C. R. Palevol 15 (2016) 855–862

Contents lists available at ScienceDirect

Comptes Rendus Palevol

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General Palaeontology, Systematics and Evolution (Vertebrate Palaeontology)

Fossil record and dynamics of Late Miocene small mammal faunas of the Vienna Basin and adjacent basins, Austria

Registre fossile et dynamique des faunes de micromammifères du Miocène supérieur du bassin de Vienne et des bassins adjacents, Autriche

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ARTICLE INFO

Article history:
Received 24 March 2015
Accepted after revision 20 June 2015
Available online 2 September 2015

Handled by Lars van den Hoek Ostende

Keywords:
Small mammals
Diversity
MN zones
Vienna Basin
Miocene
Pannonian

ABSTRACT

The Late Miocene small mammal assemblages of the hinterland of Lake Pannon in Austrian Basins are represented by 99 species-level taxa and 30,400 specimens. The fossil-bearing localities can be grouped into eight intervals spanning about three million years from the Early Vallesian to the Middle Turolian. Each time slice is characterised by the occurrence and/or dominance of certain species. The retreat of Lake Pannon is reflected by a distinct diversification. This pattern may be a regional signal due to increasing habitat availability but may also be taphonomically biased due to a rather poor Earliest Vallesian record. Nevertheless, the overall community structure is quite stable throughout the Vallesian and no indication of a Vallesian Crisis can be detected. Instead, a moderate turnover occurs with the onset of the Turolian, reflected by the increasing abundance of xerophilic taxa.

Mots clés :
Micromammifères
Diversité
Zones MN
Bassin de Vienne
Pannonien

RÉSUMÉ

Les assemblages de micromammifères du Miocène supérieur de l'arrière-pays du lac Pannon, dans les bassins autrichiens, sont constitués de 99 espèces et 30 400 spécimens. Les localités fossilifères peuvent être assignées à huit intervalles de temps couvrant environ trois millions d'années, du Vallésien inférieur au Turolien moyen. Chaque tranche de temps est caractérisée par l'occurrence et/ou la domination de certaines espèces. Le recul du lac Pannon se traduit par une nette diversification des taxa. Ce modèle peut être un signal régional induit par l'augmentation du nombre d'habitats, mais peut également être un biais taphonomique dû à la pauvreté du registre fossile à la base du Vallésien. Néanmoins, la structure de l'ensemble de la communauté est assez stable pendant le Vallésien et n'indique pas de crise vallésienne. En revanche, un renouvellement faunique modéré intervient à partir du Turolien, reflété par l'augmentation d'abondance des taxa xérophiles.

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http://dx.doi.org/10.1016/j.crpv.2015.06.008
1631-0683/

1. Introduction

The Upper Miocene small mammal assemblages studied here were recovered from 16 localities in the Vienna Basin, the northern Alpine Foreland Basin (NFAB) and the Pannonian Basin (Fig. 1). After the first discoveries early in the 20th century, more than 30,400 fossils were collected by wet screening bulk samples. Numerous publications provide comprehensive information on these small mammal assemblages (Angelone, 2009; Angelone and Veitschegger, 2015; Bachmayer and Wilson, 1970, 1978, 1980; Daxner, 1967; Daxner-Höck, 1972a, 1972b, 1977, 1980, 2004a, 2004b; Daxner-Höck and Bernor, 2009; Daxner-Höck and Höck, 2009, 2015; Harzhauser et al., 2011; Rabeder, 1973, 1985, 1998; Rögl et al., 1993; Van Weers and Montoya, 1996; Ziegler, 2006; Ziegler and Daxner-Höck, 2005 and references therein). The larger part of this material is housed in the collections of the Natural History Museum Vienna, Geological-Paleontological Department, smaller parts in the University of Vienna, Geocenter (Palaeontology).

