

Evidence for African–Iberian exchanges during the Messinian in the Spanish mammalian record

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Abstract

The thick continental record in the Fortuna Basin enables the to establishment of an accurate chronology for the main mammalian events in the Western Mediterranean between 7.6 and 4.5 my, thus covering the whole Messinian interval. A first mammalian event at about 7.2 my records a significant turnover in the murid rodent associations. A second mammalian event is characterized by the dispersal of the murid *Paraethomys* and a number of large mammals which indicates a first African–Iberian exchange at about 6.2 my. Finally, a third mammalian event dated between 5.9 and 5.3 my involved the dispersal from northern Africa of the gerbil rodents. This event is clearly associated with the Mediterranean sea level drop following the Messinian Salinity Crisis.

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1. Introduction

The Messinian is one of the most intriguing stages in Neogene history with the Mediterranean Sea experiencing its so-called “Messinian Salinity Crisis (MSC)”. Marine connections with the Atlantic progressively closed, leading to very thick evaporite deposits, and possibly even to complete desiccation, in the Mediterranean area (Hsü et al., 1973; Hsü, 1978). Obviously, this also resulted in dramatically deteriorated marine ecosystems which had major impact on marine flora and fauna evolution. With the recent advent of an astro-

nomical time scale for the Messinian, however, it is now possible to study the palaeoenvironmental and palaeoclimatological changes that took place during the MSC in a time frame of unprecedented detail (Hilgen and Krijgsman, 1999; Krijgsman et al., 1999, 2001, 2002). Consequently, the marine Messinian deposits are still subject of intensive studies which focus on detailed proxy records to understand the processes that ultimately resulted in the precipitation of massif evaporite bodies (Sierro et al., 2001). Despite numerous studies on the causes, consequences and mechanisms of the MSC, there is ongoing debate on the possible relation between Mediterranean evaporite precipitation and global climate change (Benson et al., 1991; Kastens, 1992; Hodell et al., 1994; Clauzon et al., 1996). The most recent studies linking the oxygen isotope data of the

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open ocean to the Mediterranean event stratigraphy, however, indicate that no causal relationship exists between the onset of the Messinian evaporites at 5.96 Ma (Krijgsman et al., 1999, 2002) and major changes in the palaeoclimate record (Hodell et al., 2001). The consequence of this result is that tectonic uplift processes in the Gibraltar arc must also have played an important role in the closure of the marine Mediterranean–Atlantic connection (Garcés et al., 1998; Krijgsman et al., 1999).

In contrast to the marine domain, the continental record of the peri-Mediterranean Messinian basins is only poorly studied. Attempts to quantify and qualify possible climate changes in the continental realm predominantly come from high-resolution palynological studies (Suc and Bessais, 1990; Suc et al., 1999; Fauquette et al., this volume). The main conclusion from the pollen records is that the Messinian stage was characterised by relatively humid and warm conditions, while again no evidence was found for major climatological changes during the MSC (Suc and Bessais, 1990). Compared to these palynological studies, surprisingly little palaeoclimatological data are available from studies of Messinian mammals. This is largely related to difficulties in obtaining continuous records with reliable age constraints for the mammal-bearing deposits. Many of the richest mammal localities are notoriously found in non-datable scattered outcrops, so a direct link to the Mediterranean record remains hypothetical. Inevitably, however, the progressive closure of Mediterranean–Atlantic connections should have triggered mammal migration between Africa and Europe.

The continental deposits of the Fortuna Basin of southeast Spain are exceptionally suitable for the study of fossil mammal evolution during the Messinian. Furthermore, these deposits are well known for the presence of African fauna (Jaeger et al., 1975; Agustí, 1991; Agustí and Llenas, 1996) allowing new insights of mammal migration as well. Recently, the continental sequences of the Fortuna Basin have been incorporated in detailed magnetostratigraphic studies, which resulted in the establishment of a reliable time frame for the complete Neogene basin fill (Garcés et al., 2001). These magnetostratigraphic results indicate that the transition from marine to continental environments in the Fortuna Basin took place between 7.8 and 7.6 my, and that continental deposits are continuously recorded over the time interval between 7.6 and 4.8 my. The palustrine–lacustrine units interbedded within the alluvial sequence have yielded rich small mammal fossil assemblages of latest Tortonian to Messinian and lower Pliocene age (Garcés et al.,

1998, 2001). In addition, several intervals displayed a distinct sedimentary cyclicality of grey marls and reddish silts, which has been shown to be related to astronomically forced changes in climate. Especially interesting is the fact that the astronomically calibrated interval straddles the onset of evaporite deposition in the Mediterranean Sea.

In this paper, we present data from fossil mammal localities in the continental deposits of the Fortuna Basin. The detailed mammal record allows us, furthermore, to study the zoogeographical changes that took place in southeastern Spain during the time interval from 7.6 to 4.8 Ma. Because this interval includes the MSC of the Mediterranean (5.96–5.33 my), it can be investigated if this dramatic event in the marine realm had any impact on the terrestrial ecosystems. The various African immigrant species invading Iberia during the Messinian can now be studied in a high-resolution time frame, which may significantly help to understand the geodynamic and paleogeographic evolution of the marine and continental gateways in the western Mediterranean region.

2. Geological setting of the Fortuna Basin

The Fortuna Basin was formed at the contact between the Internal and the External Betic Zones, as a result of the late Tortonian to Present NE–SW strike–slip tectonics in the Eastern Betics, in the context of the convergence between the African and Iberian plates (De Larouzière et al., 1988; Montenat et al., 1990; Sanz de Galdeano, 1990; Sanz de Galdeano and Vera, 1992) (Fig. 1).

The sedimentary infill of the Fortuna Basin is divided into three main units: (1) a Tortonian transgressive marine unit; (2) a latest Tortonian regressive marine to transitional evaporitic unit; (3) a Messinian to Pliocene thick continental alluvial and lacustrine unit (Garcés et al., 1998, 2001). Concurrently, in other basins in the Eastern Betics, rapid initial subsidence and marine transgression in the Fortuna Basin started in the Tortonian. Then, a progressive isolation of the Fortuna Basin from the open Mediterranean Basin occurred in relation to a late Tortonian tectonic uplift of the Internal Zones of the Betic chain. This basin stage was coeval with the uplift of the Central Betics and the closure of the Atlantic connection through the North Betic strait (Soria et al., 1998). The new basin configuration favoured rapid accumulation of continental alluvial sediments during the Messinian.

