ELSEVIER

Palaeogeography, Palaeoclimatology, Palaeoecology 145 (1999) 215–230

PALAEO

A succession of Miocene rodent assemblages from fissure fillings in southern France: palaeoenvironmental interpretation and comparison with Spain

Jean-Pierre Aguilar [a], Gilles Escarguel [a], Jacques Michaux [a,b,*]

[a] *Institut des Sciences de l'Evolution — UMR 5554 — Université Montpellier II, Place Eugène Bataillon, C.C. 064, 34095, Montpellier Cédex 5, France*

[b] *Laboratoire de Paléontologie des Vertébrés, E.P.H.E., UMR 5554, Université Montpellier II, Place Eugène Bataillon, C.C. 064, 34095, Montpellier cédex 5, France*

Received 11 March 1998; revised version received 23 June 1998; accepted 24 June 1998

Abstract

An Early to Late Miocene sequence of rodent assemblages from southern France has been quantitatively studied. The resulting pattern seems very similar to a contemporary sequence from central Spain (Calatayud–Teruel Basin). The fossil mammal-bearing localities are of different types: mainly karst infills in France and localities situated in sedimentary basins in Spain. In order to interpret the fossil record, a comparison has been made between southern France faunas of similar age but collected in karst infills and in basin deposits. There seems to be no difference between the two kinds of faunas and thus there is no indication that karst infills systematically give a picture of drier and more open environments. Both types of localities may give a similar relative abundance of taxa and when differences exist they can be attributed to local conditions. The comparison between southern France and the Calatayud–Teruel Basin (central Spain) shows that: (1) similar trends occurred in the two areas; (2) differences between spectra were more important during the late Early Miocene than during the Middle Miocene; (3) the shift between the late Early Miocene and the Middle Miocene environments in southern France does not seem to be correlated with a general drop in temperatures as inferred from the analysis of central Spain faunas.

Keywords: rodents; Miocene; France; Spain; karst; paleoenvironment

1. Introduction

Chronological sequences of rodent assemblages are good tools for reconstructing the evolution of Neogene environments. In order to estimate their efficiency, it is useful to see how climatic changes are recorded by rodent faunas from two adjacent geographical areas or to compare contemporary sequences from such areas. In the present case, a comparison has been made between southern France and central Spain for both areas are known by their important continental Neogene fossil record. In the last 20 years, more than 100 southern France fossil mammal-bearing localities have been discovered and studied, mainly in the Languedoc–Roussillon

* Corresponding author. Fax: +33 467 143610; E-mail: michaux@isem.univ-montp2.fr

0031-0182/99/$ – see front matter
PII: S0031-0182(98)00103-5

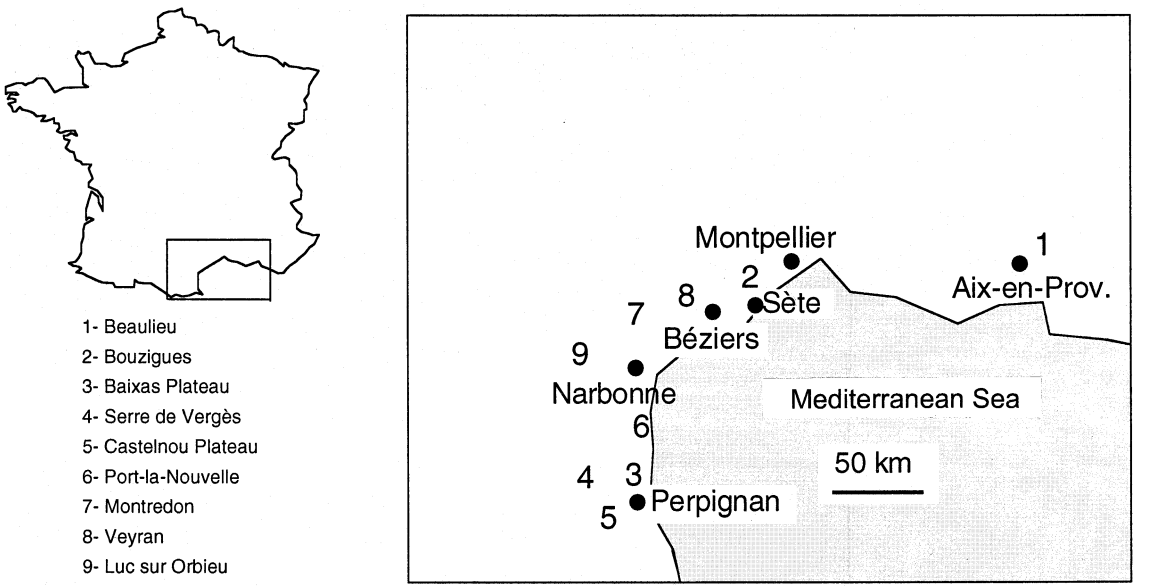

Fig. 1. Location map of the Miocene fossil mammal-bearing localities of southern France.

Province. Most of them are karst infills and many of them are Middle Miocene in age. They are distributed over a small area of a few square kilometres near Baixas (Roussillon, Eastern Pyrenees). These sites document a rich Neogene small mammal fauna, especially for a late Early Miocene to Middle Miocene time interval. Rodents but sometimes bats are especially abundant in these sites (Aguilar, 1980, 1995; Aguilar et al., 1986a,b, 1991a,b, 1994, 1995, 1996a; Escarguel and Aguilar, 1997; Faillat et al., 1990; Legendre, 1982; Sigé et al., 1996). Most of the material has been described (Aguilar and Michaux, 1990; Michaux et al., 1990). The fossil mammal-bearing localities and the list of their rodent species are given in Figs. 1 and 2, and in Appendix A.

Apart from latitudinal or other geographical differences, several factors may affect the interpretation of data. An important one is the type of fossil mammal-bearing locality. On the one hand, fossiliferous karst infills, and on the other hand sedimentary basin localities (fossils being preserved in swamp, lake, or stream sediments, etc.). One question usually raised is the possible influence of site characteristics on faunal compositions, which may distort the interpretation of the relative abundance of taxa. As assemblages are mainly collected from karst infills in France, and from sedimentary basin localities in Spain, this question must be discussed before interpreting the environmental evolution of the Miocene as recorded by the rodent faunas. Another factor that may affect the interpretation is the precision and the accuracy of the correlation of the two sequences. This point will be discussed further as there are still some disagreements between authors about the correlations.

2. The faunal sequence in southern France

2.1. Biochronology and correlation

Biochronology has been established on the basis of evolutionary lineages of rodents. 24 different biochronological levels have been recognized for a time span of ca. 10 million years (Aguilar and Michaux, 1987). The evolutionary lineages belong to Eomyidae (Escarguel and Aguilar, 1997), Eucricetodontinae (Aguilar et al., 1996a), Cricetinae — mainly *Megacricetodon* (Aguilar et al., 1994; Aguilar, 1995) — and Murinae (Aguilar et al., 1991a,b, 1995; Aguilar and Michaux, 1996). Twenty levels belong to the late Early and Middle Miocene and four to the Upper Miocene. Correlations have been established with important European fossil

