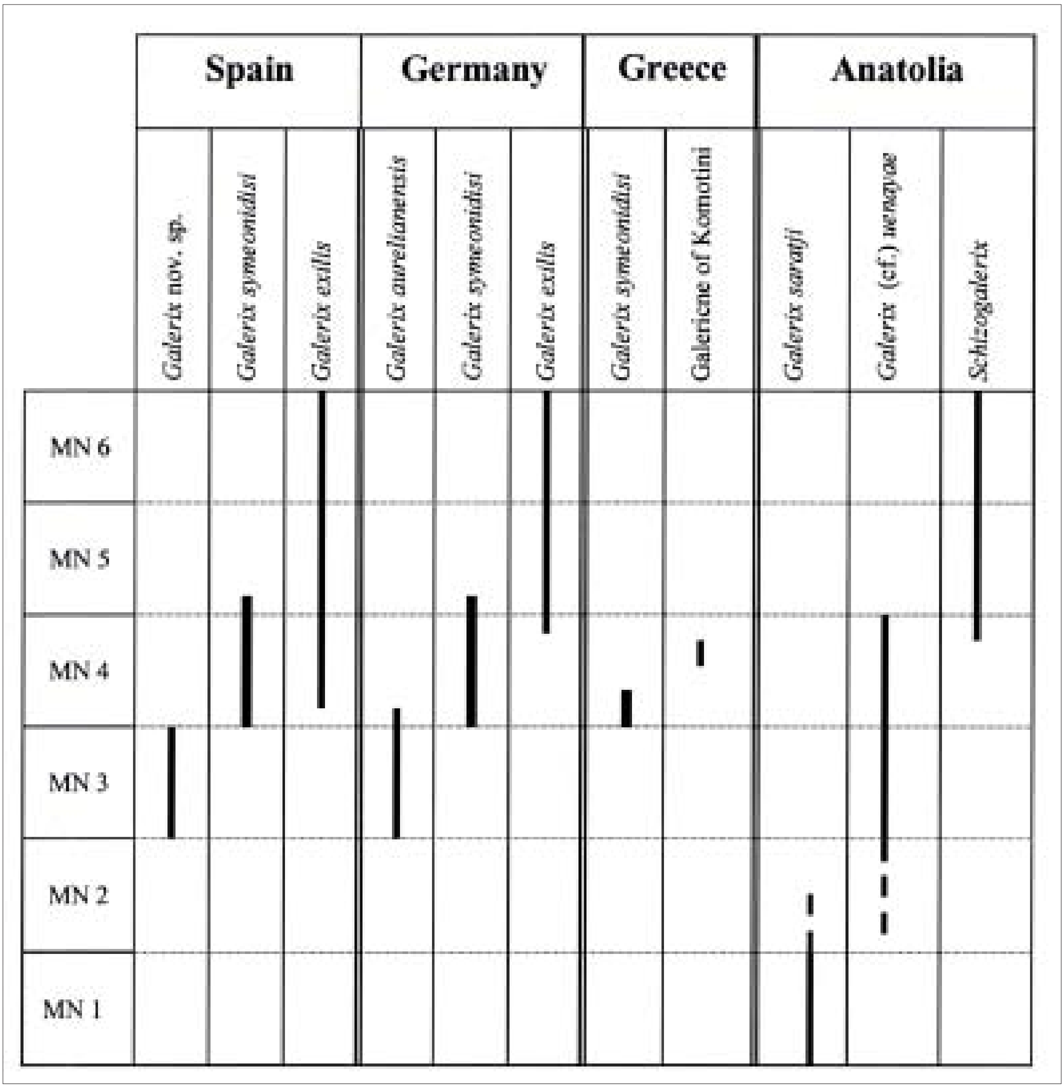

Figure 5 Distribution of *Galerix* species in Early Middle Miocene for the various regions.

palaeoenvironments of the German localities. On the basis of palaeobotanical studies on the environment and the smaller mammals they came to the conclusion that the faunas from Erkertshofen, Forsthart, Rembach and Rauscheröd lived in a wooded environment with semi-deciduous forests. According to their studies the forest gave way to a far more open landscape in MN 5-6. Van der Meulen & Daams (1992) reconstructed a similar pattern from the rodent assemblages in the Ramblian and Aragonian from the Daroca-Calamocha area. According to their model, the climate was still fairly humid in the range in which *Galerix symeonidisi* occurred in the area (zone B-Da), though not as humid as the end of the Ramblian. They assumed an open forest environment for zone B, and varied environments for zones C-Da, followed by a dryer, more open landscape in the following (sub)zones.