Several key localities, important for understanding the terrestrial mammal assemblages in central Europe during the Late Miocene, are located in the Vienna Basin. The known localities cover an interval from the Early Tortonian (Early Pannonian; ~11.2 Ma) to the Middle Tortonian (Late Pannonian; ~8.3 Ma). The relative age of the studied localities and their stratigraphic succession are well known. Most localities bear mollusc faunas, which can be correlated easily with the Lake Pannon mollusc biozones, established by Papp (1951) (Harzhauser et al., 2004; Magyar et al., 1999). In addition, some localities can be correlated with geophysical data from the thick basin fill, which attains up to 1200 m of Pannonian sediments. These deposits document a clear cyclicity, which was considered to reflect astronomic forcing (Harzhauser et al., 2004; Lirer et al., 2009). Later, this assumption was corroborated by paleomagnetic data (Paulissen et al., 2011). Thus, the age models for the Pannonian deposits of the Vienna Basin attain an accuracy of ~100 ka. The correlations with the comparatively condensed sections along the basin margins, however, lack this accuracy. Therefore, the ages of the mammal-bearing sections proposed herein may have an error of ~100–300 ka.

2. Methods

The quantitative small mammal data (specimen numbers per species; Online Appendix) are based on the collections in the NHMW and the data presented in the Catalogus Fossilum Austriae of Daxner-Höck and Höck (2015) and in Ziegler (2006). For counting we took all available specimens, i.e. skulls, partial skulls, isolated premolars, molars and jaws with or without teeth. Not included in specimen numbers are incisors and postcranials, except the humerus of Talpidae. The representation of small mammals within the various Pannonian localities of the Vienna Basin is rather inhomogeneous. The stratigraphically older assemblages are especially strongly taphonomically biased toward large mammals. Thus, Lower Pannonian localities with very few species and low specimen numbers are contrasted by extremely rich assemblages of the Upper Pannonian with thousands of specimens. A statistical comparison of these assemblages based on specimen numbers is of little significance. Therefore, we used only presence/absence data for statistical analysis, to calculate a small mammal diversity curve with the software PAST (Hammer et al., 2001) including originations and extinctions (Fig. 2). In addition, a two-way cluster analysis was performed on a reduced data set, from which singletons and persisting species were removed (Fig. 3) to illustrate

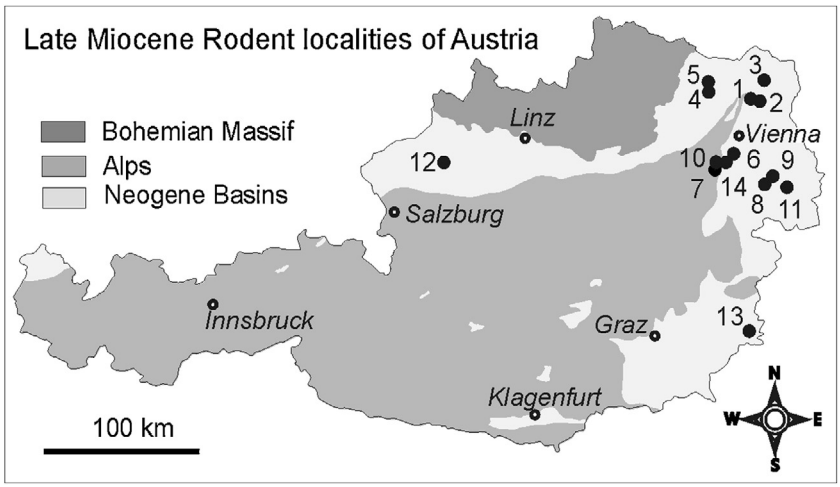

Fig. 1. Late Miocene small mammal localities of Austria. 1. Atzelsdorf (Atz), 2. Gaweinstal (Ga), 3. Bullendorf (Bu), 4. Mariathal (Mat), 5. Magersdorf (Mag), 6. Vösendorf (Vö), Inzersdorf, Hennersdorf, 7. Richardhof-Golfplatz (RH), 8. Götzendorf (Gö), 9. Stixneusiedl (Stix), 10. Richardhof-Wald (Rh), 11. Neusiedl am See (NS), 12. Schernham (Sch), 13. Kohfidisch (Ko), 14. Eichkogel (Eich).

Fig. 1. Localités à micromammifères du Miocène supérieur de l'Autriche. 1. Atzelsdorf (Atz), 2. Gaweinstal (Ga), 3. Bullendorf (Bu), 4. Mariathal (Mat), 5. Magersdorf (Mag), 6. Vösendorf (Vö), Inzersdorf, Hennersdorf, 7. Richardhof-Golfplatz (RH), 8. Götzendorf (Gö), 9. Stixneusiedl (Stix), 10. Richardhof-Wald (Rh), 11. Neusiedl am See (NS), 12. Schernham (Sch), 13. Kohfidisch (Ko), 14. Eichkogel (Eich).