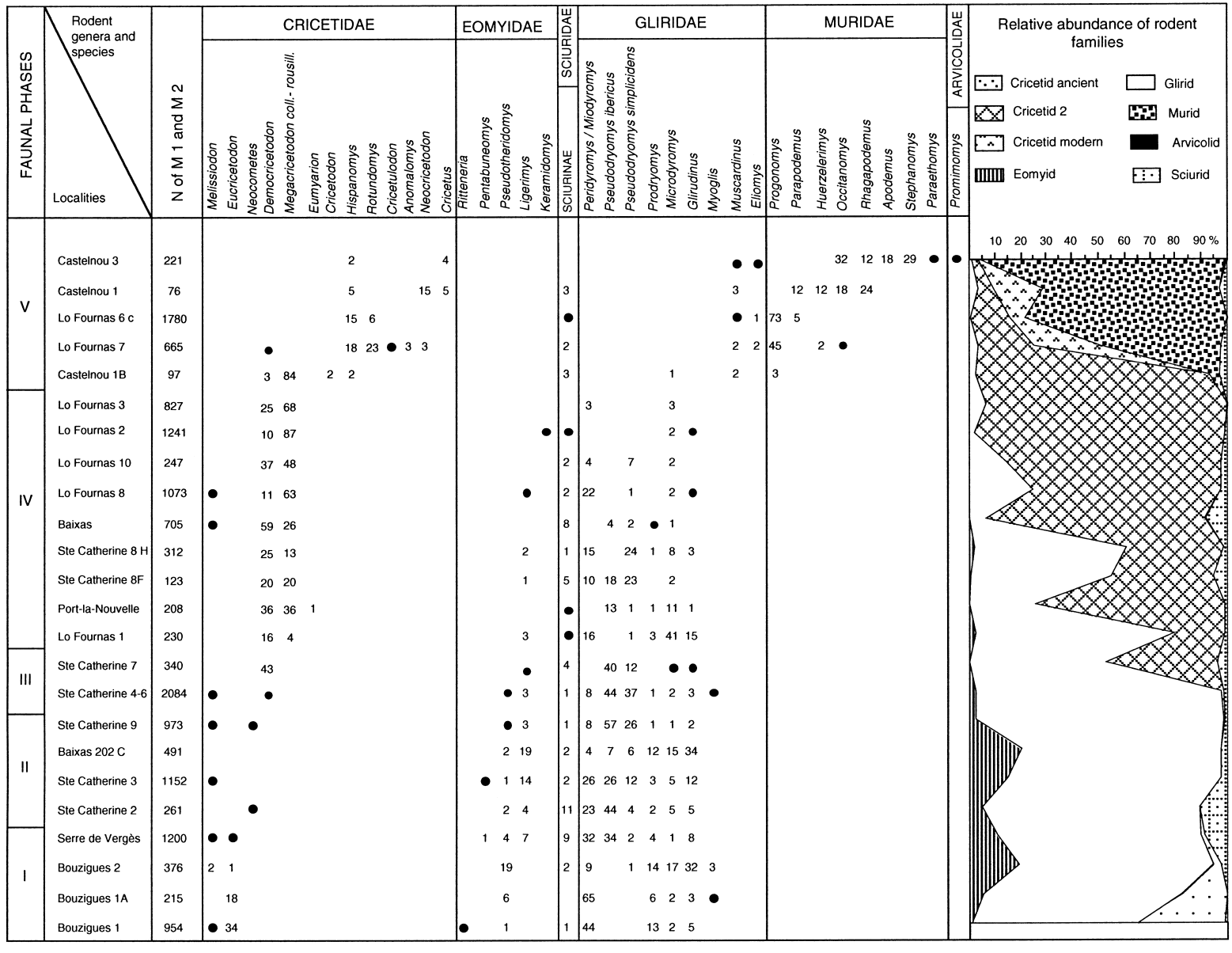

Fig. 2. Distribution and relative abundance of the rodent genera and/or species (left) and of rodent families (right) in Miocene faunas from karst infills from southern France.

mammal-bearing localities of Miocene age. They are based on evolutionary stages in lineages but faunal events have also been used: the first occurrence of *Democricetodon*, *Megacricetodon* and Murinae (for the latter, their first known occurrence in Spain and in France, respectively in Pedregueras 2c and Castelnou 1B). The characteristic time interval named the 'cricetid vacuum' (Daams and Freudenthal, 1990) has also been considered as isochronous in both areas. For the Late Miocene, the French karst infills of Castelnou 3 and Castelnou 1 are correlated (Aguilar et al., 1991a,b, 1995) respectively with La Alberca and Los Mansuetos — Lo Fournas 6c, and Lo Fournas 7 is supposed to be slightly younger than Montredon (Aguilar and Michaux, 1996). For the Middle and the late Lower Miocene, Bouzigues 2 and Serre de Vergès (Aguilar et al., 1996a; Sigé et al., 1996) are respectively older and younger than Estrepouy. The karst infills of Baixas 202 c and Ste Catherine 9 (Escarguel and Aguilar, 1997; Aguilar et al., 1997) are respectively older and younger than the basin locality of Beaulieu which has been recently radiometrically dated (Ar/Ar method): 17.5 ± 0.3 Ma (Aguilar et al., 1996b). Artenay is situated between Ste Catherine 9 and Ste Catherine 4 and 6, and La Romieu between Ste Catherine 8 and Baixas. The karst infills of Lo Fournas 8, Sansan, and Manchones are roughly contemporaneous, and similarly Lo Fournas 3 may be contemporaneous with La Grive M. Castelnou 1B is slightly younger than La Grive L3 (Aguilar, 1995; Aguilar et al., 1997).

2.2. Relative abundance of rodent taxa

The relative abundance of taxa has been calculated based on the total number of first and second molars, i.e. some 16 000 teeth from 24 localities. When several localities have a similar age, the locality used for calculation is that with the richest fauna and the most complete list of taxa. Results are given in Fig. 2. Five faunal phases, ranging from the oldest to the youngest, can be distinguished.

Phase 1 (time interval: Bouzigues 1–Serre de Vergès): abundance of glirids, and at a lesser degree of eomyids, and Eucricetodontinae the abundance of which is progressively decreasing.

Phase 2 (Ste Catherine 2–Ste Catherine 9): dominance of glirids and eomyids is characteristic. It is worth noting that *Neocometes* is present in the levels of Ste Catherine 2 and 9 (Aguilar et al., 1997). This time interval corresponds to the 'cricetid vacuum' of Daams and Freudenthal (1990).

Phase 3 (Ste Catherine 4 and 6–Ste Catherine 7): eomyids and glirids begin to decrease in number. The lower boundary of Phase 3 is determined by the first occurrence of the genus *Democricetodon*.

Phase 4 (Lo Fournas 1–Lo Fournas 3): glirids still decrease in number. The lower boundary of Phase 4 is determined by the first occurrence of the genus *Megacricetodon*.

Phase 5 (from Castelnou 1B up to Castelnou 3): first occurrence of the Murinae and of the modern cricetids; glirids are few in number and the Cricetinae disappear after Castelnou 1b.

Two remarks have to be made. First, the genus *Cricetodon*, which is listed in the karst infill of Castelnou 1b, is only known in southern France at the basin locality of Luc sur Orbieu which has the same age as Lo Fournas 8. The two latter localities are contemporaneous to Sansan (Aguilar, 1995). Second, *Paraethomys* is only known in France from La Tour and Castelnou 3: both localities are Late Miocene in age and younger than the first levels with *Paraethomys* recognized in Spain. The fossil record of this genus in France is probably much more incomplete than it is in Spain.

2.3. Comparison between karst infills and basin localities

It is frequently argued that a fauna collected in a karst infill gives a faunal spectrum different from that obtained in a basin locality. The former is considered (Van de Weerd and Daams, 1978) as indicating drier and more arid environments than the latter. In fact, it is usually observed that species related to water environments such as castorids are frequently lacking in fissure filling faunas that are otherwise rather diverse. Both characteristics can be expected because nocturnal birds of prey are generally at the origin of bone and tooth accumulations. As both types of fossil mammal-bearing localities are present in southern France, we have tried to evaluate the possible distortion introduced by the composition of the fissure filling faunas. However, as there are much more faunas from karst infills than from basin lo-

calities, the comparisons have been conducted only for two rather short time intervals. The first comparison involves late Early Miocene assemblages with the localities of Baixas 202 c, Ste Catherine 9, and Beaulieu, and the second one corresponds to Middle Miocene assemblages with the localities of Lo Fournas 8, Luc sur Orbieu, and Veyran.

2.3.1. Baixas 202 c and Ste Catherine 9 vs. Beaulieu

The Beaulieu fauna has been collected from brackish and lacustrine sediments (Aguilar, 1981; Aguilar et al., 1996b; Escarguel and Aguilar, 1997). The relative abundance of the rodent taxa are not similar in the three localities (Fig. 3a): eomyids and the genus *Melissiodon* are dominant in Beaulieu, two clear-cut differences with the spectra obtained from karst infill faunas of the same age. As eomyids are usually considered to be associated with wet environments (Alvarez Sierra et al., 1990), their abundance can be probably explained by local conditions which are also indicated by the facies of the fossiliferous sediments. *Melissiodon* is usually rare in basin localities as well as in karst infills from southern France. This rodent is also rare in the basin localities of similar age from the Iberian Peninsula. On the other hand, it is quite frequent in central Europe in karst infills as well as in basin localities (Hrubesch, 1957; Ziegler and Fahlbusch, 1986; Fejfar, 1990) and it may be indicative of a wet environment (Fejfar, 1990). Thus, the high number of *Melissiodon* in Beaulieu may simply indicate particular taphonomic and/or local environmental conditions. In the faunas of Baixas 202 c and Beaulieu, the forest glirids which are also dominant indicate similar environments. In this case, there is no distortion caused by the type of fossil mammal-bearing locality (Fig. 4).