The scenario during the Messinian was that of a poorly drained confined continental basin, with a

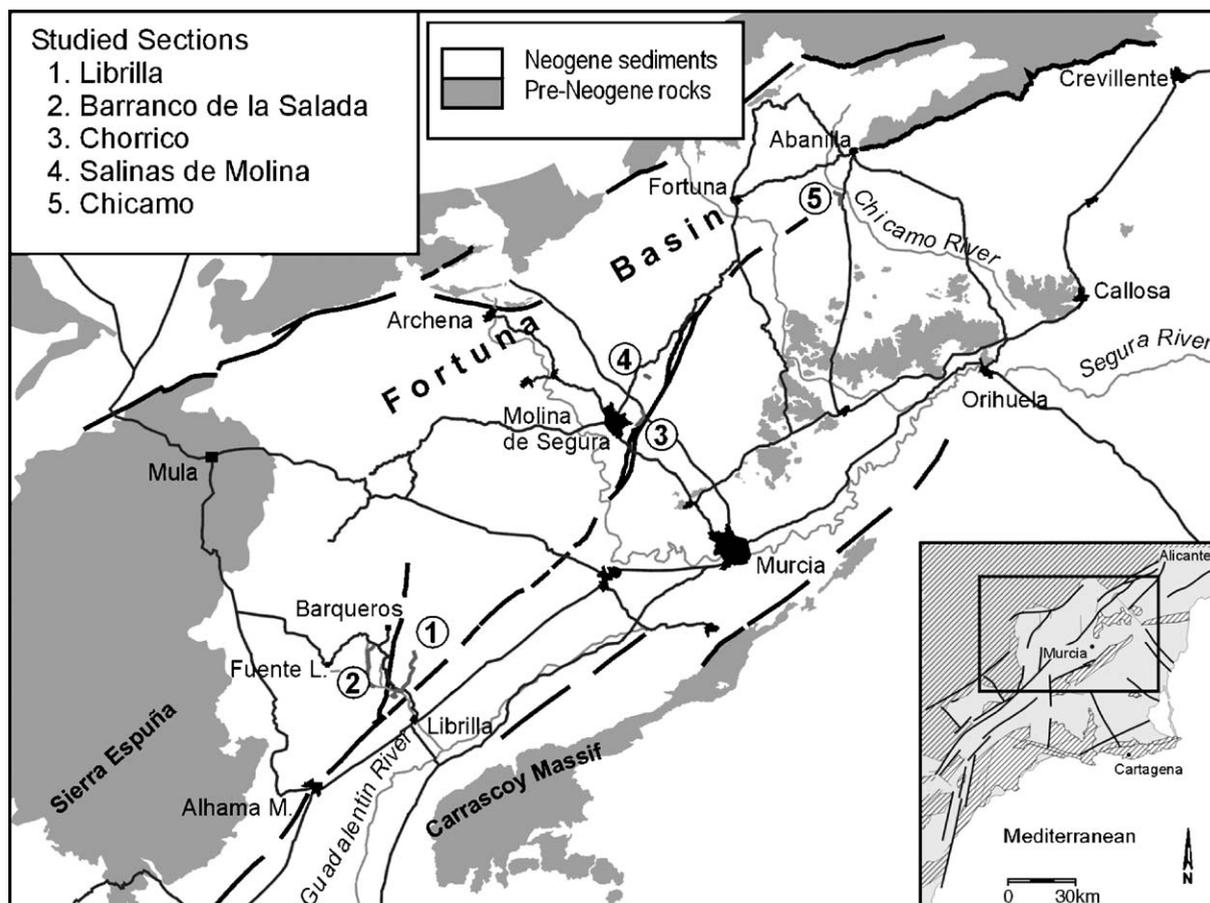


Fig. 1. Location of the studied sections in the Fortuna Basin.

punctuated development of shallow lacustrine and palustrine environments in distal areas. A marine connection existed towards the southeastern margin, where Messinian marine sediments interfinger with late Turolian continental units (Mein et al., 1973). Sea level fluctuations of the Mediterranean basin during the Messinian influenced the sedimentation in the Fortuna Basin: the sea level drop following the Messinian Salinity Crisis at 5.96 my (Krijgsman et al., 1999) correlates with a localised valley incision in the Librilla area and a sudden gravel progradation over the pre-existing mudflat and palustrine environments. The resumed normal marine conditions in the Mediterranean at the base of the Pliocene is recorded in the Fortuna Basin as a short pulse of an areally restricted transgression.

3. The late Tortonian mammalian background

Prior to the Messinian, the late Tortonian continental beds in the Fortuna Basin are characterized by typical

middle Turolian elements (MN 12, *Parapodemus barbarae* Zone of van der Weerd, 1976). This is best exemplified by the locality of Casa del Acero, close to the Chicamo section (Agustí et al., 2001; Pons-Moyà, 1987; Agustí, 1986; Garcés et al., 2001). This fauna includes a number of elements which are shared with other synchronous sites in the Teruel Basin, such as Conclud or Aljezar B: *Hipparion concudense*, *Tragoportax gaudryi gaudryi* and *Metailurus acerensis* among others. Among rodents, these middle Turolian faunas are dominated by murids and cricetids, their diversity being characteristically low (no more than five murid species per locality at the best): *P. barbarae*, *Occitanomys adroveri*, *Huerzelerimys turoliensis*, *Hispanomys adroveri*, *Cricetulodon meini* (see Table 1). Levels assigned to the middle Turolian are also present in the Chorríco (CHO-307, with *P. barbarae*) and Librilla sections (BS-141, with *H. adroveri*) (Fig. 2).

The lower boundary for these middle Turolian faunas (MN 12, *P. barbarae* zone) has been established in the Teruel Basin at 7.5 my (Krijgsman et al., 1996). The