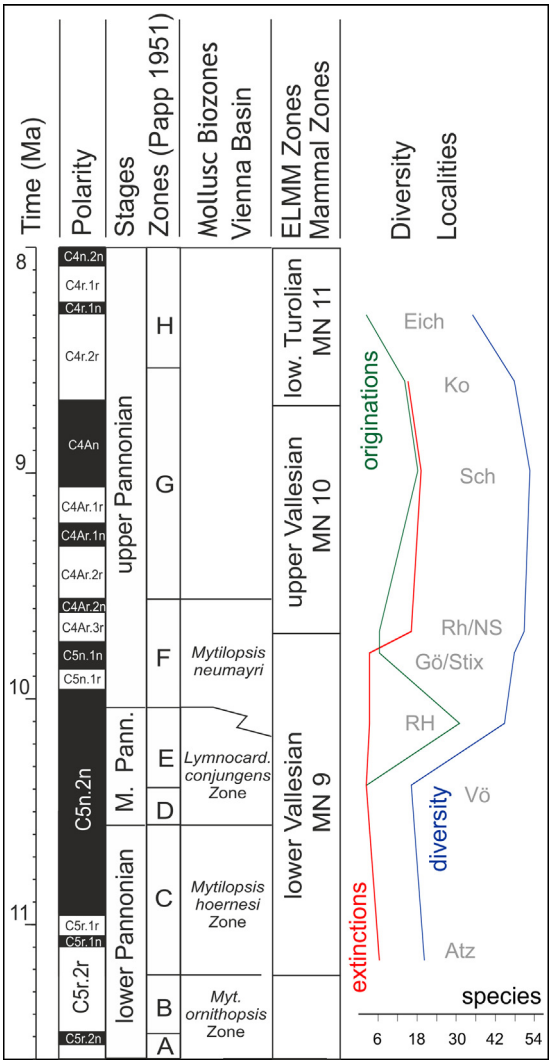

Fig. 2. (Color online.) Diversity, originations and extinctions of small mammals during the Late Miocene based on assemblages analysed herein. Stratigraphy and biozones modified from Harzhauser et al. (2004); (ELMM: European Land Mammal Mega-Zones, Steininger, 1999).
Fig. 2. (Couleur en ligne.) Diversité, apparitions et extinctions des micromammifères pendant le Miocène supérieur sur la base des assemblages analysés. Stratigraphie et biozones modifiées d'après Harzhauser et al. (2004) ; (ELMM : European Land Mammal Mega-Zones, Steininger, 1999).

similarities between the assemblages and to define species-groups, that are characteristic for certain intervals.

3. Geological setting

The deposition of limnic and fluvial sediments, and the respective mammal localities, closely related to the history of the northern Alpine Foreland Basin (NAFB), the Vienna Basin and the Pannonian Basin, and to the origin and development of Lake Pannon. At the Middle/Late Miocene transition (= Sarmatian/Pannonian boundary), i.e., at about 11.6 Ma, a glacioeustatic sea-level drop caused the final disintegration of the Paratethys Sea (Harzhauser et al., 2004). The Paratethys split geographically into the eastern Paratethys and, west of the Pannonian basin system, Lake Pannon arose. Lake Pannon attained a maximum length of 860 km (from the Karlovac Basin in the west to the Transylvanian Basin in the east) and a width of 550 km (from the Vienna Basin in the north to Belgrade in the south), covering an area of about 290,000 km^2 (Magyar et al., 1999; Harzhauser et al., 2004; Harzhauser and Mandic, 2008). In Austria, Lake Pannon covered the northern and southern Vienna Basin and the Austrian part of the Pannonian Basin.

During the Early Pannonian, the fluvial system Palaeo-Danube and its delta arose, which entered Lake Pannon in the northwestern part of the Vienna Basin. In the delta area, huge wetland environments established, as evidenced by mollusc- and vertebrate-bearing fossil sites such as Atzelsdorf, Bullendorf, Gaweinstal, Mariathal and Magersdorf. During the Middle Pannonian, a last level rise of Lake Pannon mostly destroyed these wetlands.