2.3.2. Luc sur Orbieu, and Veyran vs. Lo Fournas 8

The fossil bearing sediments of Luc sur Orbieu (Aguilar and Magné, 1978) correspond to brackish environments and those from Veyran correspond to palustrine ones (Aguilar, 1980). Both localities are contemporaneous with Lo Fournas 8 (Aguilar, 1995). Despite the presence of *Cricetodon* in Luc sur Orbieu, the three sites have similar faunal spectra.

According to these two examples, it is not possible to suggest that within the same area, karst infill faunas are indicative of drier environments than faunas collected in basin localities.

2.4. Interpretation of the sequence of karst faunas

The reconstruction of Neogene continental environments in Western Europe is often based on the analysis of sequences of small mammal assemblages (rodents but also bats) (Van de Weerd and

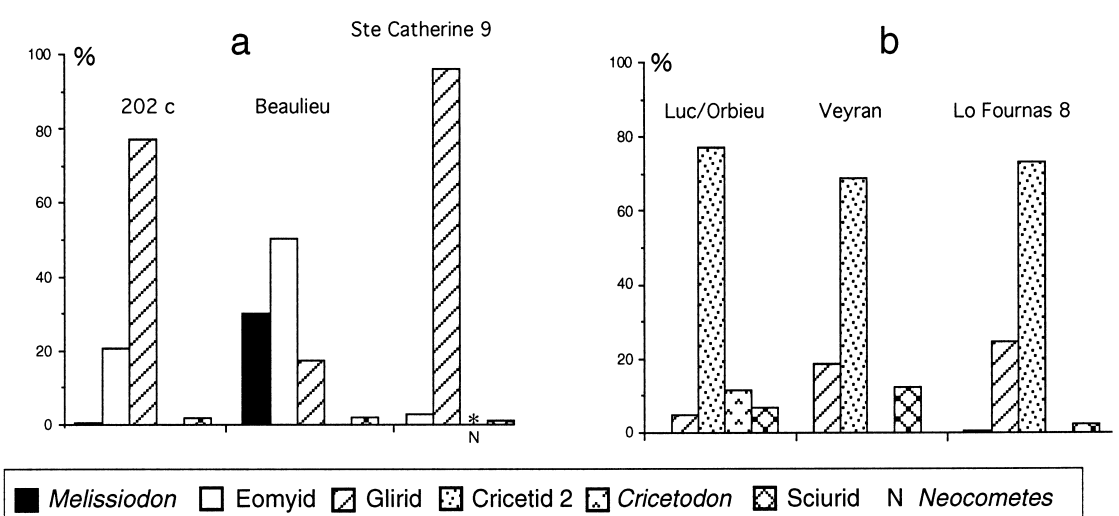

Fig. 3. Comparison between the composition of the rodent faunas from karst infills and basin localities of similar age in southern France: (a) late Early Miocene localities, and (b) Middle Miocene localities.

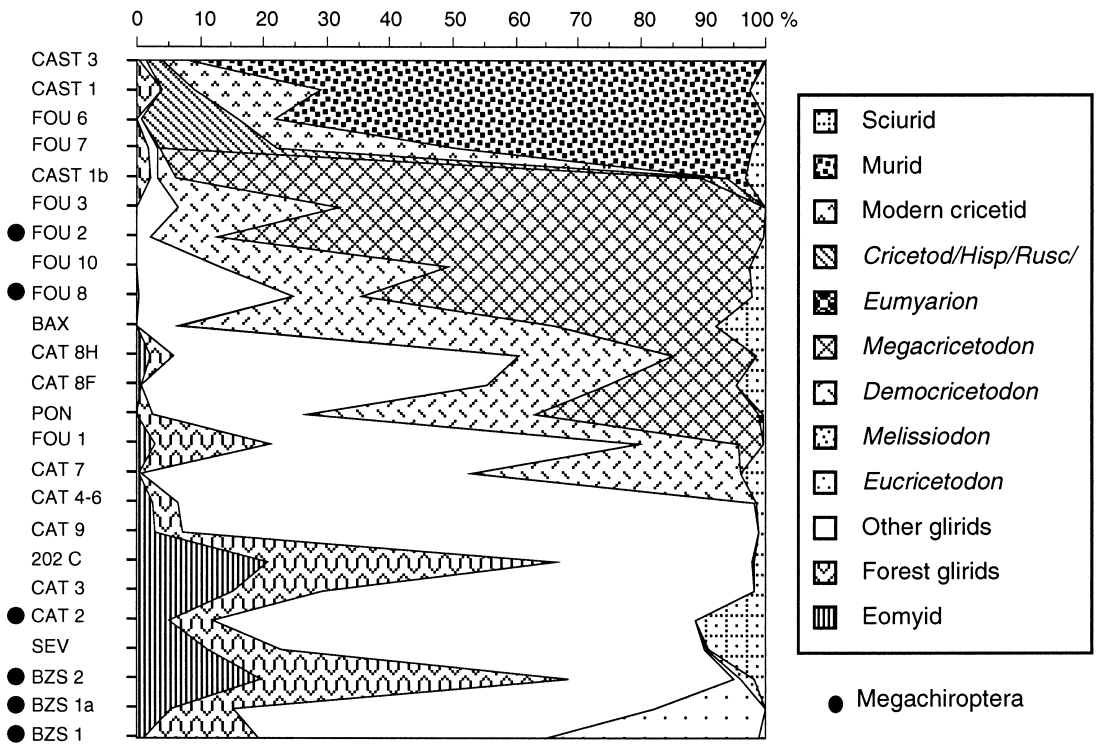

Fig. 4. Relative abundance of rodent families or genera from the late Early to Late Miocene of southern France.

Daams, 1978; Mayr, 1979; Legendre, 1982; Mein, 1984; Daams and Van der Meulen, 1984; Aguilar et al., 1986a,b, 1996b; Sigé and Aguilar, 1987; Daams et al., 1988; Aguilar and Michaux, 1990; Van der Meulen and Daams, 1992). The inference of the ecology of extinct taxa from dental characters or from their phylogenetic relationships with extant species is difficult. However, a few hypotheses about the adaptations of some extinct taxa have been proposed. Inferences from dental patterns have been done for the glirids with living relatives (Van der Meulen and De Bruijn, 1982). It is generally considered that eomyids have been living in humid environments (Van de Weerd and Daams, 1978; Daams and Van der Meulen, 1984; Alvarez Sierra et al., 1990) or in a closed environment (Daams et al., 1988; Fejfar, 1990; Van der Meulen and Daams, 1992). The recent discovery (Storch et al., 1996) of an Oligocene flying eomyid, *Eomys quercyi*, may corroborate such an interpretation. As a working hypothesis, the relative abundance of the glirids *Microdyromys* and *Peridyromys* (the former is considered to indicate rather high temperatures) (Van der Meulen and Daams, 1992) are used to infer warm conditions. In southern France (Fig. 4), there is a correlation ($r^2 = 0.772$; Student *t*-test: $t = 8.783^{***}$) between the abundance of eomyids and that of forest glirids (sensu Daams et al., 1988). During the Early and the Middle Miocene, the abundance of another glirid, *Prodryomys*, follows (Fig. 5) the curve of the forest glirids ($r^2 = 0.489$; Student *t*-test $t = 3.526^{**}$) and thus *Prodryomys* may also be indicative of a forest environment as suggested by Mayr (1979). In southern France, bats have been used for independent complementary information, a forest and warm environment being corroborated by fruit-bats. *Rousettus* is present in the three levels of Bouzigues and in Ste Catherine 2, Lo Fournas 8 and 2. According to this, a forest landscape in a sub-tropical to tropical climate can be inferred. Other bats from Bouzigues also allow one to infer a warm climate and a low forest cover, nevertheless a little more open in the case of Bouzigues 2 (Aguilar et al., 1997). Similarly, bats found at Port la Nouvelle have extant relatives living in tropical and

