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Some considerations on small mammal evolution in Southern Germany, with emphasis on Late Burdigalian–Earliest Tortonian (Miocene) cricetid rodents



Quelques considérations concernant l'évolution des petits mammifères du Sud de l'Allemagne, focalisées sur les rongeurs cricétidés de la fin du Burdigalien à la base du Tortonien (Miocène)

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ARTICLE INFO

Article history:

Received 21 April 2016

Accepted after revision 6 July 2016

Available online 30 August 2016

Handled by Isaac Casanovas-Vilar

Keywords:

North Alpine Foreland Basin

Franconian Jura

Swabian Jura

Cricetidae

Rodentia

Biostratigraphy

Faunal turnovers

ABSTRACT

The recent advances regarding the complex chronobiostratigraphy of Middle Miocene terrestrial deposits of southern Germany are reviewed. We propose new and revised correlations between the Swiss and South German faunas framework for ongoing research. We restrict our analysis to the cricetid and microtoid murid rodents, especially the *Megacricetodon* and cricetodontine groups, because of their importance for this purpose. Faunal turnovers reflect global climate changes. Species level endemism is punctuated by several immigration events, and a possible westward spread of faunal associations is suggested at around 13.8 Ma and, at the end of the Middle Miocene, by introduction of Late Miocene lineages from the east.

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R É S U M É

Les récentes avancées liées à la chronobiostratigraphie complexe des dépôts terrestres du Miocène moyen du Sud de l'Allemagne sont synthétisées. Les possibles corrélations (nouvelles et modifiées) entre les faunes suisses et du Sud de l'Allemagne sont proposées, sur la base des recherches en cours. Nous limitons l'analyse aux rongeurs muridés cricétidés et microtidés, spécialement les groupes *Megacricetodon* et cricétodontinés, à cause de

Mots clés :

Bassin nord-alpin

Jura franconien

Jura souabe

Cricetidae

Rodentia

Biostratigraphie

Renouvellements fauniques

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<http://dx.doi.org/10.1016/j.crpv.2016.08.002>

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leur importance pour ce sujet. Les renouvellements fauniques reflètent les changements climatiques globaux. L'endémisme des espèces est ponctué par plusieurs événements migratoires, et un possible déplacement vers l'ouest des associations faunistiques est suggéré à environ 13,8 Ma, ainsi qu'à la fin du Miocène moyen, par l'introduction de lignées d'origine orientale et caractéristiques du Miocène supérieur.

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1. Introduction

The North Alpine Foreland Basin (NAFB) is one of the best studied basins regarding the evolution of the Early-Middle Miocene European ecosystems. Numerous localities discovered during the last century have provided important mammal collections, which allow a local division of the Miocene deposits into several biostratigraphic units, framed in a robust chronological background based on integrated studies (e.g., Abdul Aziz et al., 2008, 2010; Kálin and Kempf, 2009; Reichenbacher et al., 2013, and references therein). Often based on small mammals, these local subdivisions basically demonstrate many similarities of the Swiss and South German records. However, some correlation problems have been intensively discussed in the recent literature (e.g., Reichenbacher et al., 2013). As a result, interpretations regarding the evolution of the terrestrial ecosystems within Europe are hazardous (e.g., van der Meulen et al., 2011).

The aim of this work is to provide the reader with an overview of the chronobiostratigraphic advances in southern Germany and some considerations on the small mammal evolution in this area as compared to the nearby Swiss record. We consider herein only the cricetid rodents, including those genera that show an initial increase of hypsodonty and that are often designated non-taxonomically as “microtoid cricetids” (Schaub, 1934). We have selected these groups because of their biostratigraphic value as well as their abundance in Early-Middle Miocene faunas. The genus *Eumyarion* is excluded from the analysis because of taxonomical problems. Finally, the main evolutionary patterns are discussed in the framework of global climate changes and their effects on these taxa in Europe.

2. Short geological overview of southern Germany

2.1. The North Alpine Foreland Basin (NAFB)

The NAFB is a classical foreland basin situated at the northern margin of the Alps and belongs to the biogeographic entity of the Paratethys (Fig. 1A). It extends from western France (Haute-Savoie) through Switzerland, South Germany to Austria. The thickness of the eroded sediments deriving from the uplifting Alps can reach up to more than 4 km near the mountains (e.g., Lemcke, 1988). In Germany, these deposits are divided into five main units based on depositional environments: the Lower Marine Molasse (UMM; Note that here we use the German abbreviations: *Untere Meeresmolasse*; Early and Middle Oligocene); the Lower Freshwater Molasse (USM; *Untere Süßwassermolasse*; Late Oligocene-Early Miocene) rich in

terrestrial fossils (e.g., Werner, 1994), the Upper Marine Molasse (OMM; *Obere Meeresmolasse*; Early Miocene); the Upper Brackish-water Molasse (OBM; *Obere Brackwassermolasse*) and the Upper Freshwater Molasse (OSM; *Obere Süßwassermolasse*; Fig. 1C). The latter two units are the main subject of this work. During the Alpine nappe tectonism, the molasse sediments were thrust, and the deposits piled up in a stack of southward dipping thrust sheets at the northern margin of the mountains, the Folded Molasse (Fig. 1B).

During the OMM (Ottangian), the Paratethys was connected with the western Mediterranean Tethys by the “Burdigalian seaway”, and a basin-wide transgression flooded the NAFB (e.g., Rögl, 1998). While the marine conditions continued in the Late Ottangian of Switzerland, the southwestern German Molasse basin was affected by a regression during the Middle Ottangian (e.g., Lemcke, 1988). The regression resulted in the development of the Graupensand River, which eroded the underlying OMM and USM (*Graupensandrinne*; e.g., Doppler et al., 2005), and the channel was infilled by the Grimmelfingen Formation, which contains land mammals in its basal part (e.g., Sach and Heizmann, 2001). The uppermost part of the overlying Kirchberg Formation, probably a short transgression of the Swiss Molasse Sea (e.g., Doppler, 2011; Lemcke, 1988; Reichenbacher, 1989), yielded the oldest *Megacricetodon* remains of the area (Reichenbacher et al., 2004).

Following the OBM, the OSM is characterized by strong temporal and lateral variability of continental facies; while radial alluvial fan sedimentation was prevalent in the southern/southwestern part of the basin, east/west fluvial deposits accumulated in the northern part leading to strong differences in the division of lithostratigraphic units from east to west (Abdul Aziz et al., 2008, 2010; Doppler, 1989; Doppler et al., 2005 and references therein). In the northern realm, some specific deposits, such as freshwater calcareous muds, with clear influence from Swabian Alb are termed as “sub-Jurassic”, and contain remarkable fossil mammals like hominoids (Böhme et al., 2011; Heizmann and Begun, 2001; Ziegler, 1995). Finally, important marker beds, derive from the consequences of a meteor impact (see below) and volcanic activities that produced several layers of bentonite, clays formed by the weathering of volcanic ash in a water-bearing environment. At least four of these volcanoclastic horizons are reported from Switzerland, and three of them have been radiometrically dated at 14.20 ± 0.08 , 14.91 ± 0.09 and 15.27 ± 0.12 Ma (U^b-isotope techniques). In South Germany, at least four horizons have also been dated (⁴⁰Ar/³⁹Ar) at 16.10 ± 0.20 , 15.6 ± 0.40 , 14.55 ± 0.19 and 14.50 ± 0.20 Ma (Abdul Aziz et al., 2008, 2010; Rocholl et al., 2008).