Table 1

Main mammalian events, faunal associations and mammal sites in the Fortuna Basin (Molina de Segura, Abanilla and Librilla areas)

| Bioevents | Faunal association | Molina de Segura–Abanilla | Librilla |
|--|---|---|-----------------------------------|
| FAD <i>Debruijnimys</i> | <i>Debruijnimys julii</i> , <i>Paraethomys miocaenicus</i> , <i>Apodemus gudrunae</i> , <i>Stephanomys medius</i> , <i>Occitanomys</i> sp., <i>Apocricetus alberti</i> , <i>Ruscinomys</i> <i>lasallei</i> , <i>Eliomys truci</i> , <i>Muscardinus vireti</i> , <i>Prolagus michauxi</i> | Molina de Segura 10 | Sifón 430, Sifón 413 |
| FOD-LOD <i>Paracamelus</i> , FOD <i>Propotamochoerus</i> , FOD <i>Paraethomys</i> | <i>Hipparion gromovae</i> , <i>Hipparion concudense</i> , <i>Propotamochoerus provincialis</i> , <i>Hexaprotodon crusafonti</i> , <i>Paracamelus aguirrei</i> , <i>Paraethomys miocaenicus</i> , <i>Apodemus gudrunae</i> , <i>Stephanomys ramblensis</i> , <i>Occitanomys</i> sp., <i>Apocricetus alberti</i> , <i>Ruscinomys</i> sp., <i>Eliomys truci</i> , <i>Muscardinus vireti</i> , <i>Prolagus michauxi</i> | Molina de Segura 3,4,7,8,9, AU 3 | Sifón 79, Sifón 71, Librilla 1 |
| FOD-LOD <i>Castromys</i> FOD <i>Ruscinomys</i> , FOD <i>Apocricetus</i> , FOD <i>Apodemus</i> , FOD <i>Stephanomys</i> | <i>Castromys kowalskii</i> <i>Apodemus gudrunae</i> , <i>Stephanomys ramblensis</i> , <i>Occitanomys</i> sp., <i>Apocricetus alberti</i> , <i>Ruscinomys</i> sp., <i>Eliomys truci</i> , <i>Muscardinus vireti</i> , <i>Prolagus michauxi</i> | Molina de Segura 1, D AU2P, 2Q, 2R, CHO17, 29, 33, Romerales, La Hornera | Sifón 52, Sifón 3, Sifón 1 |
| LAD <i>Huerzelerimys</i> , LAD <i>Cricetulodon</i> , LAD <i>Hispanomys</i> | <i>Parasorex iberica</i> , <i>Galericinae</i> indet., <i>Petenya dubia</i> , <i>Echinosoricinae</i> indet., <i>Hispanomys adroveri</i> , <i>Cricetulodon meini</i> , <i>Parapodemus barbarae</i> , <i>Occitanomys adroveri</i> , <i>Huerzelerimys turoliensis</i> , <i>Eliomys truci</i> , <i>Atlantoxerus adroveri</i> , <i>cervidae</i> indet., <i>Tragoptax gaudryi gaudryi</i> , <i>Metailurus acerensis</i> , <i>Tetralophodon</i> sp. | CHO-307, Casa del Acero | BS-141 |

youngest middle Turolian level is CHO-307 in the Chorrico section, which is placed in the reverse interval just after chron C3Br.2n, at about 7.4 my.

4. First Messinian Mammalian Event (Muroid Event)

The First Messinian Mammalian Event (MME-1), as recorded in the continuous sequence of the Fortuna Basin, involved a significant change among the small mammal faunas. This event is characterized by an increase in the diversity as well as faunal turnover in the rodent faunas. Among the murids, the genus *Huerzelerimys* became extinct, while two new genera, *Apodemus* and *Stephanomys*, appeared for the first time. *Apodemus*, represented by *Apodemus gudrunae*, is probably an in situ descendant of *P. barbarae* (van der Weerd, 1976), so its presence cannot be quoted as a true dispersal event. The same is also true for *Stephanomys* (*Stephanomys ramblensis*), whose origin probably lies very close to *O. adroveri*. However, as distinct from *Apodemus*, this was not a case of anagenesis but rather of a splitting, cladogenetic process, since *Occitanomys* coexists with *Stephanomys* at this level and even in younger levels.

Among cricetids, the replacement of the small and archaic *Cricetulodon* and *Neocricetodon* by the larger and more derived *Cricetus*-like *Apocricetus* is also

recorded at this time. This level also records the replacement of *Hispanomys* by *Ruscinomys*, the latter being characterized by its more hypsodont and selene-dont molars. In contrast to *Cricetulodon* and *Apocricetus*, in situ evolution of the first *Ruscinomys* species from the middle Turolian *H. adroveri* cannot be excluded.

The lowermost levels with this kind of small faunas in the Fortuna Basin are found in the sections of Chorrico (CHO-17, CHO-29, CHO-33) and Sifón de Librilla (SIF-1, SIF-3) at about 6.9–6.7 my (upper chron C3Ar and base of chron C3An.2n). Therefore, MME 1 took place somewhere between 7.3 my (age of the youngest middle Turolian fauna, CHO-307) and 6.8 my. It means that MME 1 (also corresponding to the MN12–MN13 and middle–late Turolian boundaries) roughly coincides with the Tortonian/Messinian boundary (placed at 7.2 my). The Tortonian/Messinian boundary records the first changes in the Mediterranean hydrography and is marked by an increase in benthic $\delta^{18}\text{O}$ values, as recorded in the Salé Briqueterie section of northwestern Morocco (Hodell et al., 1994). This $\delta^{18}\text{O}$ increase has been interpreted as a consequence of cooling and/or increased salinity that resulted from circulation changes in the Rifian Corridor and the onset of a negative water budget in the Mediterranean (Hodell et al., 1994).

At the end of this phase, a short, although significant dispersal event is the entry of the murid *Castromys*,