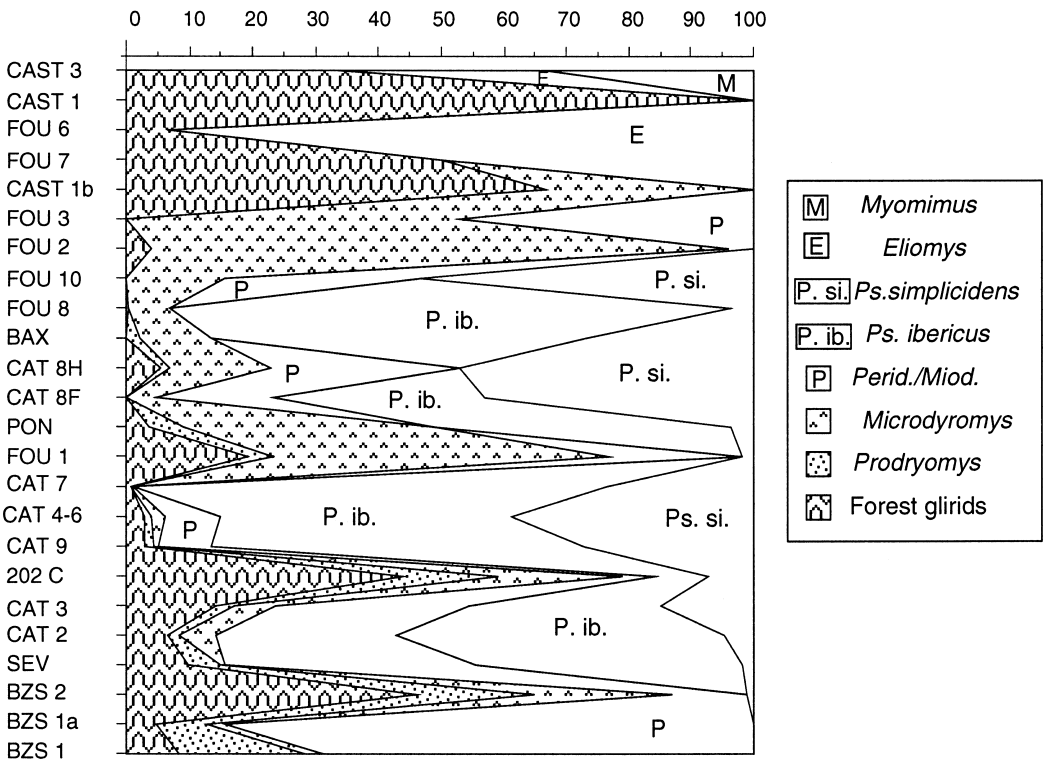

Fig. 5. Relative abundance of glirid genera in southern France from the Early to Late Miocene.

sub-tropical climates and indicate that the lowland area was characterized by a rather arid climate, a low vegetation of shrubs, but with swampy areas near the sea-shore (Legendre, 1980, 1982).

In conclusion, southern France was characterized by a rather dense cover of shrubs during the late Early Miocene (Late Aquitanian– beginning of the Burdigalian, e.g. Bouzigues 1 to Ste Catherine 9). The abundance of *Glirudinus* in Bouzigues 2 and Baixas 202c may be related with such a vegetation cover. At the end of the Burdigalian and then during the Middle Miocene, the landscape became more open. Such a change occurred at the time of the Tethys closure in the East. The new Mediterranean paleogeography and the related new climatic conditions favoured the spread of allochthonous groups of mammals such as the proboscideans or the cricetine rodents (for the latter, their first occurrence is at the level of Ste Catherine 4 and 6). There is no sign of any drop in temperatures at this time for bats indicative of warm conditions are still present (Port la Nouvelle, Lo Fournas 8, and 2) and *Microdyromys* is still abundant (Fig. 5). It is only near the Middle–Late Miocene boundary that the forest environment developed again.

3. Comparison between southern France and central Spain

Two analyses have been made: (a) of the changes in the whole rodent fauna during the Early–Late Miocene time interval, and (b) of the relative abundance of eomyids and forest glirids for the late Early to the Middle Miocene time interval.

3.1. Changes in the faunas (Fig. 6a,b)

The quantitative composition of the faunas are given in Fig. 6: on the left side for the Calatayud–Teruel basin, and on the right side for southern France. In Fig. 6a, faunal sequences are arranged according to the biochronological scale used for each region. Correspondence between the two successions

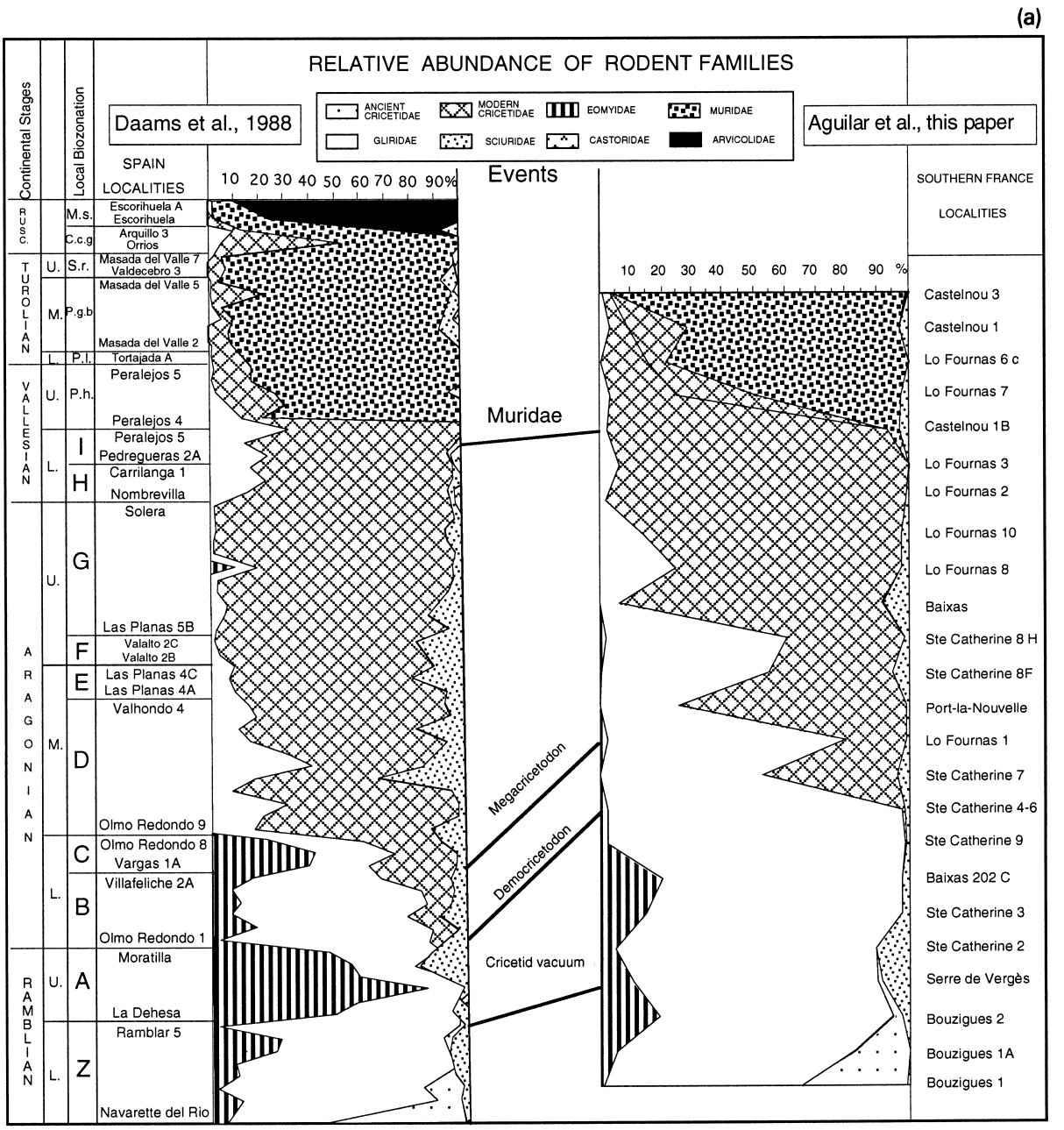

Fig. 6. Relative abundance of rodent families in southern France (right) and central Spain — Calatayud–Teruel Basin — (left) from late Early to Late Miocene: (a) heavy lines indicate possible correlation between the sequences.