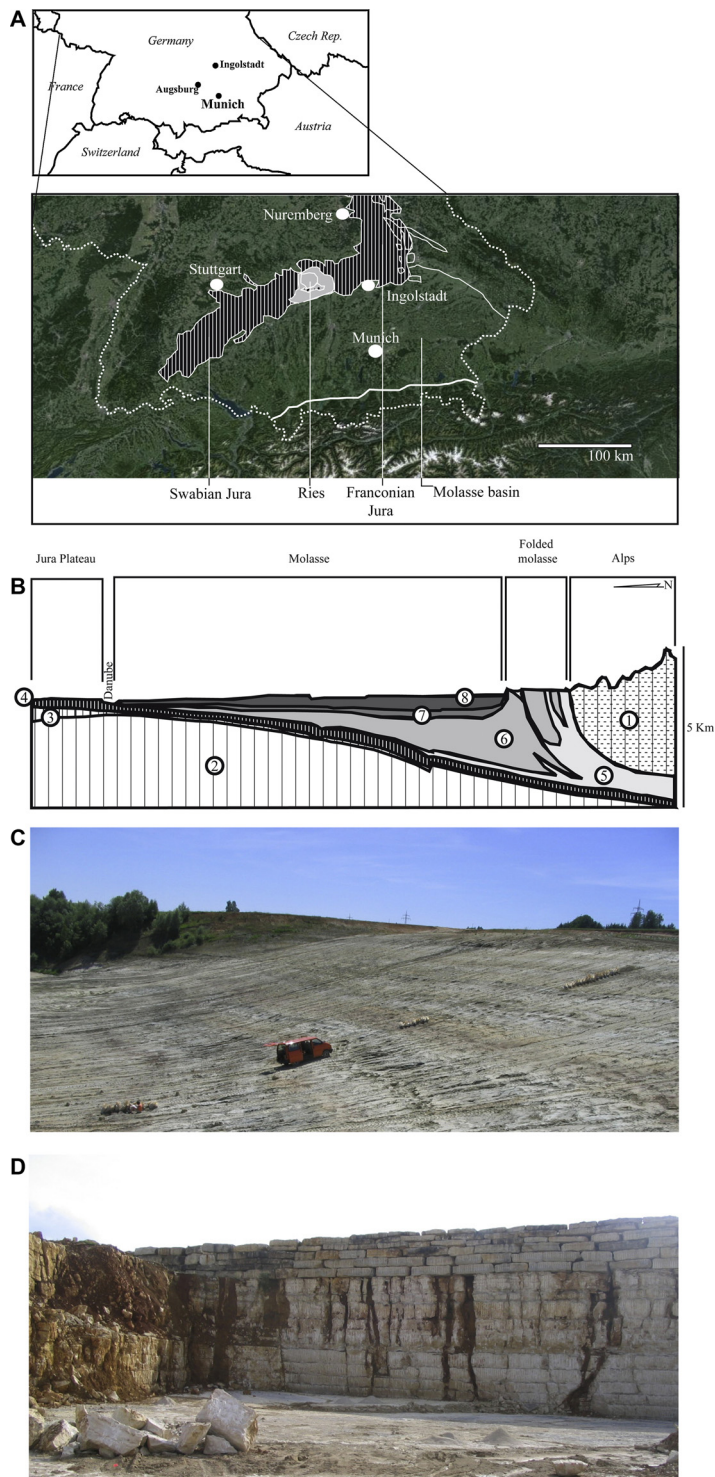


Fig. 1. A. Geographic situation of the study area. The shaded area shows the Jura Plateau. B. Schematic section along the Molasse basin. 1. Basement rock. 2. Triassic. 3. Jurassic. 4. Lower Marine Molasse. 5. Lower Freshwater Molasse. 6. Upper Marine Molasse. 7. Upper Freshwater Molasse. C. View of the Puttenhausen section (North Alpine Foreland Basin). D. View of fissure fillings from Petersbuch (Franconian Jura).

Fig. 1. A. Position géographique de la région étudiée. Les zones ombrées indiquent le plateau calcaire jurassique. B. Coupe schématique du bassin molassique. 1. Base. 2. Trias. 3. Jurassique. 4. Molasse marine inférieure. 5. Molasse d'eau douce inférieure. 6. Molasse marine supérieure. 7. Molasse d'eau douce supérieure. C. Vue de la section de Puttenhausen (Bassin nord-alpin). D. Vue de remplissages karstiques à Petersbuch (Jura franconien).

2.2. The Jura Plateau

The Swabian Jura and its eastern continuation (Franconian Jura) are part of the Jura Mountains and are separated by the Nördlinger Ries meteor crater (see below). The Jura plateau delimits the northern part of the Molasse basin in our study area (Fig. 1A). Formed during the Jurassic period, three layers of limestone are defined as the Black, Brown and White Jura. Because of its extremely high concentration of calcium carbonate, the White Jura is karstic. Fissures and cave infillings are sporadically rich in fossils so that they attracted the early mammal palaeontologists and provided spectacular specimens (e.g., Dehm, 1935; Schlosser, 1902) that range from the Oligocene to the Quaternary (e.g., Rummel, 1993, and references therein). Some quarries provided an incredible amount on fossil-enriched fissures, such as the White Jura near Petersbuch (Fig. 1D) were more than 120 fossil-bearing infillings are documented. These often contain many small mammals as the result of the accumulation of raptor pellets (e.g., Bolliger and Rummel, 1994; Klietmann, 2013; Klietmann et al., 2015; Prieto and Rummel, 2009a, 2009b, 2009c; Rosina and Rummel, 2012, and references therein).

2.3. Ries crater and Steinheim basin

The Nördlinger Ries is 24 km in diameter, whereas the Steinheim basin, formed by the impact of the smaller asteroid, is less than 4 km in diameter. This is one of the best-preserved impact structures of a binary asteroid. The age of this event is a matter of debate, but the impacts range between 14.6 and 15 Ma (e.g., Buchner et al., 2013 and references therein). Herein we follow Rocholl et al. (2011) who propose 14.94 ± 0.07 Ma for the Ries event.

Among the Ries impact ejecta, the distal ones are excellent marker beds. Isolated boulders mainly consisting of Upper Jurassic limestones are dispersed along the OSM in the form of large-sized “Reuter’scher Block” (e.g., Sach, 2014a and references therein), while smaller pieces are found in the so-called Boulder Horizon (*Brockhorizont*; e.g., Sach, 1997, 2004, 2014b) up to 180 km away from the crater (Fig. 2).

Both impact structures were filled by meteoric water forming an oligotrophic lake for the Steinheim basin and a shallow evaporitic saline lake for the Ries crater (see Tütken et al., 2006 and references therein). The deposits from Steinheim have provided an important and large collection of fossil animals and plants (Heizmann and Reiff, 2002; Tütken et al., 2006). In particular, the historical study based on the planorbid snails (Hilgendorf, 1867) is seen today as one of the first fossil evidences of Darwin’s evolutionary theory (Rasser, 2013, and references therein). The Ries lake deposits are much poorer, with the notable exception of fossil birds. Locally, important fossil-enriched layers occur, such as in the clays from Wemding, which contain a rich fauna including insects (e.g., Bolten et al., 1976). Similarly, the fissure and pocket fillings at the top of the spring mounds (travertines) may contain rich and extremely well-preserved small mammals, such as at Goldberg and Steinberg (e.g., Heizmann and Fahlbusch, 1983; Rachl, 1983; Ziegler, 1983).

2.4. Volcanigenic lakes

Maar lakes are characterized by anoxia that is a prerequisite for an exceptional preservation potential for fossils, as shown, for instance, by the Eocene Eckfeld and Messel localities. Within the scope of this paper is the Randecker Maar, which has been intensively studied by Rasser et al. (2013 and references therein; Figs. 1 and 2). It belongs to the Urach-Kirchheim volcanic field. It has a diameter of ca. 1200 m and a maximum depth of 130 m. Of the 363 taxa identified, plants and insects are the most represented groups. The mammal fauna correlates to the OSM C + D (see below).

3. Biochronology of the OSM: a historical perspective

Biostratigraphic studies of the southern German Molasse began as early as the end of the 19th century (e.g., Gümbel, 1889), and in the first half of the 20th century scholars proposed some unsatisfying approaches (e.g., Stromer, 1940). Later on, and thanks to richer fossil collections, the German OSM and its brackish-water equivalents were divided into three distinct series on the basis of the presence/absence of deinotheriid proboscideans (Dehm, 1951, 1955). The Older Series (*Altere Serien*) lacks deinotheres. The Middle Series (*Mittlere Serien*) presents *D. bavaricum* and the Younger Series (*Jüngere Serien*) *D. aff. giganteum*. The subsequent use of screen washing of fossil-rich sediments allowed Fahlbusch (1964) to propose a relative age for some German localities based on the evolutionary stage of some cricetid rodents. Afterwards a series of publications describing the cricetids, eomyids and sciurids followed (e.g., Black, 1966; Fahlbusch, 1966, 1970, 1975; Fahlbusch and Mayr, 1975). This work was completed with contributions on Swiss fauna (e.g., Engesser, 1972) or dealing with other small mammal groups such as the gliroids (Mayr, 1979). On the basis of these advances, Jung and Mayr (1980) proposed a biostratigraphy for the German Molasse basin within the framework of the MN zonation. Simultaneously, the study of the impact of the Ries meteorite on the faunas stimulated intensive fieldwork. This led to the discovery of important faunas and the characterization of a new faunal succession stratigraphically related to the boulder horizon (Fiest, 1989; Heissig, 1989; Scholz, 1986a, 1986b). This allowed Heissig (1990) to divide the Middle Series in three parts based on cricetid rodents.

In the meantime, intense fieldwork was carried out in the Swiss part of the NAFB. Following the “International Symposium on Mammalian Biostratigraphy and Palaeoecology of European Paleogene” in 1987 in Mainz, Engesser and Mayo (1987) and Engesser (1990a) proposed a biozonation for the Swiss USM and OMM, and, supported by studies based on specific mammal groups like eomyids (Engesser, 1990b), extended the biozonation to the OSM.

In the 1990’s, a number of publications provided a wealth of new data on the small mammal faunas of the Molasse basin (e.g., Bolliger, 1992a, 1992b, 1994a, 1994b, 1996, 1998, 2000; Boon, 1991; Kälin, 1993, 1997a, 1997b; Reichenbacher et al., 1998a, 1998b). This resulted in the

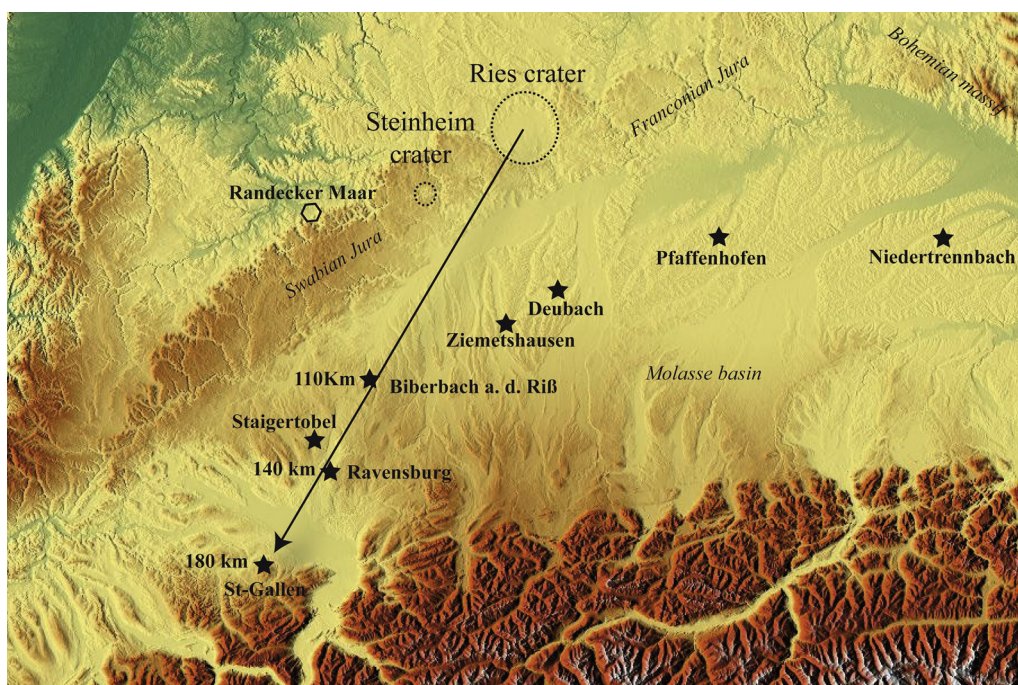


Fig. 2. Ries impact crater, Steinheim basin and Randecker Maar. Position of some distal boulder horizons (ejecta) in the North Alpine Foreland Basin.
Fig. 2. Cratère du Ries, bassin de Steinheim et Maar de Randeck. Position dans le Bassin nord-alpin de quelques horizons contenant les éjecta de l'impact.
 After Buchner et al., 2007 and Sach, 2014b.