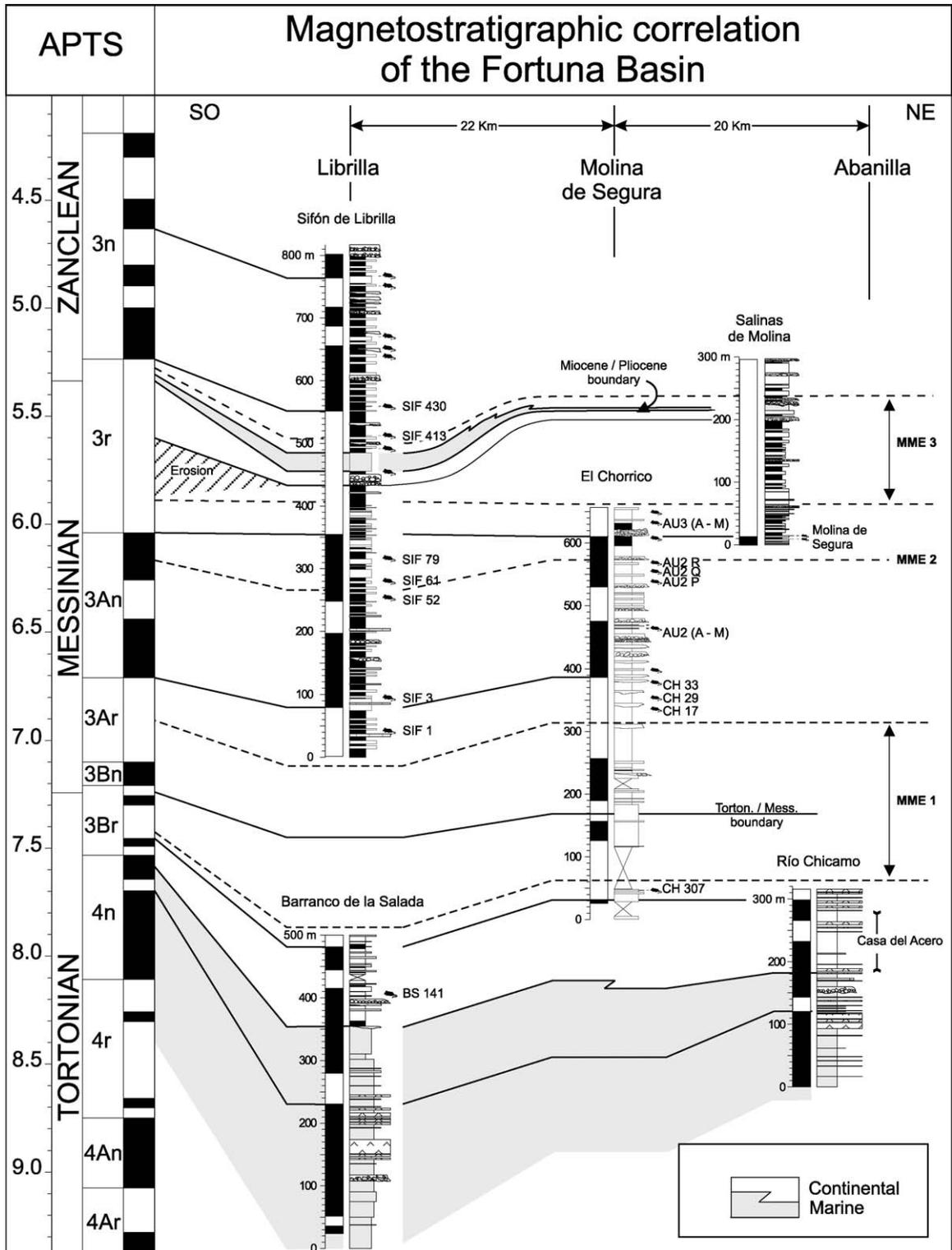


Fig. 2. Magnetobiostratigraphic correlations between the studied sections and absolute ages based on the astronomically calibrated Polarity Time Scale (Krijgsman et al., 1999).

recorded in the Salinas de Molina section. *Castromys* is a murid of Asian affinities whose origin lies close to *Parasaidomys afghanensis* from Dawrankhel 14 (Afghanistan, Brandy, 1979; Agustí and Llenas, 1996). It is represented in the Fortuna Basin by *Castromys kowalskii*, while a less derived species, *Castromys inflatus*, is present in the Teruel (Mein et al., 1990) and Crevillente basins (Martín-Suárez and Freudenthal, 1994).

5. Second Messinian mammalian event (*Paraethomys* event)

A second Messinian mammalian event (MME-2) is clearly recognized in the Fortuna Basin, as well as in other Iberian basins, after the entry of the murid *Paraethomys miocaenicus*. This dispersal event was identified very early in the 1970s as one of the main terrestrial events in the Messinian because of its zoogeographical implications (de Bruijn, 1974; Jaeger et al., 1975). The evolution of *Paraethomys* has been traced in a detailed way in northern Africa (Jaeger, 1977), while in Spain, its presence was first reported from the Fortuna, Caravaca and Guadix-Baza basins (Jaeger et al., 1975). Because of its African affinities, the first occurrence of *Paraethomys* in Southern Spain was immediately interpreted as a consequence of the Messinian Salinity Crisis. Since the spread of the early *Paraethomys* populations can be recognized all around of the Mediterranean (Jaeger et al., 1975), the biostratigraphic significance of the *Paraethomys* dispersal in the late Miocene can be compared to that of the first murids (*Progonomys*) at the beginning of the late Miocene. However, until a detailed magnetostratigraphic analysis had been carried out in these areas, little was known about the exact chronology of this event. After the chronostratigraphic framework developed in the Fortuna Basin, the dispersal of *Paraethomys* in Southern Spain has been established in chron C3An.1n, at about 6.2my (Garcés et al., 1998).

However, in contrast to what happened in MME 1, this event had little effect on the small mammal associations: *Paraethomys* simply joined the previously existing rodent taxocoenosis, without involving any kind of replacement or turnover. In contrast, this event was accompanied by a number of significant large mammal dispersals.

Probably associated with the *Paraethomys* dispersal is the entry of camels of the genus *Paracamelus* into southern Spain. *Paracamelus aguirrei* has been recorded from the Librilla section and Venta del Moro in the Cabriel Basin (Alberdi et al., 1981; Morales,

1984). In the Librilla section, *P. aguirrei* appears associated with *Hipparion gromovae gromovae*, *H. concudense*, *Parabos* cf. *cordieri*, Cervidae indet. and Suidae indet., in levels placed in the upper part of chron C3An.1n (Garcés et al., 1998). The magnetostratigraphic framework developed in Venta del Moro is also consistent with this age (Opdyke et al., 1990). *Paracamelus* is an eastern immigrant which likely entered southern Spain from northern Africa (Pickford et al., 1994). Therefore, the presence of *Paraethomys* and *Paracamelus* in the Messinian beds of southern Spain can be explained as part of the same dispersal event from the south.

A number of other large mammal dispersals that took place at this time are probably related to the former ones. For instance, the small hippo *Hexaprotodon crusafonti* is known in the Salinas de Molina section in levels with *Paraethomys*. This is also the case for other localities in the Levant areas with *Hexaprotodon*, such as Arenas del Rey in the Granada Basin and Venta del Moro in the Cabriel Basin (Morales, 1984). As stated, the chronology of Venta del Moro (Opdyke et al., 1990) is consistent with the datum of *Paraethomys* in the Fortuna Basin, that is, within chron C3An.1n, at about 6.2my. As in the case of *Paraethomys* and *Paracamelus*, *Hexaprotodon* probably entered Southern Spain from Africa, taking part of the same dispersal event. However these small hippos may have dispersed at an earlier time, since a form called *Hexaprotodon primae-vus* (= *H. crusafonti*) was quoted in the locality of El Arquillo (Teruel Basin) by Crusafont et al. (1964). The fauna from El Arquillo lacks *Paraethomys* and is probably equivalent to those of the former MME 1.