are indicated by heavy lines, each of them corresponding to a biochronological event. In Fig. 6b, the central Spain sequence of faunas has been calibrated on the basis of the southern France biochronological scale, the four biochronological events been considered isochronous in southwestern Europe. A fifth point of correlation has been added: the correlation between Lo Fournas 8 and the base of zone G. Some

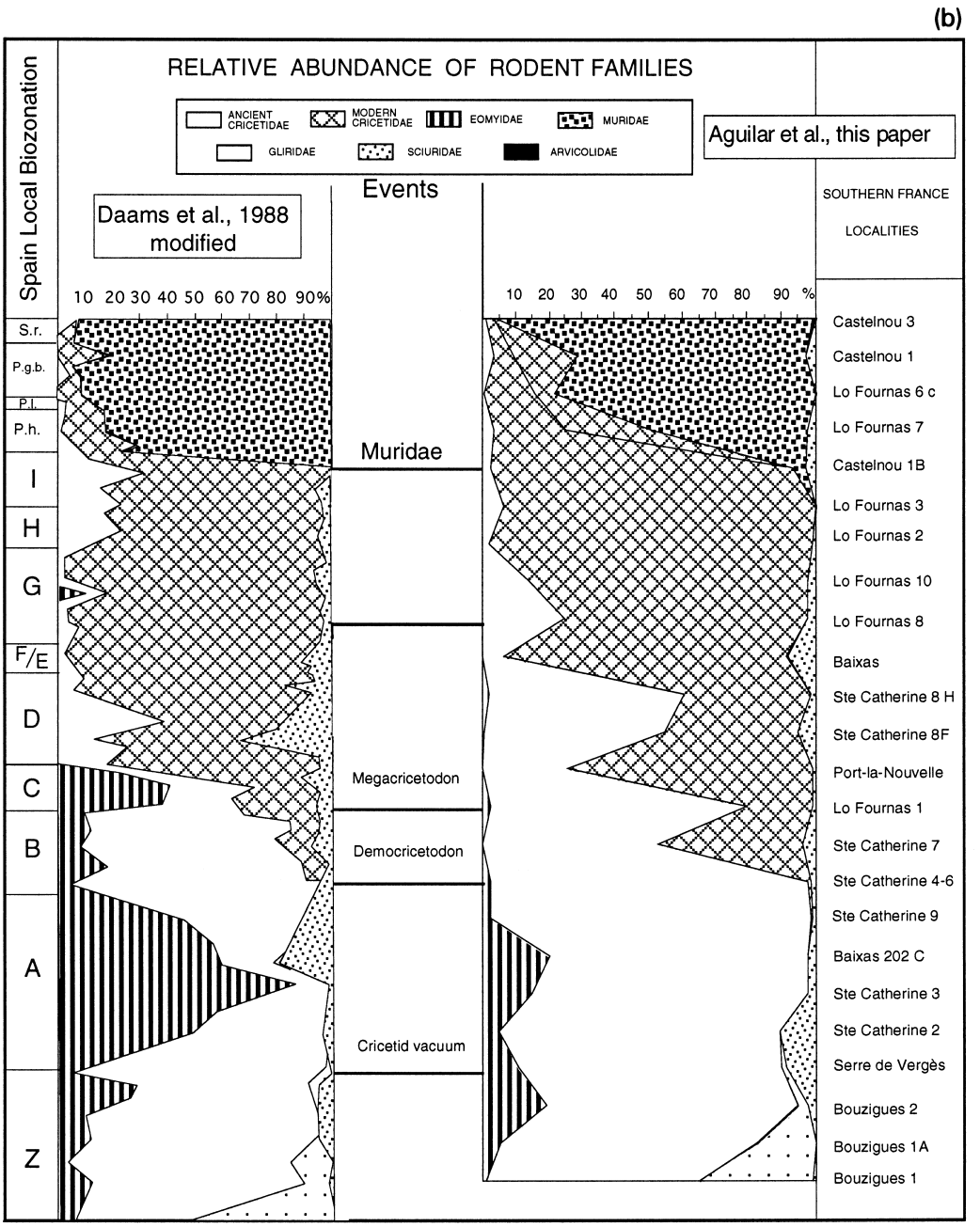

Fig. 6 (continued). (b) Same data as in (a), but the Calatayud–Teruel Basin sequence has been calibrated on the basis of the biochronological scale used for southern France.

comments are needed here for there are still different opinions about the calibration of the biochronological scales or biochronological events in Spain and in France. For example, the first occurrence of *Democricetodon* is ca. 17 to 17.5 Ma for Aguilar et al. (1996b) and ca. 16.7 Ma for Alvarez Sierra et al. (1997). The correlation between the Middle Miocene localities of Sansan, Manchones and Lo

Fournas 8 is here used. It is based on the comparison between the rodent faunas (Aguilar et al., 1994; Aguilar, 1995). But there are also other problems: the estimated age of Manchones, at the base of zone G2 (Van der Meulen and Daams, 1992), is ca. 13.3 Ma and Sansan is considered to have an age ca. 15.2 to 15 Ma according to a magnetostratigraphic study (Sen, 1996). The boundary between the Aragonian and the Vallesian is also a matter of discussion. Although more accurate correlations would be needed, comparisons can nevertheless be made. Comparisons as they result of the correlations used in the present work, show similar general patterns as well as some differences which have to be noticed:

– Eomyids are always more abundant in the Calatayud–Teruel basin than in southern France. The highest values in each area occur during the 'cricetid vacuum' or are a slightly earlier in southern France; this could correspond to the type of fossil locality, but another interpretation is possible (see below);

– Except at the beginning of the Late Miocene, glirids are always more abundant than eomyids and cricetines in southern France;

– Relative abundance of cricetids and of murines change in parallel directions in the two regions.

3.2. Change in abundance of eomyids and forest glirids

These two groups of rodents give interesting information (Fig. 7). Correlations are the same as in Fig. 6b. Eomyids are abundant in the Early and the

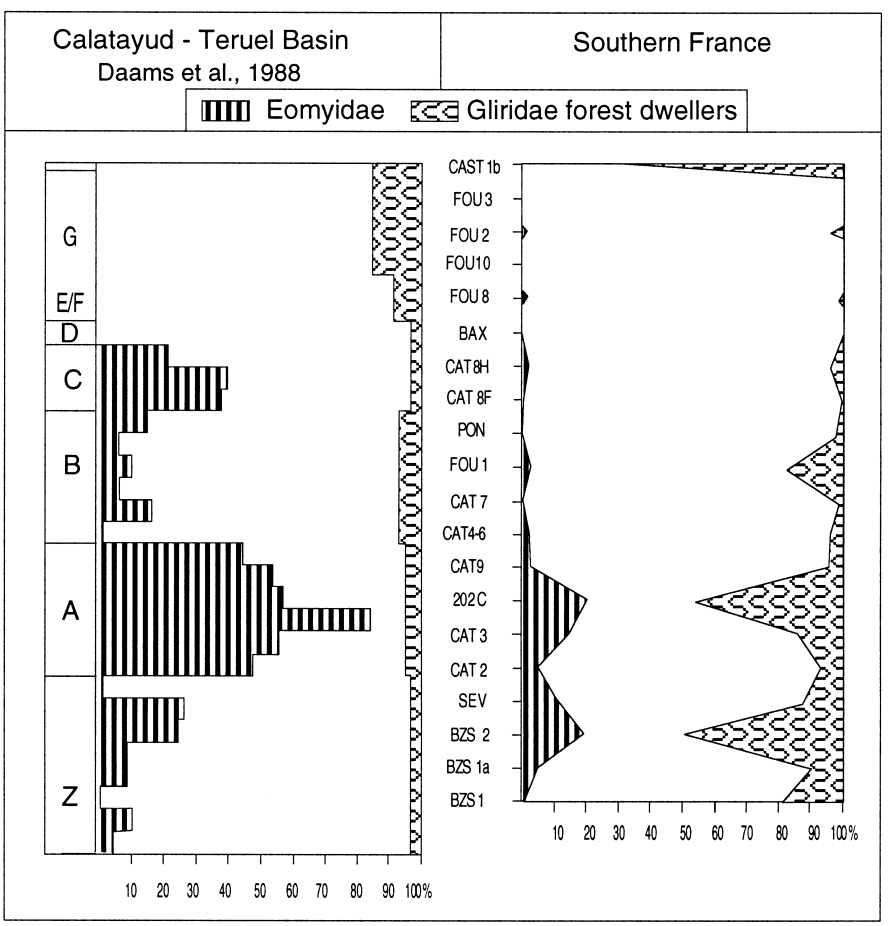

Fig. 7. Relative abundance of eomyids and forest glirids in southern France and in central Spain (Calatayud–Teruel Basin) from the late Early to Late Miocene.