first proposals of a small mammal-based biostratigraphy during the 1997 Biochrom' congress in Montpellier, France, that were published in three separate contributions in the volume devoted to that congress, Heissig (1997) divided the German part of the OSM into six biozones (OSM A–F). The Older Series are related to OSM B–D and Middle Series to OSM E–F. Kálin (1997c) completed the work of Engesser (1990a) and added three Swiss reference faunas and Bolliger (1997) added five other younger reference faunas. Finally, Sach and Heizmann (2001) presented their results concerning the mammal successions in the area of Ulm, southern Germany.

Böhme et al. (2003) re-evaluated the influence of the Ries impact in the terrestrial faunas and at the same time studied the stratigraphic distribution of the mammals in the OSM in South Germany. As a result of their work they added the OSM E' biozone.

Abdul Aziz et al. (2008) proposed an integrated stratigraphy for the OSM in eastern Bavaria. They merged the OSM C and D. Later on, Abdul Aziz et al. (2010) extended their study to the western part of Bavaria. In the meantime, Kálin and Kempf (2009) provided a high-resolution bio- and magnetostratigraphy for the Swiss molasse, and discussed the correlation of the local OSM zonation with both the European MN units and German biozonation, noting that the mammal succession in the NAFB is nearly identical for the two countries.

These results allowed van der Meulen et al. (2011) to compare in detail the faunal succession in the Aragonian type area (Spain) and the NAFB, and thus underline some synchronies and diachronies between them. These authors further discuss the use of the MN zones at the European

scale (see also Van Dam, 2003). This theme was the subject of an RCMNS workshop in Krumbad (Germany) in 2012. Reichenbacher et al. (2013) re-interpreted the previously established local magnetostratigraphy of the Early Miocene part of the OSM (see also Jost et al., 2015).

Finally, Kirscher et al. (2016) dated the locality Hammerschmiede at around 11.6 Ma, making it a chronostratigraphic tie point for the base of the Tortonian.

4. The cricetid rodent succession in South Germany: taxonomical notes

Before discussing cricetid-based biostratigraphy, we provide some taxonomical remarks on the most important taxa (mainly lineages) that are useful for correlation.

4.1. “*Megacricetodon bavaricus* group”

This group is used in the sense of Oliver Pérez and Peláez-Campomanes (2013) and Oliver Pérez (2015). It thus includes *Megacricetodon* aff. *collongensis*, *M. bavaricus*, *M. aff. bavaricus*, *M. bezianensis*, *M. lappi*, *M. aunayi* and *M. vandermeuleni*, of which the latter two have not been yet recognized from the NAFB. Berger (2010) assigns some teeth from Georgensgmünd to *M. bourgeoisi*, a species originally only known from France. This is a feasible proposal and it deserves attention, but the taxonomic assignment in our opinion lacks justification, and so does the proposed synonymy of *M. bourgeoisi* with *M. bezianensis*. Pending a detailed comparison between these taxa, we prefer to retain these species in order to simplify the biostratigraphy. In Germany, the lineage *M. aff. collongensis*–*M. lappi*

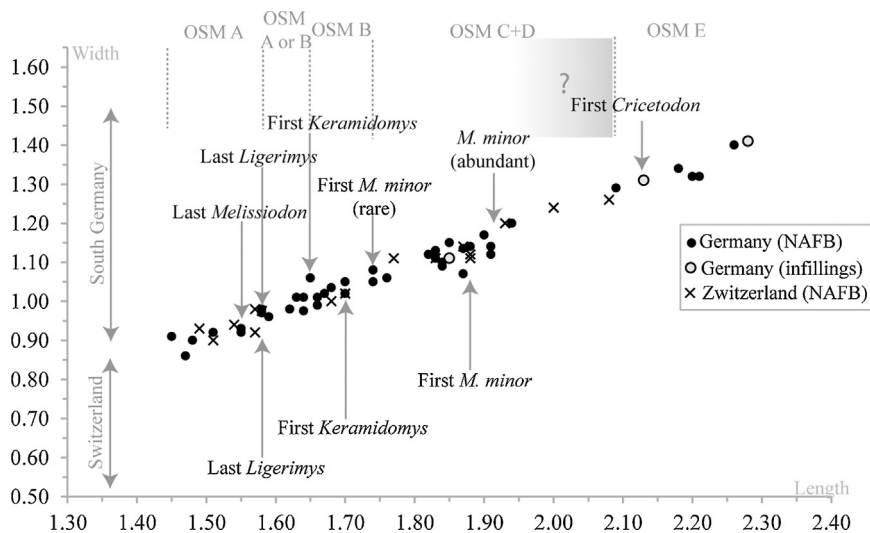


Fig. 3. Length/width diagram of the first lower molar (mean values) of “*Megacricetodon bavaricus* group” from different localities of South Germany and Switzerland. Note the anagenetic trend in size increase through time. The major stratigraphical divisions of the Molasse Basin, as well as occurrences of biostratigraphically important taxa are also included in the graph (see text for details).

Fig. 3. Diagramme de répartition des tailles moyennes de la première molaire inférieure du « groupe *Megacricetodon bavaricus* » (valeurs moyennes) de différentes localités du Sud de l’Allemagne et de Suisse. À noter la tendance anagénétique d’augmentation de taille au cours du temps. Les divisions stratigraphiques majeures du bassin molassique, ainsi que les premières apparitions de taxons importants pour la biostratigraphie sont incluses dans le graphique (se référer au texte pour les détails).

is mainly characterized by a size increase through time (Fig. 3; e.g., Abdul Aziz et al., 2010), and the limit between the closely related species is hard to define. The forms closer to *M. lappi* show a stronger lingual anterolophid than in the older species (Prieto et al., 2009). In the present work we use the size of the m1 in order to characterize the species occurring in different biostratigraphic units. We do not consider valid the proposal of Aguilar (1995) of a *M. bavaricus*–*M. germanicus* lineage. Mein and Freudenthal (1971a) defined the subgenus *Collongomys* for the species *M. lappi*. This proposal was mainly based on differences in mandibular characters, but has not been followed afterwards. Indeed, a comparison with mandibles of *M. bavaricus* is needed (M. Freudenthal, pers. com. 2012), and it could have consequences for the traditional arrangement of the lineage.

4.2. “*Megacricetodon germanicus* group”

Prieto and Rummel (2009a) describe *Megacricetodon* aff. *germanicus* from Petersbuch 68. They recognize a strong resemblance with the species from Zeglingen as stated by Kälin (1993, 1997b). The same year, Kälin and Kempf (2009) emended their original assignment into *M. gersii* without detailing their reasons. Afterwards, Maridet and Sen (2012) provided new data on the material of the type locality for this species (Sansan, France) and they further showed the similarities in size between the two species. Their morphology is also similar. As a result, the German specimens are assigned to *M. gersii*. In many aspects, *M. gersii* resembles *M. germanicus* from Anwil, and it may be justified to include them in the same lineage. On the other hand, *M. gersii* and *M. germanicus* co-occur in a single Swiss locality, namely Grat 930 m (Kälin and Kempf, 2009), together with two

other small-sized *Megacricetodon* species. Unfortunately, a detailed description is not provided, and these data likely derive from unpublished new material because Bolliger (1992a) does not report such a diversity of *Megacricetodon* in the locality. Thus we cannot judge whether *M. gersii* and *M. germanicus* are sympatric species (and define a lineage) or not in the NAFB. In addition, Prieto (2007) described the *Megacricetodon* material from different fissure fillings from Petersbuch. Especially in Petersbuch 6 and 18, he recognized m1 morphotypes that better allocated the specimens to the “*M. germanicus* group”, while other teeth correspond to a *M. gregarius*-like species. These differences are not seen in the other molars. Finally, a new *Megacricetodon* was recently described by Oliver Pérez in his thesis (2015) based on material from the late Middle Miocene of the Calatayud Basin (Spain; Las Umbrias 22; see García-Paredes et al., 2016). The species differs from *M. gersii* mainly by its larger size, while it is smaller than *M. germanicus*. The inclusion of this form in the “*M. germanicus* group” should be studied in greater detail.