Besides *Paracamelus* and *Hexaprotodon*, other immigrants of not strictly African affinities are again associated with the dispersal of *Paraethomys*. This is the case, for instance, of the suid *Propotamochoerus provincialis* and the ursid *Agriotherium roblesi*. The *Paraethomys* levels of the Salinas de Molina and Librilla sections record the presence of a suinae closely related to *P. provincialis* (Agustí et al., 1985; Van der Made, 1990). *P. provincialis* is a middle-sized suid closely related to modern pigs (*Sus*, *Potamochoerus*) which has been also recorded in the sites of Venta del Moro (Cabriel Basin) and Arenas del Rey (Granada Basin), both with *Paraethomys miocaenicus* (Van der Made, 1990). *A. roblesi* was a large ursid of modern aspect which is also associated with *P. miocaenicus* in Venta del Moro and Alcoy (Morales, 1984). Another *Agriotherium* species has been also recorded from the Pliocene of Southern Africa (*Agriotherium africanum*; Hendey, 1979). However, older species are known from

Asia (*A. paleindicum*, *A. sivalense*; Morales, 1984, and references therein), so a simultaneous settlement of Europe and Africa from the East in the late Miocene seems feasible. Thus, both *P. provincialis* and *A. roblei* are of probable Asian origin.

Therefore, a significant dispersal event took place at 6.2my, in the upper part of chron C3An.1n, involving the entry into South-Western Europe of African (*P. miocaenicus*, *P. aguirrei*) and Asian species (*P. provincialis*, *A. roblei*). The existence of similar dispersals of European taxa into northern Africa was already known and included a number of typical late Turolian European rodents: *Apodemus*, *Apocricetus* and *Eliomys* at Aïn-Guettara (Morocco; Brandy and Jaeger, 1980) and *Ruscinomys*, *Stephanomys* and *Castillomys* at Argoub Kemellal (Algeria; Coiffait et al., 1985). However, until recently, no accurate data about the chronology of this dispersal event were available. The framework developed in the Aït Kandoula Basin, in northern Morocco, enabled Benammi et al. (1996) to correlate this event with chron C3An.1n. This age is coincident with the one obtained by Garcés et al. (1998) in the Fortuna Basin for the entry into Spain of *Paraethomys* and *Paracamelus*. This means that at 6.2my exchanges between Africa and Spain took place in both directions. However, this African–Iberian exchange predates by more than 200ky the onset of the evaporite deposition at 5.96my.

Therefore, a significant restriction of the Mediterranean–Atlantic flow must have started well before the first deposition of the lower evaporites, enabling these mammalian exchanges. Intensification of the glaciation at 6.26my may have contributed significantly to this restriction of the Mediterranean before the onset of the MSC, as supported by several lines of evidence (Hodell et al., 2001). For instance, in the Mediterranean, the coiling change in *Neoglobobadrina acostaensis* from sinistral to dextral has been recognized at 6.36, 17 cycles below the onset of the evaporite deposition (Hilgen and Krijgsman, 1999). At Site 982 in North Atlantic, Hodell et al. (2001) recognize a distinct increase in the amplitude of the benthic $\delta^{18}\text{O}$ signal near the base of chron C3An.1n at 6.26my. The increase in $\delta^{18}\text{O}$ at 6.26my correlates with the transition from cycle T36 to T37 in Sicily and A43 to A44 in Sorbas (Hodell et al., 2001). This cycle coincides with a major slumping event seen in all sections of the Upper Abad Member in the Sorbas Basin (Sierro et al., 2001). This slumping as well as the unconformity observed between a bioherm and fringing reef unit in the marginal deposits of the Sorbas Basin (Braga and Martín, 1996) are probably related to sea

level lowstands during the interval of increased $\delta^{18}\text{O}$ amplitude starting at 6.26my (Hodell et al., 2001). Moreover, studies of the Niue Atoll led Aharon et al. (1993) to determine sea level changes of about 10 m amplitude from 6.14my onwards, reaching an amplitude of at least 30 m at 5.26my. This result is consistent with the one obtained by Braga and Martín (1996) in the Sorbas Basin, who estimated sea level changes of 10–30m by studying variations in the elevations of reef facies. Therefore, there is a lot of evidence suggesting that a significant restriction of the Mediterranean–Atlantic flow started at 6.2Ma, thus enabling the first African–Iberian mammalian exchanges.

6. Third Messinian Mammalian Event (Gerbil Event)

Besides the entry of *Paraethomys*, *Paracamelus* and *Hexaprotodon*, one of the main events that has been related to the Messinian Salinity Crisis is the dispersal of gerbils into Southern Spain. The gerbils are subdesertic rodents that today inhabit the dry landscapes of northern Africa and southwestern Asia. They appear as rare elements in a number of early Ruscinian localities from Southern Spain (Caravaca, Gorafe 1; de Bruijn, 1974) and have been usually interpreted as African elements having entered Spain during the Messinian, at the same time as *Paraethomys* or *Paracamelus*. This hypothesis gained further support after the discovery in Spain of fissure infillings in which other north African rodents such as the Myocricetodontine hamsters appeared associated with gerbils. This is the case in Salobreña (Aguilar et al., 1984) and Almenara M (=Casablanca M, Agustí and Galobart, 1986). In Almenara M, a surprising rodent association includes a mixture of European and Afro-Asian taxa: *A. gudrunae*, *P. miocaenicus*, *S. ramblensis*, *Occitanomys* cf. *adroveri*, *Castillomys crusafonti gracilis*, *Apocricetus alberti*, *Ruscinomys lasallei*, *Blancomys* sp., *Debruijnimys almenarensis*, *Myocricetodon* cf. *parvus*, *Calomyscus* sp., *Pseudomeriones abbreviatus*, *Eliomys truci* (Agustí, 1990). However, because of their karstic character, the exact chronology of these localities remained uncertain for years. The recent advances in the chronostratigraphy of the Fortuna Basin enables light to be shed on the dating of this particular event.

In the Fortuna Basin, as well as in other basins in the Betics, the thick evaporitic deposits that crop out at the end of the marine sedimentation were directly related to the Messinian Salinity Crisis. However, as demonstrated by Krijgsman et al. (2000), the evaporitic formations in the Lorca and Fortuna Basins deposited well before the

onset of the Messinian Salinity Crisis, are Tortonian in age. The extensive work developed in the Fortuna Basin enabled Garcés et al. (2001) to identify the equivalent levels of the MSC in the thick alluvial to lacustrine sedimentary sequences of the Sifón de Librilla and Chorríco sections. A short-lived marine transgression of basal Pliocene age overlies these units, thus indicating the return to normal marine conditions in the Mediterranean.