Middle Miocene of the Calatayud–Teruel basin, and the two first peaks of the curve for central Spain are also observed for southern France. However forest glirids are much less abundant in central Spain than in southern France.

The quantitative analyses of the rodent faunas in southern France and Spain give basically very similar pictures. If the criteria used to interpret the environmental significance of some groups of rodents are valid, it can be inferred that during the late Early Miocene, the Calatayud–Teruel basin, which has a central position in the Iberian Peninsula, was more humid or the forest cover was more closed than in southern France near the Mediterranean sea. Such a difference can be explained by the fact that the Calatayud–Teruel area was a large basin with lakes contrary to southern France which was dryer because of the nature of its substratum, mostly composed of Mesozoic limestones.

4. Conclusion

Two successions of Miocene rodent faunas, one from karst infills in southern France, and one from basin localities from the Calatayud–Teruel basin, central Spain, give very similar information about the evolution of the environment. In southern France, the environment was warm and the landscape rather closed during the Late Aquitanian and the Lower Burdigalian. This result is consistent with other information provided by bats. Southern France was probably densely covered by bushes and shrubs, and woodlands may have been more abundant in the Calatayud–Teruel basin. At the end of the Early Miocene, a general shift occurred towards a more open environment. As a working hypothesis, this shift may have occurred with the eastern closure of the Tethys. However, at that time temperatures remain still rather high as indicated by the presence of fruit-bats in southern France.

Acknowledgements

The authors wish to thank the two referees, H. de Bruijn and R. Daams, whose comments have improved the manuscript. B. Marandat and D. Vernier helped to improve the English text. Publication I.S.E.M. no. 98065.

Appendix A

Bouzigues 1

Euericetodon aquitanicus
Melissiodon dominans
Pseudotheridomys parvulus
Ritteneria manca
Peridyromys murinus
Prodryomys brailloni
Prodryomys prosper
Microdyromys koenigswaldi
Glirudinus modestus
Palaeosciurus cf. *fissurae*
Heteroxerus aff. *lavocati*

Bouzigues 2

Eucricetodon aquitanicus-infralactorensis
Melissiodon dominans
Pseudotheridomys parvulus
Pseudotheridomys bouziguensis
Pseudodryomys simplicidens
Miodyromys cf. *biradiculus*
Prodryomys brailloni
Prodryomys gregarius
Microdyromys koenigswaldi
Glirudinus aff. *modestus*
Glirudinus aff. *gracilis*
?*Glirudinus minutus*
Myoglis houlezi
?*Paraglirulus infralactorensis*
?*Vasseuromys*
Palaeosciurus fissurae
Sciuridé indet

Ste Catherine 2

Neocometes cf. *similis*
Pseudotheridomys parvulus
Pseudotheridomys bouziguensis
Ligerimys antiquus
Ligerimys lophidens
Peridyromys murinus
Miodyromys biradiculus
Prodryomys brailloni
Pseudodryomys julii
Pseudodryomys ibericus
Pseudodryomys simplicidens
Microdyromys koenigswaldi
Microdyromys legidensis
Glirudinus modestus
Glirudinus minutus
Glirudinus gracilis-undosus
Atlantoxerus sp.
Palaeosciurus fissurae
Spermophilinus bredai

Baixas 202 C
Melissiodon cf. *dominans*
Pseudotheridomys parvulus
Ligerimys antiquus
Ligerimys lophidens
Pseudodryomys ibericus
Pseudodryomys simplicidens
Prodryomys brailloni
Miodyromys biradiculus
Microdyromys koenigswaldi
?*Microdyromys legidensis*
Glirudinus modestus
Glirudinus minutus
Glirudinus gracilis-undosus
Atlantoxerus sp.
Palaeosciurus sp.

Ste Catherine 4
Democricetodon franconicus
Melissiodon cf. *dominans*
Ligerimys antiquus-florancei
Ligerimys lophidens
Pseudotheridomys bouziguensis
Pseudodryomys ibericus
Pseudodryomys simplicidens
?*Pseudodryomys robustus*
Prodryomys brailloni
Myoglis sp.
Miodyromys biradiculus
Microdyromys koenigswaldi
Microdyromys legidensis
Glirudinus modestus
Glirudinus gracilis-undosus
Atlantoxerus sp.
Spermophilinus sp.

Ste Catherine 6
Democricetodon franconicus
Ligerimys antiquus-florancei
Ligerimys lophidens
Pseudotheridomys sp.
Pseudodryomys ibericus
Pseudodryomys simplicidens
Miodyromys biradiculus
Prodiyomys brailloni
Microdyromys koenigswaldi
Microdyromys legidensis
Glirudinus modestus
Glirudinus gracilis-undosus
Atlantoxerus sp.
Palaeosciurus fissurae

Lo Fournas 1
Megacricetodon collongensis
Democricetodon aff. *mutilus*
Democricetodon gracilis
Ligerimys florancei
Pseudodryomys simplicidens
Miodyromys koenigswaldi
Prodryomys sp.
Glirudinus gracilis-undosus
Glirudinus modestus
Microdyromys koenigswaldi
Microdyromys legidensis
Atlantoxerus sp.

Ste Catherine 8 H
Megacricetodon collongensis
Democricetodon franconicus
Democricetodon sp.
Ligerimys florancei
Pseudodryomys simplicidens
Prodryomys brailloni
Miodyromys sp.
?*Peridyromys murinus*
Microdyromys koenigswaldi
Microdyromys legidensis
Glirudinus modestus
Glirudinus gracilis-undosus
Atlantoxerus sp.

Lo Fournas 8
Megacricetodon gersii
Megacricetodon minor
Democricetodon sp.
Melissiodon sp.
Ligerimys florancei
Miodyromys aegercii
Pseudodryomys simplicidens
Microdyromys koenigswaldi
Glirudinus undosus
?*Palaeosciurus*
Heteroxerus huerzeleri
Spermophilinus bredai or *bessana*

Luc sur Orbieu
Cricetodon sansaniensis
Megacricetodon gersii
Megacricetodon minor
Democricetodon aff. *affinis*
Microdyromys koenigswaldi
Microdyromys miocaenicus
Miodyromys aegercii
Spermophilinus bredai
Heteroxerus huerzeleri
Heteroxerus grivensis

Lo Fournas 10
Megacricetodon lemartinelli
Megacricetodon minor
Democricetodon aff. *affinis*
Miodyromys biradiculus
Miodyromys aegercii
Pseudodryomys simplicidens
Microdyromys koenigswaldi ?*Heteroxerus grivensis*
?*Palaeosciurus*

Lo Fournas 3
Megacricetodon roussillonensis

Megacricetodon minor or *similis*
Democricetodon aff. *affinis*
Democricetodon gracilis
Miodyromys aegercii
Microdyromys koenigswaldi
?*Microdyromys legidensis*

La Grenatière
Megacricetodon gregarius
Megacricetodon minor
Fahlbuschia larteti
Heteroxerus grivensis

Montredon
Hispanomys mediterraneus
Rotundomys montisrotundi
Anomalomys gaillardi
Progonomys cathalai
Eomyops catalaunicus
Muscardinus hispanicus
Muscardinus heintzi
Eliomys cf. *truci*
Spermophilinus bredai
Heteroxerus cf. *grivensis* or *Atlantoxerus*

Lo Fournas 6
Hispanomys mediterraneus
Rotundomys montisrotundi
Progonomys cf. *hispanicus*
Progonomys clauzoni
Parapodemus lugdunensis
Parapodemus pasquierae
Spermophilinus sp.
Muscardinus sp.
Eliomys sp.