4.3. *Megacricetodon* cf. *gregarius*

Megacricetodon m1s with a clearly divided anteroconid are easily recognizable in the NAFB, yet rarely recorded, most probably because of their short stratigraphic range (Fig. 4E). *M. gregarius*-like species are only reported in Germany from Steinheim and Petersbuch 31 (e.g., Prieto, 2007; Fig. 4F). As noted above, some m1s from Petersbuch 6 and 18 show also a clearly divided anteroconid. Prieto (2007) concluded that the *Megacricetodon* material from these localities belonged to one highly variable species (*M. aff. germanicus*). Indeed, a revision of these forms is needed, as the presence of two species could not be discarded. First

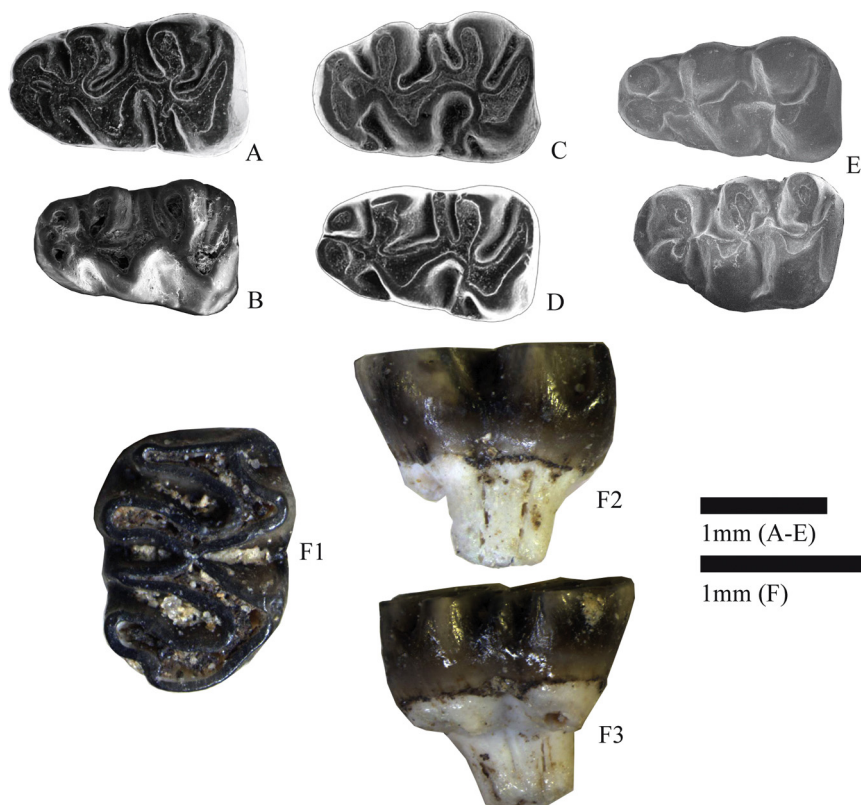


Fig. 4. A. ?*Collimys* sp. m1 from Kleineisenbach. B. *Collimys* sp. m1 from Mörgen. C. *Collimys hiri* m1 from Hammerschmiede. D. *Collimys doboosi* m1 from Hillenloh. E. *Megacricetodon* cf. *gregarius* from Steinheim (above: m1; under: M1). F. *Microtracricetus* sp. M2 from Mörgen (F1: occlusal view; F2: labial view; F3: lingual view).

Fig. 4. A. ?*Collimys* sp. m1 de Kleineisenbach. B. *Collimys* sp. m1 de Mörgen. C. *Collimys hiri* m1 de Hammerschmiede. D. *Collimys doboosi* m1 de Hillenloh. E. *Megacricetodon* cf. *gregarius* de Steinheim (au-dessus : m1 ; au-dessous : M1). F. *Microtracricetus* sp. M2 de Mörgen (F1 : vue occlusale ; F2 : vue labiale ; F3 : vue linguale).

of all, the assignment of the remains from Steinheim and Petersbuch 31 has not been, in our opinion, sufficiently discussed, and the same applies to the Swiss material (Bolliger, 1994a, 1994b; Kälin et al., 2001). The “*M. gregarius*” morphotypes from Petersbuch 6 and 18 differ slightly from the species from Steinheim, and are assigned as *M. cf. gregarius*.

4.4. “*Collimys transversus* group”

The low-crowned species *C. transversus* was defined by Heissig (1995) on the basis of a few molars from Steinheim. Prieto and Rummel (2009c) added *C. gudrunae* from Petersbuch 31 to this genus. *Collimys gudrunae*, though also low-crowned, is clearly larger than *C. transversus*. An intermediate form is recognized in Petersbuch 26 and currently assigned as *C. aff. transversus*. These three forms represent a single lineage.

A questionable record of *C. gudrunae* corresponds to a single m1 from Petersbuch 18. Kälin and Kempf (2009) reported *Collimys* in Anwil. Prieto (2007) and Prieto and Rummel (2009c, 2009d) did not identify the genus in neither Kleineisenbach nor in Giggenhausen, perhaps due to its strong resemblance with *Democricetodon freisingensis*. Indeed, one single tooth from Kleineisenbach might be

attributed to *Collimys* (Fig. 4A), but is not included in the “*C. transversus* group”.

4.5. “*Collimys longidens* group”

In Germany, and possibly in the NAFB as well, the lineage *Collimys hiri*–*C. longidens*–*C. doboosi* is mainly marked by size increase of the molars (Prieto and Rummel, 2009d) (Fig. 4B–D). In addition, Prieto et al. (2011) included a single m1 from Aumeister in this group. The anagenetic trend in size increase of the molars led Prieto and Rummel (2009d) to propose that the lineage is of great use for biostratigraphic purposes at the transition between the Middle and the Late Miocene. In contrast, this has been nuanced by Prieto et al. (2014) who suggest that given the present state of knowledge these taxa should not be used for long-distance correlations. Finally, the *Collimys* molars from Mörgen are relatively small and show a trilobed anteroconid (Fig. 4B). This character is observed in some specimens of *C. doboosi* (Hír, 2005).

4.6. Genus *Lartetomys*

The study of the *Lartetomys* material is currently ongoing by the authors and colleagues. Initial results indicate

that two species are present. *Lartetomys* (= *Mixocricetodon*) *dehmi* is present in the NAFB and fissure fillings (e.g., Ziemetshausen 1b, Petersbuch 39; Rummel, 1997). A second smaller species is scarcely recorded in Petersbuch 41 and Burg-Balzhausen (Rummel, 1997; Seehuber, 2009). The reader is referred to Prieto (2012a) and Prieto and Scholz (2013) for useful references regarding the species assigned to *Lartetomys* and *Karidomys*, and a discussion of previous synonymies.

4.7. Genus *Mirrabella*

Mirrabella is one of the rarest genera in the Miocene of Germany. A single M1 is reported from Rembach (Ziegler and Fahlbusch, 1986; as *Cricetidae* n. g. n. sp., Plate 10, fig. 2; see also De Bruijn and Saraç, 1992: Plate 13, fig. 3). De Bruijn et al. (2013) ascribe this specimen to *Mirrabella* cf. *tuberosa*, a species only recorded in the Early Miocene from Greece and Turkey.

5. Biostratigraphy of the South German Miocene deposits on the basis of the cricetid rodent succession

In this section, the German record is compared to the local biozonation for the Swiss molasse as proposed by Kälin and Kempf (2009). We follow the new correlations provided by Reichenbacher et al. (2013) for the pre-Riesian deposits. Our results are summarized in Table 1 and Fig. 5.

5.1. Pre-Riesian faunas

There is no fauna equivalent to the Swiss *Democricetodon franconicus*–*Megacricetodon collongensis* interval zone (Glovelier) in the German molasse because the deposits of the OMM have not provided any small mammals. In contrast, the German fissure fillings from Petersbuch and Erkertshofen have provided a nice picture of the small mammal faunas of this period (Fahlbusch, 1966, 1970; Heissig, 1978; Rummel, 1993; Wu, 1993; Ziegler, 1989; Ziegler and Fahlbusch, 1986).

In Germany, the differences between OSM A and OSM B are indeed characterized by the presence/absence of some eomyid rodent taxa. Kälin and Kempf (2009) remark that the first occurrence (FO) of *Keramidomys* in Switzerland is not contemporaneous with the last occurrence (LO) of *Ligerimys*, because both genera are never found in association, and because some localities from the same period do not record any Eomyidae at all. However, both genera occur in Germany. First, Sach and Heizmann (2001) listed them in Langenau 1. The size of the *Megacricetodon*, very small in this locality, is not in agreement with the expected size at the initial occurrence of *Keramidomys*. The fossil material has never been described, and our first observations (JP) show that the presence of *Keramidomys* is indeed doubtful. Secondly, Prieto (2015) reviewed the material from Eitensheim, originally assigned to *Keramidomys* n. sp. by Fahlbusch (1975). Indeed two genera are present in the collection, namely *Keramidomys* and a small *Ligerimys* species. However, we cannot exclude that the material of this site mixes fossils of slightly different ages, and question the

biostratigraphic value of such purported co-occurrence. In Germany, *Ligerimys*, as well as *Melissiodon*, become very rare near the end of the OSM A (herein as OSM A-REI). No Eomyidae are recorded in Reisensburg (Seehuber, 2015), but the locality contains *Melissiodon*. In contrast, a single tooth of *Ligerimys* is present in Günzburg 2. The first occurrence of *Keramidomys* is in Pöttmes (e.g., Prieto, 2010). As a consequence, some localities lacking eomyids are difficult to assign to a given OSM zone.

Heissig (1997) proposed that the German OSM B is defined by *M. bavaricus* and the first occurrence of *Democricetodon gracilis*, *D. mutilus* and *Anomalomys minor*. However, *D. gracilis* is present at the end of the OSM A (Forsthart, Reisensburg; see above). Regarding *D. mutilus*, Seehuber (2015) could not discard the presence of the species in Reisensburg. Therefore, we do not consider it a good index for OSM B. The stratigraphic range of *A. minor* has been emended by Böhme et al. (2003) and does not allow discrimination of OSM A from OSM B. For this reason, it is considered herein that the older documented occurrence of *Keramidomys* (Pöttmes, *Megacricetodon* m1 mean length 1.65 mm) should be used at present as reference for the base of the OSM B. Similarly the discrimination between OSM B and C + D deserves some comments. Heissig (1997) recognized an increase in *Megacricetodon* size in OSM C, as well as the first occurrence (FO) of *M. minor*-like species and the FO of *Neocometes similis*. The oldest locality containing *M. minor* is Roßhaupten, but the species is only documented by a single m2 (Fahlbusch, 1964). The localities Engelswies/Schellenberg and Untereichen 540 m lack the small *Megacricetodon*, while *Neocometes* is present in Engelswies/Schellenberg (Ziegler, 1995). The latter localities are thus considered the oldest belonging to OSM C + D in southern Germany.