In contrast to *Paratehomys*, *Paracamelus* or *Hexaprotodon*, gerbils are absent from the thick Messinian sequence in the Fortuna Basin, prior to the incision produced by the MSC. Their first record is found just after the basal Pliocene transgression, at the level Sifón 413. It seems highly improbable that subdesertic gerbils reached southern Spain from northern Africa during the basal Pliocene transgression. Most likely, their presence in Europe is probably directly related to the onset of the MSC and the effective desiccation and spread of subdesertic conditions in the Western Mediterranean Basin. A palynological validation of this scenario would be the spread to the north of the Poaceae *Lygeum* during the MSC, as documented in the Maccarone section (Fauquette et al., this volume). *Lygeum* is a taxon adapted to arid to semi-arid conditions which now is characteristic of the south Mediterranean steppes. The fact that the gerbil dispersal is only properly recorded in fissure infillings like Salobreña or Almenara-M can be easily explained because of the erosional regime produced by the MSC and the lack of corresponding fluvio-lacustrine sediments of this precise age in the Betics. This interpretation is confirmed by the finding of the gerbil *D. almenarensis* (first recorded in Almenara M) in the latest Messinian reddish continental beds of the Zorreras Formation, in the Sorbas Basin (Martín-Suárez et al., 2000). The Zorreras Member consists of dominant silts and sandy clays containing caspibrackish ostracod species that are characteristic of the Lago Mare fauna and indicate the presence of large salt lakes in the area (Krijgsman et al., 2001). It corresponds to the upper evaporites and consists of eight cycles deposited between 5.5 and 5.33 my (Hodell et al., 2001). Therefore, the presence of *D. almenarensis* in the Zorreras Member confirms that the dispersal of gerbils took place during the deposition of the upper evaporites. This late dispersal of gerbils in Iberia during the MSC also explains why these rodents are usually recorded in southern Spain in early Pliocene (Ruscinian) levels and not in the late Miocene (late Turolian) pre-MSC ones. After their entry, gerbils persisted in Southern Spain until the middle Pliocene (Asta Regia; Castillo and Agustí, 1996).

The absence in the Iberian record of localities exactly associated with the MSC makes it difficult to gain a clear picture of the mammalian exchanges during this crucial period of the Mediterranean history. However, a number of large mammals are present in Almenara M, a site that probably deposited during the MSC, according to the occurrence of the gerbil *D. almenarensis* in the Zorreras Member of the Sorbas Basin. The list of large mammals from Almenara M includes *Macaca* sp., *Pliohyrax graecus*, Bovidae indet., cf. *Nyctereutes* sp. and Felidae indet. (Agustí and Galobart, 1986; Pickford et al., 1997; Kohler et al., 2000). Particularly significant is the presence of the cercopithecoid monkey *Macaca* sp. Cercopithecoid monkeys had been present in Eastern Europe since the early Turolian (late Tortonian), but they were represented by members of the Subfamily Colobinae (*Mesopithecus*). *Macaca*, of likely African origin, is the first Cercopithecinae monkey recorded in Eurasia and its presence in Almenara M can be clearly related to the MSC. Further evidence of African dispersal at this time is provided by the presence of the large cricetid *Protolophiomys ibericus* in the locality of Salobreña, in southern Granada (Aguilar and Thaler, 1987). The Lophiomyiinae are restricted today to eastern Africa, although their geographic range in the past probably covered the whole south Mediterranean belt (Aguilar and Thaler, 1987).

As in the case of gerbils, the sudden occurrence of new large mammals in basal Pliocene localities is probably the result of dispersals during the MSC, rather than during the early Pliocene flooding. This is the case, for instance, of the first members of the genus *Sus*. An archaic species of *Sus* (*Sus arvernensis*) is present for the first time in the early Ruscinian sites of Alcoy and Gorafe 4 (Agustí, 1986; Van der Made, 1990). Its appearance in the early Pliocene is again best explained as a consequence of the MSC.

7. Conclusions

A first Messinian mammalian event (MME 1), close to the Tortonian/Messinian boundary at about 7.2 my, can be recognized in the continental beds of the Fortuna Basin. It involved a significant small mammal turnover affecting the Muroid taxocenosis (murids and cricetids) and led to an increase in the diversity of this group.

A second Messinian mammalian event (MME 2) is recorded at about 6.2 Ma, involving significant east–west and north–south mammalian exchanges. Among the small mammals, this event is characterized by the widespread dispersal of the murid *Paraethomys*. Among the large mammals, the presence of eastern immigrants,

such as the suid *P. provincialis* and the ursid *A. roblesii* must be pointed out. The presence of *Paracamelus* at this time also points, as in the case of *Paraethomys*, to the existence of African–Iberian exchanges. This is confirmed by the presence of European rodents at a similar age in Morocco. These exchanges between the two shores indicate the existence of a significant level of constriction of the two gateways of the Mediterranean (Betic and Rifian corridors) at least 200ky before the onset of the evaporite deposition linked to the MSC.

A third Messinian mammalian event (MME 3), following the MSC and most likely preceding the basal Pliocene transgression, took place between 5.96 and 5.33 my, involving the dispersal into the Western Mediterranean of typical subdesertic rodents of African and South-Western Asian affinities. Because of the erosional character of the MSC in the continental realm, this event is very rarely recorded in MSC-equivalent continental deposits (Salobreña, Almenara M, Zorreras), but in basal Pliocene ones (Sifón 413, Alcoy, Gorafe 1 and 4). This event also explains the case of some generalist large mammals, such as *Macaca* and *Sus*, which are present for the first time in latest Miocene or basal Pliocene beds in Spain. Gerbils persisted during the early and middle Pliocene in southern Spain (Asta Regia in the Jerez Basin; Castillo and Agustí, 1996).