In the Late Pannonian, Lake Pannon disappeared from the Vienna Basin step by step, and established its northwestern coast in the Hungarian Basin (Magyar et al., 1999). Consequently, the drainage systems from the Alps and the NAFB entered the central Vienna Basin and formed extended floodplains with oxbows, rivulets and floodplain-lakes as reconstructed for the localities Götzendorf, Stixneusiedl and Neusiedl am See (Harzhauser and Tempfer, 2004), and a fringe of freshwater lakes became established along the western margin of the central Vienna Basin as reconstructed for the localities Richardhof-Golfplatz, Richardhof-Wald and Eichkogel (Daxner-Höck and Höck, 2009; Harzhauser and Tempfer, 2004).

In the western part of Austria, the drainage system of the Alps transported gravels and sands northwards into the NAFB of Upper Austria. The highest and youngest member of this sequence is the "Hausruck Gravel". Its interbedded sandy-silty layers yielded the Upper Miocene vertebrate fauna Schernham (Daxner-Höck, 2004b).

4. Stratigraphy and regional position of the fossil sites

The Upper Miocene small mammal record of the Vienna Basin and adjacent basins is one of the best in Central Europe. Stratigraphically, the studied sections provide mammal faunas or groups of mammal faunas from eight time intervals of the Pannonian Stage (Figs. 1 and 2):

1. Atz: The Lower Pannonian localities Atzelsdorf (Atz: E 16°32′39″ N 48°30′37″), Gaweinstal, Bullendorf, Mariathal and Magersdorf are part of the "Hollabrunn-Mistelbach" Formation in Lower Austria. All these localities can be correlated with the *Mytilopsis hoernesi* Zone (= Pannonian Zone C) and roughly range around 11.2 to 11.0 Ma (Harzhauser et al., 2004). Moreover, in these localities the lower boundary of the Vallesian and Mammal Zone MN9 is indicated by the first occurrence of *Hipparion* s.l. This unit represents sediments of the Paleo-Danube and its delta. The depositional environments range from fluvial channels and crevasse splays to oxbow lakes. Large mammals (e.g. *Hipparion* s.l.) are very abundant in these deposits whilst the number of small mammals is rare. To achieve a representative number we united the findings of Atzelsdorf, Bullendorf, Gaweinstal, Magersdorf