Originally, Heissig (1997) discriminated the OSM C and the OSM D based on the presence of two species of *Anomalomys*. This argumentation did not convince Böhme et al. (2003), who merged the two units. In contrast, Kälin and Kempf (2009) still keep them separated, considering as an important criterion the presence/absence of a (new) small-sized *Megacricetodon* species. This leads to some problems. Indeed, no sized-based criterion allows for clear distinctions between *M. bavaricus* and *M. aff. bavaricus*. Thus, the Swiss *Megacricetodon* aff. *bavaricus*–*Megacricetodon* cf. *minor* interval zone of Kälin and Kempf (2009) can also be referred to the OSM B in Germany. Indeed, prior to Oggenhof, the (very) small-sized *Megacricetodon* species (Fig. 6) is extremely rare although it occurs in some Bavarian localities. As a result the Swiss *M. aff. bavaricus*–*M. cf. minor* interval zone is not convincingly recognized in Germany. In addition, correlating this interval zone to the OSM C as defined by Heissig (1997), also implies a correlation to Sandelzhausen (reference fauna), which is not likely if one takes into account the faunal content (high number of small-sized *Megacricetodon* *minor*; Wessels and Reumer, 2009). Molar size comparable to *Megacricetodon minor* is not achieved in localities preceding *Cricetodon* occurrences (OSM E, see below; Fig. 6). Prior to that, only a few Bavarian localities provided a representative molar sample of the smaller form (Sandelzhausen, UA 565 m), thus limiting this analysis. The Swiss *Megacricetodon* cf.

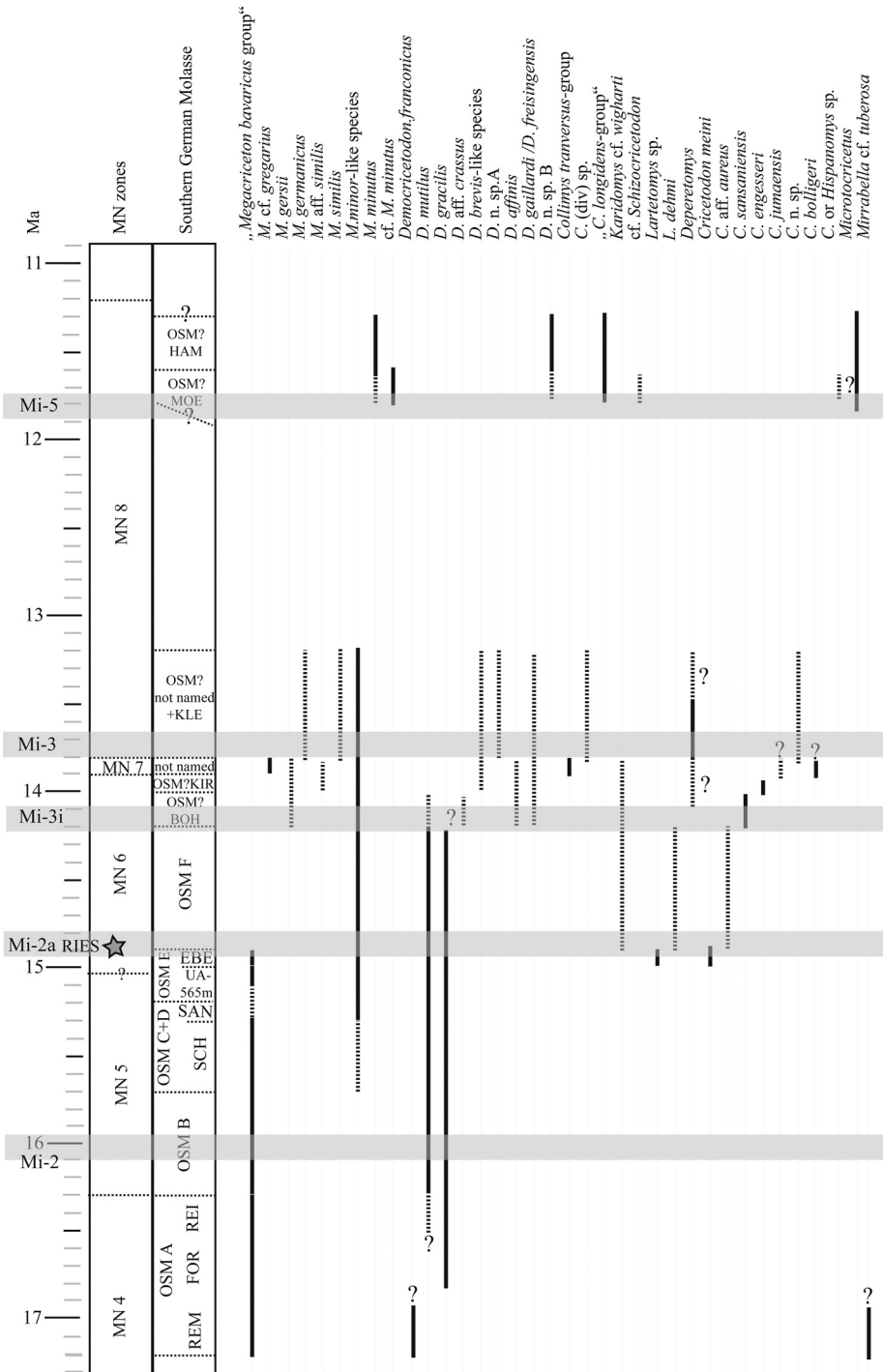


Fig. 5. Observed stratigraphic ranges of the cricetid rodents during the Late Burdigalian–Earliest Tortonian (Miocene) in South Germany. The shaded time intervals underline the oxygen isotope events. The dating of the Ries meteoritic impact (star) follows Rocholl et al. (2011). The dotted lines refer to uncertain stratigraphic ranges (see text for details). The MN zonation mainly follows Kálin and Kempf (2009). Unlike these authors, (I) we correlate the questionable “base” of the MN 6 to the OSM E–EBE; (II) we consider the youngest localities to be correlated to MN 8 instead of MN 9 because they lack hipparionin horses (see Kirscher et al., 2016). *Schizocricetodon* is recognized in Petersbuch 121 (pers. data MR).

Fig. 5. Domaines stratigraphiques observés des rongeurs cricétidés au cours du Burdigalien tardif–Tortonien basal (Miocène) du Sud de l’Allemagne. Les intervalles de temps ombrés soulignent les stades isotopiques de l’oxygène. La datation de l’impact météoritique du Ries (étoile) suit Rocholl et al. (2011). Les lignes pointillées concernent les domaines stratigraphiques incertains (se référer au texte pour les détails). La zonation MN suit principalement Kálin et Kempf (2009). À la différence de ces auteurs, (I) nous corrélons la « base » discutable de la MN 6 à la OSM E–EBE; (II) nous considérons les localités les plus jeunes comme appartenant à la MN 8 au lieu de la MN 9, car elles ne contiennent pas les chevaux hipparioninés (voir Kirscher et al., 2016). *Schizocricetodon* est présent à Petersbuch 121 (données personnelles MR).

Table 1

Preliminary local biozonation for the South German Late Burdigalian–Earliest Tortonian (Miocene) as compared to the equivalent zonation from the Swiss part of the North Alpine Foreland Basin.

Tableau 1

Biozonation locale préliminaire des dépôts du Burdigalien tardif–Tortonien basal (Miocène) en Allemagne du Sud, comparée à son équivalent suisse du Bassin nord-alpin.