Castelnou 1
Hispanomys cf. *mediterraneus*
Neocricetodon seseae
Cricetus cf. *kormosi*
Cricetus sp.
Parapodemus barbarae
Rhagapodemus primitivus
Huerzelerimys turoliensis
Occitanomys faillati
Occitanomys sp.
Karnimata cf. *intermedia*
Muscardinus hispanicus
Glirídé indet cf. *Glirulus*
Atlantoxerus cuencae

Bouzigues 1h
Eucricetodon aquitanicus-infralactorensis
Pseudotheridomys parvulus
Pseudotheridomys bouziguensis
Miodyromys cf. *biradiculus*
?*Prodryomys brailloni*
?*Prodryomys gregarius*
Prodryomys prosper
Microdyromys koenigswaldi
Glirudinus modestus
Myoglis houlezi

Serre de Vergès
Eucricetodon infralactorensis
Melissiodon dominans
Pseudotheridomys parvulus
Pseudotheridomys bouziguensis
Pentabuneomys cf. *rhodanicus*
Ligerimys antiquus
Ligerimys lophidens
Miodyromys cf. *biradiculus*
Prodryomys brailloni
Prodryomys prosper
Prodryomys gregarius
Pseudodryomys ibericus
Pseudodryomys simplicidens
Microdyromys koenigswaldi
Glirudinus aff. *modestus*
Glirudinus aff. *gracilis*
Palaeosciurus cf. *fissurae*
Atlantoxerus sp.
?*Spermophilinus bredai*

Ste Catherine 3
Melissiodon dominans
Pseudotheridomys parvulus
Pseudotheridomys bouziguensis
Ligerimys antiquus
Ligerimys lophidens
Pentabuneomys cf. *rhodanicus*
Miodyromys biradiculus
Prodryomys brailloni
?*Prodryomys prosper*
Pseudodryomys ibericus
Pseudodryomys simplicidens
?*Pseudodryomys robustus*
?*Pseudodryomys julii*
Microdyromys koenigswaldi
Microdyromys legidensis
Glirudinus modestus
Glirudinus gracilis
Atlantoxerus sp.
Spermophilinus bessana or *bredai*

Ste Catherine 9
Neocometes cf. *brunonis*
Melissiodon cf. *dominans*
Pseudotheridomys parvulus
Ligerimys antiquus
Pseudodryomys ibericus
Pseudodryomys simplicidens
Pseudodryomys julii
Pseudodryomys robustus
Prodryomys gregarius
Prododryomys brailloni
Miodyromys biradiculus
Microdyromys koenigswaldi

Glirudinus modestus
Glirudinus minutus
Glirudinus undosus
Palaeosciurus cf. *fissurae*
Atlantoxerus sp.

Ste Catherine 5
Democricetodon cf. *franconicus*
Ligerimys antiquus-florancei
Pseudodryomys ibericus
Pseudodryomys simplicidens
?*Pseudodryomys robustus*
Miodyromys biradiculus
Prodryomys brailloni
?*Prodryomys prosper*
Microdyromys
Glirudinus modestus
Glirudinus gracilis-undosus
Atlantoxerus sp.
?*Palaeosciurus* sp.

Ste Catherine 7
Democricetodon franconicus
Ligerimys florancei
Pseudodryomys ibericus
Pseudodryomys simplicidens
Pseudodryomys julii
Microdyromys biradiculus
Glirudinus modestus
Atlantoxerus sp.
Palaeosciurus fissurae

Port la Nouvelle
Megacricetodon collongensis
Democricetodon aff. *mutilus*
Democricetodon brevis
?*Prodryomys satus*
Eumyarion aff. *medius*
Pseudodryomys aff. *ibericus*
Pseudodryomys simplicidens
Microdyromys koenigswaldi
Glirudinus modestus/gracilis
Spermophilinus bredai

Ste Catherine 8 F
Megacricetodon collongensis
Democricetodon franconicus
?*Democricetodon* sp.
Ligerimys florancei
Pseudodryomys ibericus
Pseudodryomys simplicidens
Miodyromys sp.
?*Peridyromys murinus*
Microdyromys koenigswaldi
Atlantoxerus sp.

Baixas
Megacricetodon collongensis-gersii
?*Megacricetodon minor*
Democricetodon cf. *mutilus*
Melissiodon dominans
?*Prodryomys satus*
Pseudodryomys ibericus
Pseudodryomys simplicidens
Microdyromys koenigswaldi
Atlantoxerus sp.
Spermophilinus bredai

Ste Catherine 1
Megacricetodon gersii
Megacricetodon minor
Democricetodon aff. *affinis*
Miodyromys aegercii
Pseudodryomys ibericus
Microdyromys koenigswaldi
Heteroxerus huerzeleri or *grivensis*
Spermophilinus bredai
Palaeosciurusfissurae

Veyran
Megacricetodon gersii
Democricetodon aff. *mutilus* or aff. *affinis*
Eumyarion sp.
Microdyromys koenigswaldi
Microdyromys miocaenicus
Miodyromys aegercii
Bransatoglis cadeoti
Spermophilinus bredai
Palaeosciurus fissurae

Lo Fournas 2
Megacricetodon fournasi
Megacricetodon minor
Democricetodon aff. *affinis*
Democricetodon brevis
Democricetodon gracilis
Keramidomys carpathicus
Microdyromys koenigswaldi
Glirudinus undosus
Miodyromys sp.
Heteroxerus huerzeleri or *grivensis*

Lo Fournas 5
Megacricetodon gregarius
Megacricetodon minor
Fahlbuschia larteti
Democricetodon sp.
Hispanomys bijugatus
Heteroxerus grivensis

Castelnou 1B
Progonomys hispanicus
Megacricetodon gregarius
Megacricetodon similis
Democricetodon affinis
Cricetodon sp.
Hispanomys sp.
Microdyromys miocaenicus

Muscardinus sp. 1
Muscardinus sp. 2
Heteroxerus grivensis
Spermophilinus bredai

Lo Fournas 7
Hispanomys mediterraneus
Rotundomys montisrotundi
Neocricetodon sp.
Cricetulodon sp.
Democricetodon sulcatus
Anomalomys cf. *gaillardi*
Progonomys castilloae
Huerzelerimys vireti
Occitanomys faillati
?*Muscardinus hispanicus-heintzi*
Eliomys sp.
Spermophilinus sp
Heteroxerus or *Atlantoxerus*

Castelnou 3
Cricetus barrierei
Ruscinomys cf. *lasallei*
Hispanomys cf. *mediterraneus*
Myocricetodon sp.1
Promymomys sp.
Stephanomys dubari
Occitanomys adroveri
Occitanomys sp.
Paraethomys anomalus
Rhagapodemus primaevus
Apodemus dominans
Apodemus gudrunae
Apodemus jeanteti
Muscardinus sp.
Eliomys truci
Myomimus dehmi

References

Aguilar, J.-P., 1980. Rongeurs du Miocène inférieur et moyen en Languedoc. Leur apport pour les corrélations marin-continental et la stratigraphie. Palaeovertebrata 9 (6), 155–203.

Aguilar, J.-P., 1981. Evolution des rongeurs miocènes et paléogéographie de la Méditerranée occidentale. Thèse Doctorat Sciences, Montpellier, 203 pp.

Aguilar, J.-P., 1995. Evolution de la lignée *M. collongensis* – *M. roussillonensis* (Cricetidae, Rodentia, Mammalia) au cours du Miocène inférieur et moyen dans le sud de la France. Palaeovertebrata 24 (1), 1–45.

Aguilar, J.-P., Magné, J., 1978. Nouveaux gisements à rongeurs dans des formations marines miocènes du Languedoc méditerranéen. Bull. Soc. Geol. Fr. 7 (20), 803–805.

Aguilar, J.-P., Michaux, J., 1987. Essai d'estimation du pouvoir séparateur de la méthode biostratigraphique des lignées évolutives chez les rongeurs néogènes. Bull. Soc. Geol. Fr. 3 (6), 1113–1124.

Aguilar, J.-P., Michaux, J., 1990. A paleoenvironmental and paleoclimatic interpretation of a Miocene rodent faunal succession in southern France. Critical evaluation of the use of rodents in paleoecology. In: Evolution climatique dans le domaine méditerranéen au Néogène. Paleobiologie Cont. XVII, 311–327.

Aguilar, J.-P., Michaux, J., 1996. The beginning of the age of Murinae (Mammalia: Rodentia) in the southern France. Acta Zool. Cracov. 39 (1), 35–45.

Aguilar, J.-P., Calvet, M., Crochet, J.-Y., Legendre, S., Michaux, J., Sigé, B., 1986a. Première occurence d'un Megachiroptère Ptéropodidé dans le Miocène moyen d'Europe (gisement de Lo Fournas II, Pyrénées-Orientales, France). Palaeovertebrata 16 (3), 173–184.