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References

- Aguilar, J.P., Thaler, L., 1987. *Protolophiomys ibericus*, n. gen., n. sp. (Mammalia, Rodentia) du Miocène supérieur de Salobreña (Sud d'Espagne). C. R. Acad. SC. Paris, 304, Ser. 2, 14, 859–862.
- Aguilar, J.P., Brandy, L.D., Thaler, L., 1984. Les Rongeurs de Salobreña (Sud de l'Espagne) et le problème de la migration messinienne. Paleobiol. Cont. 14 (2), 3–17.
- Agustí, J., 1986. Nouvelles espèces de cricétidés vicariantes dans le Turolien moyen de Fortuna (prov. Murcia, Espagne). Geobios 19, 1, 5–11. 2 pl. Lyon.
- Agustí, J., 1990. The Miocene Rodent Succession in Eastern Spain: a zoogeographical appraisal. Lindsay, Fahlbusch and Mein: European Neogene Mammal Chronology. Plenum Press, New York, pp. 375–404.
- Agustí, J., 1991. Gerbilidés fossils d'Europe occidentale. In: Le Berre, Guelte (Eds.), Le Rongeurs et l'Espace, R. Chabaud Editeur, Paris, pp. 177–182.
- Agustí, J., Galobart, A., 1986. La sucesión de micromamíferos en el complejo cárstico de Casablanca (Almenara, Castellón): problemática biogeográfica. Paleontol. Evol. 20, 57–62.
- Agustí, J., Llenas, M., 1996. The late Turolian murid rodent succession in eastern Spain. Acta Zool. Cracov. 39 (1), 47–56 (Kraków).
- Agustí, J., Moyà Sola, S., Gibert, J., Guillén, J., Labrador, M., 1985. Nuevos datos sobre la bioestratigrafía del Neógeno continental de Murcia. Paleontol. Evol. 18, 83–94 (Sabadell).
- Agustí, J., Cabrera, L., Garcés, M., Krijgsman, W., Oms, O., Parés, J. M., 2001. A calibrated mammal scale for the Neogene of Western Europe. State of the art. Earth Sci. Rev. 52, 247–260.
- Aharon, P., Goldstein, S.L., Wheeler, C.W., Jacobson, G., 1993. Sea-level events in the South Pacific linked with the Messinian Salinity Crisis. Geology 21, 771–775.
- Alberdi, M., Morales, J., Moyà, S., Sanchiz, B., 1981. Macrovertebrados (Reptilia y Mammalia) del yacimiento finimioceno de Librilla (Murcia). Est. Geol. Sect. 37, 307–312.
- Benammi, M., Calvo, M., Prévot, M., Jaeger, J.J., 1996. Magnetostratigraphy and paleontology of Aït Kandoula basin (High Atlas, Morocco) and the African–European late Miocene terrestrial fauna exchanges. Earth Planet. Sci. Lett. 145, 15–29.
- Benson, R.H., Rakic-El Bied, K., Bonaduce, C., 1991. An important reversal (influx) in the Rifian Corridor (Morocco) at the Tortonian–Messinian boundary: The end of Tethys Ocean. Paleoceanography 6 (1), 164–192.
- Braga, J.C., Martín, J., 1996. Geometries of reef advance in response to relative sea-level changes in a Messinian uppermost Miocene) fringing reef (Cariatiz Reef, Sorbas Basin, SE Spain). Sediment. Geol. 107, 61–81.
- Brandy, L.D., Jaeger, J.J., 1980. Les échanges de faunes terrestres entre l'Europe et l'Afrique nord-occidentale au Messinien. C. R. Acad. Sci., Paris 291, 465–468.
- Castillo, C., Agustí, J., 1996. Early Pliocene rodents (Mammalia) from Asta Regia (Jerez basin, Southwestern Spain). Proc. Kon. Ned. Akad. Wetensch. 99 (1–2), 25–43 (Utrecht).
- Clauzon, G., Suc, J.-P., Gautier, F., Berger, A., Loutre, M.-F., 1996. Alternate interpretation of the Messinian salinity crisis: controversy resolved? Geology 24 (4), 363–366.
- Coiffait, B., Coiffait, P.E., Jaeger, J.J., 1985. Découverte en Afrique du Nord des genres *Stephanomys* et *Castillomys* (Muridae) dans un nouveau gisement de microvertébrés néogènes d'Algérie orientale: Argoub Kemellal. Proc. Kon. Ned. Akad. Wetensch. 88 (2), 167–183 (Utrecht).
- Crusafont, M., Adrover, R., Golpe, J.M., 1964. Découverte dans le Pikermien d'Espagne du plus primitif des hippopotames: *Hippopotamus (Hexaprotodon) primaevus* n. sp. C. R. Acad. Sci., Paris 258, 1572–1575.
- de Bruijn, H., 1974. The Ruscinian rodent succession in Southern Spain and its implications for the biostratigraphic correlation of Europe and North Africa. Senckenbergiana Lethaea 55, 435–443.
- De Larouzière, F.D., Bolze, J., Bordet, P., Hernández, J., Montecat, C., Ott d'Estevou, P., 1988. The Betic segment of the lithospheric Trans-Alboran shear zone during the late Miocene. Tectonophysics 152, 41–52.
- Garcés, M., Krijgsman, W., Agustí, J., 1998. Chronology of the late Turolian of the Fortuna Basin (SE Spain): implications for the Messinian evolution of the eastern Betics. Earth Planet. Sci. Lett. 163, 69–81.