Swiss units after Kälin and Kempf (2009)	Swiss reference localities	Germany Unit names	Characteristic taxa	Other relevant taxa	German localities (Fissures and other)	German localities (NAFB)	Questionable localities	Range (Ma)
		OSM?-HAM	<i>Microtocrictetus molassicus</i> abundant	<i>Democricetodon</i> sp. nov.		Hammerschmiede , Unterföhring, Aumeister, Hillenloh		~11.30–~11.60
Not defined	Nebelbergweg	OSM?-MOE	FO: <i>Microtocrictetus</i> (rare) <i>Megacricetodon minutus</i> , “ <i>Collimys longidens</i> ” group	cf. <i>Megacricetodon robustus</i> <i>Cricetodon</i> vel <i>Hispanomys Cricetodon</i> n. sp.	Petersbuch 14?, 121?	Mörgen , Markt1?		?–~11.60
<i>Deperetomys hagni</i> taxon range zone	Anwil	OSM?-KLE	Localities containing <i>Deperetomys</i> and <i>Megacricetodon similis</i>			Kleineisenbach , Giggerhausen		
		Not named	Localities containing <i>Deperetomys</i> and <i>Megacricetodon</i> aff. <i>similis</i>	<i>Democricetodon freisingensis</i> <i>Collimys</i> sp.	Petersbuch ?35, 48			~13.20–~13.80
<i>Megacricetodon gregarius</i> – <i>Deperetomys hagni</i> interval zone	Helsighausen	Not named	Localities containing <i>Megacricetodon</i> cf. <i>gregarius</i>	FO <i>Collimys</i> with “ <i>C. transversus</i> group” <i>Cricetodon bolligeri</i> <i>C. jumaensis</i>	Steinheim (with <i>M. gregarius</i>), Petersbuch 26, 31		Petersbuch 6, 10, 18, Derndorf, Tiefenried, Eppishausen Steinheim (Heizmann's excavations) Petersbuch 68	~13.80–~13.90
? <i>Megacricetodon similis</i> – <i>Megacricetodon gregarius</i> interval zone	Mettlen-Weid	OSM?-KIR	Localities containing <i>Cricetodon engesseri</i> - and <i>Megacricetodon similis</i> -related species	Possible <i>Democricetodon brevis</i> <i>D. affinis</i> and <i>D. fail-lardi/freisingensis</i>		Kirrburg Sandgrube , K.-Tongrube		~13.90–~14.00
? <i>Megacricetodon gersii</i> – <i>Megacricetodon similis</i> interval zone	Oeschgraben	OSM?-BOH	Localities containing species related to <i>Cricetodon sansaniensis</i> and <i>Megacricetodon gersii</i>	Possible <i>Democricetodon crassus</i> and <i>D. affinis</i>		Bohlinger Schlucht 3 and 4		~14.00–~14.20
<i>Megacricetodon lappi</i> – <i>Democricetodon gracilis</i> interval zone + <i>Democricetodon gracilis</i> – <i>Megacricetodon gersii</i> interval zone	Uzwil-Nutzenbuech + Rumikon	OSM F	Localities containing larger members of the <i>Cricetodon meini</i> – <i>C. aff. aureus</i> lineage; <i>Lartetomys dehmi</i>	FO <i>Karydomys</i>	Petersbuch 32, 33, 38, 39, Steinberg, Goldberg	Laimering 3, Thannhausen, Ziemetshausen 1b, 1d, Laimering 2, 4a, Unterzell, Göttschlag, Gallenbach 2b, Unterneul 1c, Unterzölling Göttschlag 1b, Unterzölling 1a, Höll, ? Laimering 4b, ?5 ?Hohenraunau		~14.20–~14.88
		OSM E	Localities containing the larger members of the “ <i>Megacricetodon bavaricus</i> group” of mean m1 size > 2.09 mm					~14.88–~15.20
		OSM E-EBE	“ <i>Megacricetodon bavaricus</i> group” of mean m1 size > 2.09 mm and/or with <i>Cricetodontini</i> (<i>Cricetodon meini</i> -sized)	FO <i>Lartetomys</i>	Petersbuch 41	?Denckendorf, Edelbeuren-M aurerkop f, Burg-Balzhausen, Ebershausen , Unterneul 1a, Mohrenhausen, Ziemetshausen 1c, Eberstetten, Derching 1b		~14.88–~15.00

Table 1 (Continued)

Swiss units after Kälin and Kempf (2009)	Swiss reference localities	Germany Unit names	Characteristic taxa	Other relevant taxa	German localities (Fissures and other)	German localities (NAFB)	Questionable localities	Range (Ma)
Top of <i>Megacricetodon lappi</i> taxon range zone	Aspitobel 520m	OSM E-UA565m OSM C + D	" <i>Megacricetodon bavaricus</i> group" of mean m1 size > 2.09 mm and without <i>Cricetodontini</i> Localities containing " <i>Megacricetodon minor</i> group" and/or <i>Neocometes</i> and/or with " <i>Megacricetodon bavaricus</i> group" of mean m1 size comprised between 1.74 mm and (at least) 1.94 mm			Untereichen-Altenstadt 565m Randecker Maar		~15.00--~15.20 ~15.20--~15.90
<i>Megacricetodon</i> cf. <i>minor</i> – <i>Megacricetodon</i> aff. <i>bavaricus</i> overlap zone	Tobel Hombrechtikon	OSM C + D-SAN	" <i>Megacricetodon bavaricus</i> group" forms of mean m1 size > 1.90 mm; The upper range is unknown because of a gap (see Fig. 3); <i>M. minor</i> -related forms are well represented or even dominant			Oggenhof, Oggenhausen 2, Sandelzhausen , Burtenbach lb + lc, Affalterbach		~15.20--~15.30
<i>Megacricetodon</i> aff. <i>bavaricus</i> – <i>Megacricetodon</i> cf. <i>minor</i> interval zone	Vermes 1	OSM C + D-SCH	" <i>Megacricetodon bavaricus</i> group" of mean m1 size comprised between 1.74 mm and < 1.90 mm; <i>M. minor</i> -related forms might be present but always rare		Rothenstein 1/13	Engelwies 1, Schellenfeld 2–4 , Roßhaupten, Untereichen-Altenstadt 540m, Jettingen, Walda 2, Puttenhausen classic, Bubenhausen, Ichenhausen 7, Edelstetten, Gisseltshausen lb, Betlinshausen, Puttenhausen E, Maßendorf, Schönenberg Pöttmes, Langenmoosen , Bellenberg 1 + 2, Niederaichbach, Ichenhausen 3 + 6		~15.30--~15.90
<i>Keramidomys</i> – <i>Megacricetodon bavaricus</i> overlap zone	Oberkulm-Sämlen	OSM B	Localities containing <i>Keramidomys</i> and/or with " <i>Megacricetodon bavaricus</i> group" of mean m1 size comprised between 1.65 mm–< 1.74 mm			Offingen 2, Georgensgmünd, Hessellohe, Attenfeld, Gietlhausen, ?Ichenhausen 1		~15.90--~16.30
? <i>Keramidomys</i> – <i>Megacricetodon bavaricus</i> overlap zone	?Oberkulm-Sämlen	OSM A or B	Localities lacking eomyids and with " <i>Megacricetodon bavaricus</i> group" of mean m1 size comprised between 1.58 mm–1.65 mm					?~16.30--~15.70
<i>Megacricetodon collongensis</i> – <i>Keramidomys</i> interval zone	Tägernaustrasse	OSM A OSM A-REI OSM A-FOR OSM A-REM	Base: FO <i>Megacricetodon</i> (<i>M. cf. collongensis</i>) Top: LO: <i>Ligerimys</i> " <i>Megacricetodon bavaricus</i> group" of mean m1 size > 1.55 mm Base: FO: <i>Democricetodon gracilis</i> Top: LO: <i>Democricetodon franconicus</i>	<i>Ligerimys</i> and <i>Melissiodon</i> extremely rare Rare <i>Mirrabella</i>		Günzburg2, Reisensburg Forsthart Rembach , Raucheröd	Eitensheim, Langenau 1	~17.20–?~16.30
<i>Democricetodon franconicus</i> – <i>Megacricetodon collongensis</i> interval zone	Glovilier	Not provided	<i>Democricetodon franconicus</i> (as single "modern cricetid") <i>Melissiodon dominans</i>		Petersbuch 2, Erkersthoften 1 + 2			~18.00--~17.20

The diagnostic criteria for each local biozone, as well as the correlation of sectioned sites (reference localities in bold), are also included. Les critères diagnostiques de chaque biozone locale, ainsi que les corrélations d'une sélection de sites (localités références en gras), sont aussi inclus.

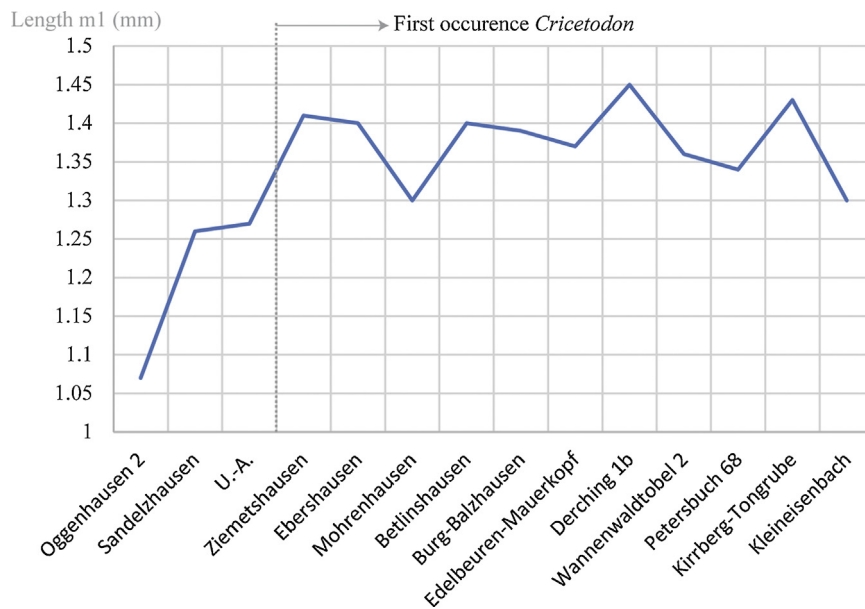


Fig. 6. Size variation in *Megacricetodon minor*-like species based on the length of the first lower molar. Note that the species occurring prior to the first appearance of *Cricetodon* is very small.

Fig. 6. Variation de la taille des espèces proches de *Megacricetodon minor*, basée sur la première molaire inférieure. À noter que l'espèce présente avant l'apparition de *Cricetodon* est très petite.

minor-*Megacricetodon* aff. *bavaricus* overlap zone has as reference locality Tobel Hombrechtikon. Members of the “*M. bavaricus* group” are missing. However, this could be the result of sampling bias. This assumption is supported by the abundance of *M. minor* in Sandelzhausen. Indeed, the larger-sized *Megacricetodon* species were not recognized by Fahlbusch (1964), but after intensive sampling, the species was reported by Wessels and Reumer (2009). As a result, the German OSM C + D-SCH correlates most probably to the *Megacricetodon* aff. *bavaricus*-*Megacricetodon* cf. *minor* interval zone from Switzerland, but this assumption is only based on the size of representatives of the “*M. bavaricus* group”. In southern Germany, the OSM C + D-SAN correlates to the Swiss *Megacricetodon* cf. *minor*-*Megacricetodon* aff. *bavaricus* overlap zone. *Anomalomys minutus* from Tobel Hombrechtikon (Switzerland) is only a bit smaller than *A. minor* and no clear morphological differences are observed (Bolliger, 1992a). We thus agree with Böhme et al. (2003) in not considering this taxon as relevant for biostratigraphic purposes. The absence of *Megacricetodon* in the Randecker Maar precludes any precise correlations (Rasser et al., 2013), but the presence of *Keramidomys* and *Neocometes* supports a correlation of the locality to the OSM C + D.