Aguilar, J.-P., Calvet, M., Michaux, J., 1986b. Découverte de faunes de micromammifères dans les Pyrénées-Orientales (France) de l'Oligocène supérieur au Miocène supérieur; espèces nouvelles et réflexion sur l'étalonnage des échelles Cont. et marine. C. R. Acad. Sci. Paris II 303, 755–760.

Aguilar, J.-P., Calvet, M., Michaux, J., 1991a. Présence de *Progonomys* (Muridae, Rodentia, Mammalia) dans une association de rongeurs de la fin du Miocène moyen (Castelnou 1B, Pyrénées-Orientales, France). Géobios 24 (4), 503–508.

Aguilar, J.-P., Michaux, J., Bachelet, B., Calvet, M., Faillat, J.-P., 1991b. Les nouvelles faunes de rongeurs de la limite Mio-Pliocène en Roussillon. Implications biostratigraphiques et biogéographiques. Palaeovertebrata 20 (4), 145–172.

Aguilar, J.-P., Calvet, M., Michaux, J., 1994. Les rongeurs de Castelnou 6 (Pyrénées-orientales, France) et les corrélations entre faunes ibériques et françaises au Miocène moyen. N. Jahrb. Geol. Paläontol. Monatsch. 192 (1), 109–131.

Aguilar, J.-P., Calvet, M., Michaux, J., 1995. Les rongeurs du gisement karstique Miocène supérieur de Castelnou 1 (Pyrénées-Orientales, France). Géobios 28 (4), 501–510.

Aguilar, J.-P., Escarguel, G., Crochet, J.-Y., Sigé, B., Sudre, J., 1996a. Nouveaux sites d'âges variés dans les remplissages karstiques du Miocène inférieur de Bouzigues (Hérault, Sud de la France). Partie II: faunes 2 (Rongeurs), biochronologie et corrélations. Géobios, M.S. 20 (Rongeurs), 485–491.

Aguilar, J.-P., Clauzon, G., De Goër de Herve, A., Maluski, H., Michaux, J., Welcomme, J.-L., 1996b. The MN3 fossil mammal-bearing locality of Beaulieu (France): biochronology, radiometric dating, and lower age limit of the Lower Neogene renewal of the mammalian fauna in Europe. Newsl. Stratigr. 34 (3), 177–191.

Aguilar, J.-P., Escarguel, G., Michaux, J., 1997. Biochronologie du Miocène inférieur et moyen du sud de la France à partir des faunes karstiques. Le problème du genre *Neocometes*. In: Aguilar, J.-P., Legendre, S., Michaux, J. (Eds.), BiochroM '97 Biochronologie mammalienne du Cénozoïque en Europe et domaines reliés. Mém. Trav. E.P.H.E., Inst. Montpellier 21, 575–579.

Alvarez Sierra, M.A., Diaz Molina, M., Lacomba, J.L., Lopez Martinez, N., 1990. Taphonomic and sedimentary factors in the fossil record of Mammals. In: Lindsay, E., Fahlbusch, V., Mein, P. (Eds.), European Neogene Mammal Chronology, pp. 461–474.

Alvarez Sierra, M., Daams, R., Van der Meulen, A.J., Pelaez-Campomanes, P., 1997. A new time scale for the Aragonian. In: BiochroM '97, Montpellier, Résumé, pp. 18

Daams, R., Van der Meulen, A.J., 1984. Paleoenvironmental and paleoclimatic interpretation of micromammal faunal successions in the Upper Oligocene and Miocene of north central Spain. Paléobiol. Cont. 14, 241–257.

Daams, R., Freudenthal, M., 1990. The Ramblian and Aragonian: limits, subdivision, geographical and temporal extension. In: Lindsay, E., Fahlbusch, V., Mein, P. (Eds.), European Neogene Mammal Chronology, pp. 51–59.

Daams, R., Freudenthal, M., Van der Meulen, A.J., 1988. Ecostratigraphy of micromammal faunas from the Neogene of the Calatayud–Teruel Basin. In: Freudenthal, M. (Ed.), Biostratigraphy and Paleoecology of the Neogene Micromammalian Faunas from the Calatayud–Teruel Basin. Scri. Geol. Spec. Issue 1, 287–302.

Escarguel, G., Aguilar, J.-P., 1997. Les Eomyidés *Pseudotheridomys* et *Ligerimys* (Rodentia, Mammalia) du Miocène inférieur du sud de la France, Evolution et biostratigraphie. Palaeontographica 247 (1–4), 25–58.

Faillat, J.-P., Aguilar, J.-P., Calvet, M., Michaux, J., 1990. Les fissures à remplissages fossilifères néogènes du plateau de Baixas, Pyrénées-Orientales, France), témoins de la distension oligo-miocène. C. R. Acad. Sci. Paris II 311, 205–212.

Fejfar, O., 1990. The Neogene VP sites of Czechoslovakia: a contribution to the Neogene terrestric biostratigraphy of Europe based on rodents. In: Lindsay, E., Fahlbusch, V., Mein, P. (Eds.), European Neogene Mammal Chronology, pp. 211–236.

Hrubesch, K., 1957. Zahnstudien an tertiären Rodentia als Beitrag zu deren Stammesgeschichte. Über die Evolution der Melissiodontidae, eine Revision der Gattung *Melissiodon* . Bayer. Akad. Wiss. Math.-Naturwiss. Kl. Abh, N.F. 83, 1–101.

Legendre, S., 1980. Un Chiroptère Emballonuridé dans le Néogène d'Europe occidentale: considérations paléobiogéographiques. Géobios 13 (6), 839–847.

Legendre, S., 1982. La faune de micromammifères du gisement burdigalien de Port-la-Nouvelle (Aude). Compléments et indications paléoécologiques. Bull. Soc. Geol. Fr. 24 (2), 383–387.

Mayr, H., 1979. Gebissmorphologische Untersuchungen an miozänen Gliriden (Mammalia, Rodentia) Süddeutschlands. Dissertation, Universitat Munchen, 380 pp.

Mein, P., 1984. Composition quantitative des faunes de mammifères du Miocène moyen et supérieur de la région lyonnaise. Paléobiol. Cont. 14 (2), 339–346.

Michaux, J., Aguilar, J.-P., Bachelet, B., 1990. La faune des rongeurs du sud de la France et sa dynamique au Néogène supérieur. Vie Milieu 40 (23), 130–136.

Sen, S., 1996. Present state of magnetostratigraphic studies in the continental Neogene of Europe and Anatolia. In: Bernor, R.L., Fahlbusch, V., Mittmann, H.W (Eds.) The Evolution of Western Eurasian Neogene Mammal Faunas, pp. 56–63.

Sigé, B., Aguilar, J.-P., 1987. L'extension stratigraphique des mégachiroptères dans le Miocène d'Europe méridionale. C. R. Acad. Sci. Paris II 304, 469–474.

Sigé, B., Crochet, J.-Y., Sudre, J., Aguilar, J.-P., Escarguel, G., 1996. Nouveaux sites d'âges variés dans les remplissages karstiques du Miocène inférieur de Bouzigues (Hérault, Sud de la France). Partie I: sites et faunes 1 (Insectivores, Chiroptères, Artiodactyles). Géobios, M.S. 20, 477–483.

Storch, G., Engesser, B., Wuttke, M., 1996. Oldest fossil record of gliding in rodents. Nature 379, 439–441.

Van der Meulen, A.J., De Bruijn, H., 1982. The mammals from the Lower Miocene of Aliveri (Island of Evia, Greece). Part 2, The Gliridae. Proc. K. Ned. Akad. Wet. B 85 (4), 485–524.

Van der Meulen, A.J., Daams, R., 1992. Evolution of Lower–Middle Miocene rodent faunas in relation to long-term paleoenvironmental changes. Palaeogeogr. Palaeoclimatol. Palaeoecol. 93, 227–253.

Van de Weerd, A., Daams, R., 1978. Quantitative composition of rodent faunas in the Spanish Neogene and paleoecological implications. Proc. K. Ned. Akad. Wet. B 81 (4), 448–473.

Ziegler, R., Fahlbusch, V., 1986. Kleinsäuger-Faunen aus der basalen Oberen Süsswasser-Molasse Niederbayerns, Zitteliana. Abh. Bayer. Staatssamml. Paläontol. Hist. Geol. 14, 3–80.