A second indication that *G. symeonidisi* had a preference for humid environments is found in the accompanying faunas. In the type locality of Aliveri several rodent species indicative for a humid, wooded environment were found, such as a beaver (De Bruijn & Van der Meulen 1979), four species of flying squirrel (De Bruijn *et al*. 1980) and an eomyid (Alvarez Sierra *et al*. 1987). The insectivores of the locality also suggest a humid environment. *Heterosorex* is believed to be a forest dweller (Doukas 1986) and a dimylid was found. The dentition of Dimylidae is adapted for a diet consisting of snails (Hürzeler 1944; Müller 1967). Since snails thrive best in humid conditions, Dimylidae can be considered indicative for moist environments. So far, accompanying faunas confirm this ecological preference for the family. Finally, two species of mole, *Myxomygale* and *Desmanodon*, were found. Burrowing moles need moist soils to make their tunnels. Moles that make surface tunnels through the litter are also indicative for wooded environments.

Many of the indicators of a humid environment found in Greece, are also known from the German faunas with *Galerix symeonidisi*. According to Heissig (1978) beavers were found in Petersbuch 2 and Erkertshofen 2, although these are not mentioned by Ziegler & Fahlbusch (1986). They mention the presence of beavers in Erkertshofen 1 and Rauscheröd. Flying squirrels are rare in the German fauans. They are represented in Petersbuch 2 by one element only and are not known from Erkertshofen 2 or Rauscheröd, but have been found in Erkertshofen 1, Rembach and Forsthart (Ziegler & Fahlbusch 1986). Eomyids are found in all of the faunas. The insectivore faunas from the German localities are also similar to that of Aliveri. Both *Heterosorex* and Dimylidae are present, and the mole diversity is even higher than in Greece.

In contrast, the Spanish faunas in which *Galerix symeonidisi* occurs contain very few humid species. No beavers have been found and only two elements of flying squirrels are known from zones B-Da. Eomyids are found in zones B and C and in the oldest locality of zone Da (Col A). Dimylids have not been found and mole diversity is low (*Desmanodon* is the only talpid). Notably, many of the localities in zone C contain *Heterosorex*. We do not consider the absence of these indicators of humidity in contradiction to our hypothesis that *G. symeonidisi* prefers a relatively wet environment. It is clear that the environment was dryer than in the coeval German and Greek localities, but *G. symeonidisi* is here also more rare than in those areas and is often found in mixed assemblages. Furthermore, an analysis of all rodents shows that the environment in zones B-Da was at least more humid than in the following period (van der Meulen & Daams 1992).

Galerix aurelianensis probably preferred even more humid environments than *G. symeonidisi*. We base this assumption on the sudden demise of the species at the beginning of the Aragonian in Spain, which coincides with a drop in humidity (van der Meulen & Daams 1992). In Germany, which as we noted above was probably more humid at that time, *G. aurelianensis* continued into MN 4. According to Ziegler (1983) *G. exilis* lived in relatively dry environments. This is corroborated by the absence of the species in the MN 5/6 lignites of Germany (Hambach: Ziegler & Mörs 2000) and Poland (Belchatów B: Rzebik-Kowalskae pers. comm.), and the presence in the ‘dry’ locality of Somosaguas (Luis & Hernandez 2000).