The occurrence of *Cricetodon* in OSM C + D is reported by Heissig (1997) but without details, so this occurrence is not considered herein (see comments in Prieto and Scholz, 2013: 306). Seehuber (2009) correlates Hohenraunau (Germany) to the OSM F, but reports a single M1 of *Megacricetodon lappi*. This specimen was found 5 m under the lowest reworked Boulder Horizon (Seehuber, 2009: 22). In contrast, the *Cricetodon* remains derive from reworked sediments and are thus younger. (Seehuber, 2009: 220) could not exclude that the fauna is mixed. For this rea-

son, the locality is not considered to be relevant here. A representative sample of *Cricetodon meini* has been recovered in Burg-Balzhausen (Germany). That these are almost the smallest representatives of the group in the NAFB lead Seehuber (2009) to correlate the locality to the OSM E. Surprisingly, the locality lacks *M. lappi*, although numerous fossils have been recovered. Here we preliminarily consider the absence of this species as a sampling effect (see above: comments on *Megacricetodon* aff. *bavaricus* from Sandelzhausen). Similarly, the absence of *Cricetodon* in Mohrenhausen (Germany) is hard to explain. Kälín and Jost (2014) argue that OSM E-EBE equivalents have not been yet discovered in Switzerland. Indeed, *M. lappi* is smaller there and the localities lack Cricetodontini (equivalent to OSM E-UA565 m).

5.2. Riesian and post-Riesian faunas

The German unit OSM E' is briefly described in Böhme et al. (2003) who noted that it differs from OSM E only by a cricetid rodent species, called in that work *Megacricetodon* aff. *gersii*, but the authors do not provide further details on this taxon. This unit is restricted to Derching 1b, a locality that has not been well studied although it is considered to just precede the Ries impact. In the context of this work, the small mammal material from Derching has been studied, and we have not found cogent arguments to attribute this material to *M. aff. gersii*, but consider it a somewhat large *M. minor* (see Fig. 6). For this reason, the locality is included in OSM F herein. Heissig (2006) introduced OSM?F for Laimering 5 (Germany) on the basis of differences in the sedimentary cycle. From a biostratigraphic point of view, there are no differences with the OSM F species and we place the locality into this unit. Kälín

and Kempf (2009) correlate the Swiss *Megacricetodon lappi*–*Democricetodon gracilis* interval zone, the *Democricetodon gracilis*–*Megacricetodon gersii* interval zone and the *Megacricetodon gersii*–*Megacricetodon similis* interval zone to the OSM F. The *Megacricetodon lappi*–*Democricetodon gracilis* interval zone records the first entry of *Cricetodon* in the Swiss part of the NAFB. As shown above, the genus occurs earlier in the German part (OSM E-EBE) but these faunas are not documented in Switzerland. Kälin and Kempf (2009) also recognized *Anomalomys* cf. *gaudryi* as an important newcomer into this unit. A revision of the German *Anomalomys* is indeed necessary to decide on the relevance of the genus for biostratigraphic purposes in Bavaria. However, Abdul Aziz et al. (2008) recognized the FO of *A. gaudryi* at the base of the OSM F in the same area. The characteristic occurrence of *Karydomys/Lartetomys* in Switzerland is also observed in Germany. The following Swiss interval zone (*Democricetodon gracilis*–*Megacricetodon gersii* interval zone) differs basically from the former by the LO of *D. gracilis*. Notably, eomyids and *Anomalomys* are completely missing. The LO of *D. gracilis* is at present not well defined in Germany. Finally, the Swiss *Megacricetodon gersii*–*Megacricetodon similis* interval zone is characterized by a species assemblage strongly resembling the fauna of the French site Sansan. In Germany, the distinction between *C. aureus* and *C. sansaniensis* is not always clear in the literature and the recognition of the species in the NAFB is in general a matter of debate. Rummel and Kälin (2003) assigned the collection from Zeglingen to *Cricetodon sansaniensis*, and preliminarily attributed some other Swiss material to this species (see also Bolliger, 2000). They also discussed that these forms differ slightly from the type material in size and morphology. Regarding the German record, they consider the fossils from Petersbuch 31 and Kirrberg Tongrube as *C. cf. sansaniensis* (see also Rummel, 2000; Seehuber, 2009). Some other German occurrences are more problematic. *Cricetodon sansaniensis* is reported in Höll (Scholz, 1986a, 1986b), but this sample has not been re-studied. Only the measurements of a single specimen have been given (Heissig, 1990; see also comments in Prieto and Scholz, 2013). The large collections from Steinberg and Goldberg, originally assigned to this species by Heizmann and Fahlbusch (1983), are now thought to belong to *C. aff. aureus* (Rummel, 2000). *Cricetodon sansaniensis* is described from the Bohlinger Schlucht (Giersch, 2004). The fauna contains both *M. minor* and *M. aff. gersii* and is tentatively correlated to the Swiss *Megacricetodon gersii*–*Megacricetodon similis* interval zone herein (OSM?-BOH).

Even more tentative is the correlation of the Kirrberg faunas (Kirrberg Tongrube and Kirrberg Sandgrube, Bavaria) to the Swiss *Megacricetodon similis*–*Megacricetodon gregarius* interval zone. It is based on the presence of *Cricetodon* cf. *engesseri* in these two sites (Seehuber, 2009), a rare species at present only reported in Switzerland from this interval zone from the site Chräzerentobel 505 m. The composition of the Kirrberg faunas allowed Seehuber (2009) to exclude a correlation to younger assemblages.

The *Megacricetodon* species with clearly divided anteroconid (*M. gregarius*-like; see taxonomical notes) is considered by Kälin and Kempf (2009) an excellent index fossil in the Swiss record. They extend their analysis to Steinheim and conclude that the presence of the species represents a very short interval, named as “*gregarius* event” by Heissig (1997). The species is, according to this scheme, never found in co-occurrence with *Deperetomys*, an index taxon for the following Swiss biostratigraphic unit (Anwil). In contrast to Steinheim, some German localities cannot be so easily correlated. In Bavaria, the sites from Derndorf, Tiefenried and Eppishausen are close in age, but not rich in small mammals. These localities postdate the FO of the pig *Listriodon* (Seehuber, 2009), which is seen also as a newcomer in Hellsighausen (Switzerland; Kälin and Kempf, 2009). The first occurrence of *Listriodon splendens* in Central Europe occurs at around 14.2 Ma in Klein-Hadersdorf (Austria; Böhme et al., 2012). In Germany, Seehuber (2009) considers the material of this species from Stätzing to be probably older than 11.4 Ma. Furthermore, *Deperetomys* may be present in Tiefenried, indicating an earlier entry of the genus in the NAFB than generally accepted (Prieto, 2012b; Seehuber, 2009). The German fissure filling Petersbuch 31 (upper part) contains *M. cf. gregarius* (Rummel, 1997; see Prieto, 2007, figs. 36F and I), but the species is found in association with *Cricetodon sansaniensis*, which disappears earlier in Switzerland. Petersbuch 6 and 18 may contain two medium-sized *Megacricetodon* species that can only be distinguished on the basis of the m1. One resembles *M. gersii* or *M. germanicus*, and the second one shows a better divided anteroconid (Prieto, 2007, see taxonomical notes). These fissures contain also some rare *Deperetomys* teeth. And finally, Prieto and Rummel (2009a) consider Petersbuch 68 to be older than Steinheim on the basis of the size of *M. gersii*. Among the *Cricetodontini*, the presence of rare *Cricetodon engesseri* molars and the absence of *Collimys* agree with this correlation. A very variable *Deperetomys* is also present and abundant (MR and JP, pers. data). Finally, the fissure fillings of Petersbuch 35 and 48, rich in *Deperetomys*, are considered to be slightly older than Anwil (Prieto, 2007). To sum up, it can be concluded from these localities that the faunal succession around the “*M. gregarius* event” is characterized by intense but short dispersal waves that complicate the correlation of the faunas. Herein, we propose the succession of Table 1 and Fig. 6, but emphasize that it is not well supported for the faunas near in age to Steinheim.

As shown above, the *Deperetomys hagni* taxon range zone as defined by Kälin and Kempf (2009) for the Swiss molasse might be in need of revision in the view of the German record. In addition, they noticed that the genus is absent in the younger localities assigned to MN 8. In any case, the reference locality Anwil is the Swiss equivalent of Kleisenbach and Giggenshausen (Prieto, 2007).