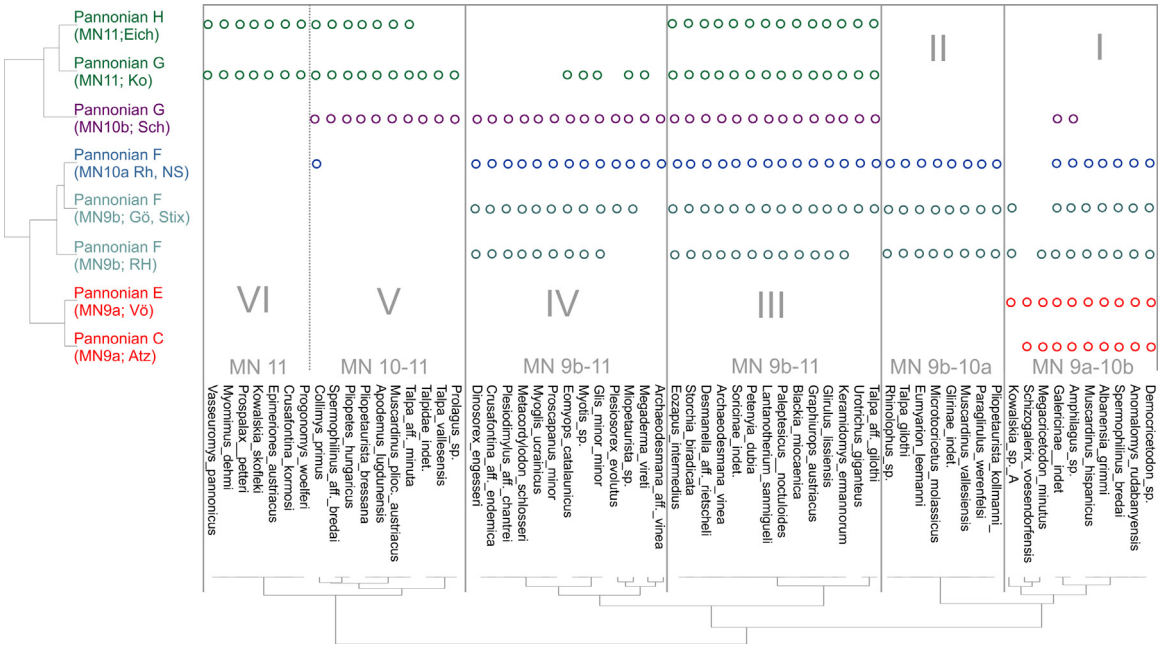

Fig. 3. (Color online.) Two-way cluster analyses (Ward's method) based on presence/absence data of species occurring in at least two time slices (singletons removed, range-through assumption).
Fig. 3. (Couleur en ligne.) Analyse hiérarchique à deux entrées (méthode de Ward) sur la base des données de présence/absence des espèces observées dans les deux derniers intervalles de temps (occurrences isolées exclues, extensions stratigraphiques supposées).

and Mariathal. Nevertheless, only twenty small mammal species represented by 92 specimens are recorded from this interval. For detailed data on stratigraphy, sedimentology, taphonomy and taxonomy of these localities see Daxner-Höck (1996, 2004a), Daxner-Höck and Bernor (2009), Harzhauser (2009), Harzhauser et al. (2003, 2004, 2011), Nehyba and Roetzel (2004), Steininger (1999).

2. Vö: The Middle Pannonian localities Vösendorf (Vö), Inzersdorf and Hennersdorf (E 16°19-21′ N 48°06-07′) are situated at the western margin of the central Vienna Basin in Lower Austria. These localities can be correlated with the *Lymnocardium schedelianum* Zone (= Pannonian E) and range around 10.4 to 10.5 Ma (Kern et al., 2012). They represent pelitic offshore clays of Lake Pannon. Rare levels with terrestrial mammals were formed by transport from the shores during high energy events of Lake Pannon. Again, large mammals are predominant whilst small mammals are very rare in the samples of Vösendorf, Inzersdorf and Hennersdorf. Only seven species were detected, represented by only 178 specimens. They indicate the first part of the Lower Vallesian (MN 9a). For data on sedimentology, taphonomy and taxonomy of these localities see Daxner (1967), Harzhauser and Mandic (2004), Harzhauser et al. (2003, 2004), Kern et al. (2012, 2013), Papp (1951) and Papp and Thenius (1954).

3. RH: The Upper Pannonian fauna of Richardhof-Golfplatz (RH: E 16°16′13″ N 48°03′27″) is situated in the central Vienna Basin in Lower Austria. In the course of the Upper Pannonian Lake Pannon disappeared from the Vienna Basin and freshwater deposits established. The vertebrate- and gastropod fauna of a 7-m thick sediment sequence from Richardhof-Golfplatz reveals a swampy freshwater lake environment. The gastropod *Prososthenia sepulcralis* is indicative for Pannonian Zone F (around 10.1 Ma). The small mammal assemblage comes from intercalated silty clay layers and comprises 42 species represented by 1274 specimens. They indicate the second part of the Lower Vallesian (MN9b). Data on sedimentology, stratigraphy and taxonomy are presented in Daxner-Höck and Höck (2009, 2015), Harzhauser and Binder (2004), Harzhauser and Tempfer (2004), Harzhauser et al. (2004) and Ziegler (2006).

4. Gö/Stix: The Upper Pannonian localities Götzendorf (Gö: E 16°34′59″ N 48°00′27″) and Stixneusiedl (Stix: E 16°40′13″ N 48°03′12″) are situated in the southern Vienna Basin in Lower Austria. The depositional environment was characterized by floodplains and wetlands. The mollusc fauna indicates a correlation with the *Mytilopsis neumayri* Zone (= Zone F of Papp, 1951). The mammal fauna correlates with the Lower Vallesian (MN9b). The two coeval small mammal faunas yielded 34 species represented by 1163 specimens. The localities range around 9.7 to 9.9 Ma. More data are provided by Bernor et al. (1993), Daxner-Höck (2004a), Daxner-Höck and Höck (2009, 2015), Harzhauser and Tempfer (2004), Harzhauser et al. (2004), Rögl et al. (1993).