EXPLAINING THE PATTERN

Both in Germany and in Spain *Galerix symeonidisi* appears in the oldest MN 4 localities. This suggests that it was one of the immigrants that entered Europe at the beginning of the Aragonian. Whether *G. symeonidisi* is of Anatolian origin, as suggested by Van den Hoek Ostende (1992), is open to doubt. As was already indicated in that paper, a direct descent from the Anatolian MN 3 species *G. uenayae* is unlikely, and the proposed evolutionary model in which *G. symeonidisi* is a split-off from the *saratji*-*uenayae* lineage seems cumbrous. *Galerix symeonidisi* spread quickly through Europe. Its success cannot be explained by migration only. Probably ecological factors played a role as well. This could explain why the species quickly replaced the preceding *Galerix* species in Spain, whereas the change was more gradual in Germany. While spreading, the species underwent some changes. The geographical variation observed may be related to the adaptation to local environments. It is noteworthy that the largest morphological differences exist between the *symeonidisi* assemblages from the wettest (the Greek) and the dryest (the Spanish) localities.

After the Early Aragonian (MN 4), conditions in Europe became dryer still. This probably lead to the extinction of *Galerix symeonidisi*. The species was gradually replaced by *G. exilis*, which was presumably better adapted to less humid conditions. This gradual replacement is best observed in the records from the Daroca-Calamocha area. They also show a gradual impoverishment of the insectivore fauna. *Heterosorex* disappears before *G. symeonidisi*, *Desmanodon* soon after. In Germany the *Galerix symeonidisi* faunas are also followed by *G. exilis*.

The record of the Galericinae in the eastern Mediterranean for the Early Miocene is far more incomplete than the western European record. There is a fairly complete record in Anatolia, that shows that *Galerix*, which was present throughout the Early Miocene, is being replaced by the genus *Schizogalerix*. The oldest and most primitive representative of this genus, *S. pasalarensis*, was described from the MN 5 locality of Pasalar (Engesser 1980), but the assemblage from Hisarçik shows that the genus was already present in MN 4, at which time it co-occurred with *Galerix*. In Anatolia too, conditions became less humid near the MN 3/MN 4 transition (de Bruijn *et al*. 1996), which may have played a role in the faunal change. However, the youngest *Galerix* species in that region is not *G. symeonidisi* but *G. uenayae*.

In Greece we have two MN 4 localities, Aliveri and Karidia. Although geographically close to Anatolia, the Greek record cannot simply be combined with the Anatolian one since the faunas from the two areas represent two different bioprovinces in the Early Miocene (van den Hoek Ostende 2001b). Still, the record of the Galericinae in the two areas may be linked, since an evolutionary lineage can be reconstructed from *G. symeonidisi*, through the Karidia galericine to *Schizogalerix*. *G. symeonidisi* already resembles *Schizogalerix* in some aspects. Like *Schizogalerix*, this species invariably bears a hypocone on the P3. The posterior cingulum of the lower molars of *Schizogalerix* connects to the entoconid-hypoconid ridge. This character, which is also found in *G. symeonidisi* from Aliveri, is in *S. pasalarensis* not yet fully developed. The evolutionary stage for this character is similar for the assemblages from Aliveri and Pasalar.

In *Schizogalerix* the posterior arm of the metaconule of the M1 and M2 connects to the postero-labial corner of the molar. This configuration is not known from Aliveri, but is found in the galericine of Karidia. Thus *Galerix symeonidisi* seems to be a plausible ancestor for *Schizogalerix pasalarensis*. Possibly conditions in the eastern Mediterranean changed less dramatically at the beginning of the Middle Miocene than they did in western Europe.

Whereas the *symeonidisi* populations in western Europe became extinct, they had the chance to evolve into *Schizogalerix* in the east. An indication for this less dramatic change is the continuing presence in Anatolia of the talpid *Desmanodon* (Engesser 1980), a taxon found in all faunas in which *Galerix symeonidisi* was encountered.

The distribution of a species in time and space is controlled by physical barriers and environment. Once the environment changes, there are two options for the species living in that environment. Either they become extinct, or, if circumstances allow it, they adapt to the changing environment. It is our working hypothesis that both scenarios apply to *Galerix symeonidisi*. In western Europe the species was gradually replaced and disappeared, in southeastern Europe and southwestern Asia it adapted and evolved into a new genus. Further study of the Greek and Anatolian assemblages from MN 4 is needed to confirm this hypothesis.

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