5.3. Faunas at the Middle–Late Miocene transition

Clear similarities are observed between Nebelbergweg (Switzerland) and Hammerschmiede (Germany), although the Swiss locality lacks *Microtocricetus* (Kälin and Engesser,

2001). The genus is recorded in Nebelberg TGL localities (Switzerland). Recent advances show that the rich and diverse faunas from Hammerschmiede can be correlated to the base of the Tortonian, at 11.6 Ma, while Hillenloh is probably a bit younger, with an estimated age of 11.3 Ma (Fuss et al., 2015; Kirscher et al., 2016; Prieto et al., 2011). The relative age of Nebelbergweg is indeed much more controversial, and the argumentation proposed by Prieto and Rummel (2009d) based on *Collimys* has to be critically evaluated (Prieto et al., 2014). In this context, the German locality Mörge is highly relevant. Seehuber (2009) places it between Anwil and Nebelbergweg, and excludes a correlation to MN 9 based on the presence of *Miodiomys aegercii*, *Euprox furcatus* and *Dorcatherium crassum*. He recognizes some uncanny similarities with Nebelbergweg. Both localities share a very large *Miodiomys* species, as well as similar *Democricetodon* species and *Collimys* of the “*C. longidens* group”. In Mörge, two *Megacricetodon* forms are recognized although they have not been identified to the species level. The smallest one resembles in many points *M. minutus*, while the larger is characterized by an m1 with a well-divided anteroconid. Seehuber (2009) refrains from ascribing it to *M. robustus*, a species endemic to Nebelbergweg, mainly because of the presence of a well-developed anterolophid on the German teeth. The specimens from Mörge belong in our opinion to the same *Megacricetodon* grade as *M. robustus* or *M. crusafonti*. The tribe Cricetodontini is not reported from Nebelbergweg, but the group is represented in Nebelberg by *Hispanomys* sp. (Kälin and Kempf, 2009). *Cricetodon* sp. from Mörge also resembles this form, being at the same time similar to *C. nievei* and early *Hispanomys* species. Recently, a single tooth of *Microtocricetus* has been found in this German locality. It is an M2 that fits within the lower size range of *Microtocricetus molassicus* (1.72×1.33 mm; see Kretzoi and Fejfar, 2005). From a morphological point of view, this specimen differs from the type material in its reduced lingual anterocone (Fig. 4F; nomenclature follows Daxner-Höck and Höck, 2015). These data link strongly Mörge to the Swiss localities, but their biostratigraphic arrangement is still unclear. As noticed above, the proposal of Prieto and Rummel (2009d) that Hammerschmiede is older than Nebelbergweg is open to discussion. On the other hand, the lack/rarity of *Microtocricetus*, might imply, among other possibilities, an older age for the Swiss site. Similarly, the German locality Markt (Bavaria) is considered to be older than Hammerschmiede, although this conclusion is based on third molar morphology of *Microtocricetus* (Fahlbusch and Mayr, 1975). This conclusion is also partly followed by Kowalski (1993). In addition, the locality also contains the large-sized eomyid *Eomyops* sp., a species currently not recognized elsewhere in Europe (Prieto, 2012a). Finally, the presence of *Collimys* cf. *longidens* and *Democricetodon* n. sp. in Chräzentobel 655 m allows for a clear correlation of the Swiss fauna to the localities mentioned above. In conclusion, the relative ages of the localities proposed here is a working hypothesis, requiring of additional material for many sites and if possible of independent stratigraphical data.

6. German cricetid turnover events and their correlation with Eurasian faunal dispersals and major climatic changes

The beginning of the deposition of the OSM and its brackish equivalents occurred during the warmest period during the Neogene, the Miocene Climate Optimum (MCO; beginning ~17 Ma; Zachos et al., 2001). The “modern” cricetid rodents in Europe radiated successfully at that time. Influence of Eastern European/Anatolian faunas is evidenced by the rare occurrence of *Mirrabella* for instance (see also van den Hoek Ostende et al., 2015). The OSM A is the theatre of the slow disappearance of characteristic Early Miocene forms such as *Melissiodon* or the eomyid *Ligerimys*, the latter being replaced by *Keramidomys*. Until ~15 Ma no major changes occur among cricetids, but the genus *Megacricetodon* shows a regular size increase through time. An exception is a small-sized species of *Megacricetodon* after ~15.9 Ma (OSM C+D), which becomes abundant during the OSM C+D-SAN. It correlates to the second faunal event observed by García-Paredes et al. (2016) in the Calatayud-Montalbán basin at the Lower/Middle Aragonian transition. These authors correlate this event to the cooling period of the isotopic event Mi2. Interestingly this period documents also the entry in Spain of *Megacricetodon vandermeuleni*, a species linked to the “*M. bavaricus* group” (Oliver Pérez and Peláez-Campomanes, 2013). Members of this group are completely missing in Austria although the earliest populations occur in the Czech Republic as newcomers of a second *Megacricetodon* migration wave (Oliver Pérez and Peláez-Campomanes, 2013). This might indicate isolation between the terrestrial communities from western and central Paratethys during this time. Interestingly, Jost et al. (2015) recognize in the Swiss part of the Middle Miocene NAFB the onset of seasonality between 16.1 Ma and 15.8 Ma [corresponding here roughly to the transition (OSM B-OSM C+D)] and lower annual precipitation in relation to the eccentricity minimum at 15.57 Ma.

In sharp contrast, the migration of the Cricetodontini in Eastern/Central Europe is a widespread event recorded in France, the NAFB and the Pannonian Basin (OSM E; Daxner-Höck, 2003; Fejfar, 1974; Hír, 2013; Hír et al., 2016; Mein and Freudenthal, 1971b). In Germany, this event is also characterized by the FO of a second cricetodontine (*Lartetomys*) and marks the demise of the “*M. bavaricus* group”. A small faunal turnover is also recorded in the Iberian Peninsula, but characterized by the extinction of taxa linked to humid habitats (García-Paredes et al., 2016) at the end of the MCO.

At around 14.2 Ma, major changes occurred in the cricetid assemblages in the NAFB. In a relatively short span of 400 ka, species diversity increased incredibly, but some species have a very short stratigraphic range, such as *Megacricetodon* cf. *gregarius*. This species evidences a migration of western origin, while other taxa, as in the earlier faunal turnovers, have an oriental origin, indicating a period of strong instability and turnover at a larger scale. This includes the disappearance of marsupials from Europe (Kälin and Kempf, 2009; Prieto and Rummel, 2015), and the end of the crocodile era (Böhme, 2003). These events, related to the Middle Miocene Climate Transition (MMCT;

isotopic events Mi-3a, Mi-3) are widely documented but faunal response differs from one area to another (see García-Paredes et al., 2016; Hír et al., 2016). Böhme et al. (2011) recognized that the gradient in the mean annual precipitation between Central Europe and Southern Europe neared zero for this period, both areas receiving the same precipitation relative to the present, which might have been a positive factor for the faunal interchanges.

During the beginning of the Miocene cooling trend, the ecosystems found again a certain degree of stability, so that the *Deperetomys* fauna contains forms of possible western European origin (*M. germanicus*), but there are numerous central Paratethyan elements (see Hír et al., 2016) indicating probably a westward shifting of the ecosystems. The palaeobiogeographic isolation is marked, as the *Deperetomys* fauna is not recorded as such outside the NAFB.

As shown by Hír et al. (2016), the small mammal faunas ranging from ~13.2 Ma to ~11.6 Ma are a rarity in the central and eastern European fossil record, highlighting the importance of the Hungarian and Romanian sites for this time span (Late Badenian–?Earliest Pannonian). The quality of the Vallès–Penedès Basin record is better for this time interval (Late Aragonian; Casanovas-Vilar et al., 2016). The faunas are highly diversified because of the presence of taxa – most often forest-dwellers – poorly or unrecorded elsewhere in the Iberian Peninsula. This basin could be seen as a transitional area between the arid Iberian and the more humid Central European faunas. Noteworthy, *Microtocrictetus* never reached Spain, its westernmost occurrence being reported from east of France (Welcomme et al., 1991). In addition, the Iberian record is characterized by the successful radiation of the Cricetodontini, while in the NAFB and the Pannonian Basin the tribe slowly declined. Regarding the cricetid rodents, the early *Microtocrictetus* faunas are characterized by the association *Megacricetodon minutus* + *Democricetodon* n. sp. (sensu Kálin and Engesser, 2001) + “*C. longidens* group”, species present at least as early as the late Sarmatian in the Pannonian Basin. Other rare forms are characterized by their short stratigraphical range and also evidence, at least for some, a western influence (*Galerix* cf. *exilis*, Prieto et al., 2011).

7. Conclusions

The German cricetid and microtid cricetid rodent succession can be traced for around 6 My in the OSM, and for a bit longer in its Swiss counterpart, the early Ottnangian equivalents being documented in Bavaria by fauna deriving from fissure fillings. The biozonation provided by Kálin and Kempf (2009) can be mirrored in the German deposits although some periods are apparently missing or are less well documented in that basin. The faunal turnovers mostly coincide with major climatic changes, as observed in other regions, especially in the Iberian Peninsula. The most important of those is observed at the end of the MMCT, and the cricetid assemblage suffered drastic changes, with species of short stratigraphic range invading the NAFB from both western and eastern regions. This important period is documented in the Swiss Molasse, but most of the information in southern Germany derives from fissure fillings and crater lakes, making the relative

dating of the fauna harder. Interestingly, the fauna accumulated during cooler late middle Miocene climates might be regarded as deriving from assemblages found earlier in the Pannonian Basin, suggesting a shifting of the ecosystems westwards.

The gap observed in Switzerland and Germany between ~13.2 Ma and ~11.6 Ma corresponds to the latest Badenian and Sarmatian, with faunas known from Hungary and Romania. In this region, the FO of *Microtocrictetus* is almost synchronous with the NAFB. After decades of study, the faunal sequence of southern Germany has gained a central position in the discussions on chronostratigraphy and ecosystem development in western Eurasia. Our review, only considering a restricted group of small mammals, shows, however, that some fine-tuning is still necessary to elucidate the relative chronological position of localities within the NAFB and the relationship to localities in other parts of Europe.

Acknowledgments

This study was funded by grant BO1550/16 of the Deutsche Forschungsgemeinschaft (DFG) to JP. We deeply appreciate the comments by the two reviewers, L.W. van den Hoek Ostende (Leiden) and an anonymous reviewer, as well as by the guest editor, Isaac Casanovas-Vilar (Barcelona). We also especially thank Lawrence J. Flynn (Cambridge) for kindly polishing the English.

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