- Garcés, M., Krijgsman, W., Agustí, J., 2001. Chronostratigraphic framework and evolution of the Fortuna Basin (Eastern Betics) since the late Miocene. *Basin Res.* 13, 199–217.
- Hendey, Q.B., 1979. *Agriotherium* (Mammalia, Ursidae) from Langebaanweg, South Africa, and relationships of the genus. *Ann. South Afric. Mus.* 81, 1–109.
- Hilgen, F.J., Krijgsman, W., 1999. Cyclostratigraphy and astrochronology of the Tripoli diatomite formation (pre-evaporite Messinian, Sicily, Italy). *Terra Nova* 11, 18–22.
- Hodell, D.A., Benson, R.H., Kent, D.V., Boersma, A., Rakic-El Bied, K., 1994. Magnetostratigraphic, biostratigraphic, and stable isotope stratigraphy of an upper Miocene drill core from the Salé Briqueterie (northwestern Morocco): a high-resolution chronology for the Messinian stage. *Paleoceanography* 9, 835–855.
- Hodell, D.A., Curtis, J.H., Sierro, F.J., Raymo, M., 2001. Correlation of late Miocene to early Pliocene sequences between the Mediterranean and North Atlantic. *Paleoceanography* 16 (2), 164–178.
- Hsü, K.J., 1978. Stratigraphy of the lacustrine sedimentation in the Black Sea. *Initial Reports of the Deep Sea Drilling Project*, vol. 42B, pp. 509–524.
- Hsü, K.J., Cita, M.B., Ryan, W.B.F., 1973. The origin of the Mediterranean evaporites. *Initial Reports of the Deep Sea Drilling Project*, vol. 42, pp. 1203–1231.
- Jaeger, J.-J., 1977. Les Rongeurs du Miocène moyen et supérieur du Maghreb. *Palaeovertebrata* 8 (1), 1–166 (Montpellier).
- Jaeger, J.J., Michaux, J., Tähler, L., 1975. Présence d'un rongeur muridé nouveau, *Paraethomys miocaenicus* n. sp., dans le Turolien supérieur du Maroc et d'Espagne. Implications paléogéographiques. *C. R. Acad. Sci., Paris* 280, 1673–1676.
- Kastens, K.A., 1992. Did glacio-eustatic sea level drop trigger the Messinian salinity crisis? New evidence from Ocean Drilling Program Site 654 in the Tyrrhenian Sea. *Paleoceanography* 7, 333–356.
- Kohler, M., Moyà, S., Alba, D.M., 2000. *Macaca* (Primates, Cercopithecidae) from the late Miocene of Spain. *J. Hum. Evol.* 38, 447–452.
- Krijgsman, W., Garcés, M., Langereis, C.G., Daams, R., van Dam, J., van der Meulen, A., Agustí, J., Cabrera, L., 1996. A new chronology for the middle to late Miocene continental record in Spain. *Earth Planet. Sci. Lett.* 142, 367–380.
- Krijgsman, W., Hilgen, F.J., Raffi, I., Sierro, F.J., Wilson, D.S., 1999. Chronology, causes and progression of the Messinian salinity crisis. *Nature* 400, 652–655.
- Krijgsman, W., Garcés, M., Agustí, J., Raffi, I., Taberner, C., Zachariasse, W.J., 2000. The Tortonian salinity crisis of the eastern Betics (Spain). *Earth Planet. Sci. Lett.* 181, 497–511.
- Krijgsman, W., Fortuin, A.R., Hilgen, F.J., Sierro, F.J., 2001. Astrochronology for the Messinian Sorbas basin (SE Spain) and orbital (precessional) forcing for evaporite cyclicity. *Sediment. Geol.* 140, 43–60.
- Krijgsman, W., Blanc-Valleron, M.M., Flecker, R., Hilgen, F.J., Kouwenhoven, T.J., Merle, D., Orszag-Sperber, F., Rouchy, J.-M., 2002. The onset of the Messinian salinity crisis in the Eastern Mediterranean (Pissouri Basin, Cyprus). *Earth Planet. Sci. Lett.* 194, 299–310.
- Martín-Suárez, E., Freudenthal, M., 1994. *Castromys*, a new genus of Muridae (Rodentia) from the late Miocene of Spain. *Scr. Geol.* 106, 11–43 (Leiden).
- Martín-Suárez, E., Freudenthal, M., Krijgsman, W., Ritger Fortuin, A., 2000. On the age of the continental deposits of the Zorreras Member (Sorbas basin, SE Spain). *Geobios* 33 (4), 505–512.
- Mein, P., Bizon, G., Bizon, J.J., Montenat, C., 1973. Le gisement de Mammifères de La Alberca (Murcia, Espagne méridionale). Corrélations avec les formations marines du Miocène terminal. *C. R. Acad. Sci., Paris*, D 276, 3077–3080.
- Mein, P., Adrover, R., Moissenet, E., 1990. Biostratigraphie du Néogène supérieur du bassin de Teruel. *Paleontol. Evol.* 23, 121–139 (Sabadell).
- Montenat, C., Ott d'estevou, P., Coppier, G., 1990. Les Bassins Neogenes entre Alicante et Cartagena. *Doc. Trav. IGAL, Mem. Hors-Ser.* 12–13, 313–368.
- Morales, J., 1984. Venta del Moro: su macrofauna de mamíferos y biostratigrafía continental del Mioceno terminal mediterráneo. PhD thesis, Edit. Univ. Complut. Madrid, pp. 1–340.
- Opdyke, N., Mein, P., Moissenet, E., Pérez-González, A., Lindsay, E., Petko, M., 1990. The magnetic stratigraphy of the late Miocene sediments of the Cabriel Basin, Spain. *Lindsay, Fahlbusch and Mein: European Neogene Mammal Chronology*. Plenum Press, New York, pp. 507–514.
- Pickford, M., Morales, J., Soria, D., 1994. Fossil camels from the upper Miocene of Europe: implications for biogeography and faunal change. *Geobios* 28 (5), 641–650.
- Pickford, M., Moyà, S., Mein, P., 1997. A revised phylogeny of Hyracoidea (Mammalia) based on new specimens of Pliohyracidae from Africa and Europe. *N. Jb. Geol. Palaontol. Abb.* 205 (2), 265–288 (Stuttgart).
- Pons-Moyà, J., 1987. *Fortunictis acerensis* nov. sp., nuevo Metailurino (Mammalia, Carnivora) del Mioceno superior de la Península Ibérica. *Paleontol. Evol.* 21, 63–68 (Sabadell).
- Sanz de Galdeano, C., 1990. Geologic evolution of the Betic Cordilleras in the Western Mediterranean, Miocene to the present. *Tectonophysics* 172, 107–119.
- Sanz de Galdeano, C., Vera, R., 1992. Stratigraphic record and palaeogeographical context of the Neogene basins in the Betic Cordillera, Spain. *Basin Res.* 4, 21–36.
- Sierro, F.J., Hilgen, F.J., Krijgsman, W., Flores, J.A., 2001. The Abad composite (SE Spain): a Messinian reference section for the Mediterranean and the APTS. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 168, 141–169.
- Soria, J.M., Viseras, C., Fernández, J., 1998. Late Miocene–Pleistocene tectono-sedimentary evolution and subsidence history of the central Betic Cordillera (Spain): a case study in the Guadix intramontane basin. *Geol. Mag.* 135, 565–574.
- Suc, J.P., Bessais, E., 1990. Pérennité du climat thermo-xérique en Sicilie avant, pendant et après de la crise de salinité messinienne. *C. R. Acad. Sci., Paris* 310, 1701–1707.
- Suc, J.P., Fauquette, S., Bessedik, M., Bertini, A., Zheng, Z., Clauzon, G., Suballyova, D., Diniz, F., Quézel, P., Feddi, N., Clet, M., Bessais, E., Bachiri, N., Meon, H., Comborieu-Nebout, N., 1999. Neogene vegetation changes in West European and West circum-Mediterranean areas. In: Agustí, J., Rook, L., Andrews, P. (Eds.), *Evolution of Neogene Terrestrial Ecosystems in Europe*. Cambridge University Press, pp. 378–388.
- Van der Made, J., 1990. Iberian Suoidea. *Paleontol. Evol.* 23, 83–97 (Sabadell).
- van der Weerd, A., 1976. Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alfambra region, Spain. *Utrecht Micropaleontol. Bull.* 2, 1–217.