5. Rh/NS: The Upper Pannonian locality Richardhof-Wald (Rh: E 16°16′15″ N 48°03′35″) is situated at the western margin of the central Vienna Basin in Lower Austria, and Neusiedl am See (NS) at the eastern margin of the southern Vienna Basin in Burgenland. The small mammals of these two faunas indicate a correlation with

the first part of the Upper Vallesian (MN10a). The lacustrine (Rh) and fluvial deposits (NS) are correlated with the uppermost Pannonian Zone F. The first occurrence of the murid *Progonomys hispanicus* indicates mammal zone MN10 (Agusti et al., 1997; Garces et al., 1996; Van Dam, 1997). Consequently, the age is around 9.7 Ma. Both fossil layers yielded together 1632 specimens representing 39 species. Details on the sections are presented by Daxner-Höck (1996, 2004a), Daxner-Höck and Höck (2009, 2015), Rögl et al. (1993) and Ziegler (2006).

6. Sch: The locality Schernham (Sch: E 13°36′38″ N 48°10′40″) is situated in the NAFB in Upper Austria. The estimated age ranges around 8.9 to 9.1 Ma. From the sand and gravel pit Schernham 45 small mammal species are represented by 2307 specimens. The mammals indicate a correlation with the second part of the Upper Vallesian (MN10b). Information on taxonomy and stratigraphy is given in Daxner-Höck (2004a, 2004b), Daxner-Höck and Höck (2009, 2015) and Ziegler (2006).

7. Ko: The Upper Pannonian deposit Kohfidisch (Ko: E 16°20′39″ N 47°08′52″) is situated in the Pannonian Basin in Burgenland near Kirchfidisch and represents a karstic cave and fissure system in Devonian limestones. The mollusc assemblages point to a correlation with the Pannonian zone G of the Vienna Basin. The mammal assemblage corresponds to the Lower Turolian (MN11). The estimated age is around 8.5 to 8.6 Ma. Numerous excavation campaigns resulted in a huge collection of 21,754 specimens; nevertheless, the number of species (41) is lower than in Schernham and Richardhof-Golfplatz. Details on regional geology and taxonomy are presented by Bachmayer and Zapfe (1969), Bachmayer and Wilson (1970), Daxner-Höck (2004a) and Daxner-Höck and Höck (2009).

8. Eich: The youngest assemblage was collected at Eichkogel (Eich: E 16°17′32″ N 48°03′55″) at the western margin of the Vienna Basin in Lower Austria. The mollusc and small mammal fauna was excavated from silty clay about 10–12 m below the freshwater limestone forming the top of the Eichkogel hill. The extraordinarily rich mollusc fauna of the lacustrine clay and limestone is the type fauna for the Upper Pannonian Zone H. The mammal assemblage represents the Lower Turolian (MN11). Its estimated age is 8.3 Ma. From the Eichkogel clay 2029 specimens of 35 species were collected. Details on stratigraphy, taxonomy and further references are given in Daxner-Höck (2004a), Daxner-Höck and Höck (2009, 2015), Harzhauser and Binder (2004), Harzhauser et al. (2004) and Ziegler (2006).

5. Small mammal record and faunal change

From these localities the fossil record is partly rare and partly very rich. Totally, almost hundred small mammal species were identified, i.e. 51 Rodentia, 36 Eulipotyphla ("Insectivora"), seven Chiroptera and five Lagomorpha (details in Online Appendix). Some species or groups of taxa are characteristic for certain stratigraphic levels and allow correlation with the European land Mammal Zones MN9 to MN11 of the Vallesian and Lower Turolian (Steininger, 1999).

5.1. Assemblages of the Lower Vallesian (lower part): MN9a

Despite the rather large stratigraphic gap of ~0.8 Ma between the assemblages Atz (Atzelsdorf, Gaweinstal, Bullendorf, Magersdorf, Mariathal) and Vö (Vösendorf, Inzersdorf, Hennersdorf) no major taxonomic difference can be detected. About 30% of the species are residents (Van der Meulen et al., 2005), e.g., *Neopetes hoeckarum, Spermophilinus bredai, Hispanomys bijugatus, Megacricetodon minutus, Steneofiber* sp., *Euroxenomys minutus, Plesiodimylus chantrei*. All assemblages are characterised by low origination- and extinction numbers (Fig. 2), by low diversities and by low individual numbers (due to taphonomic bias). The cluster analysis clearly shows a well-defined cluster I of taxa (Fig. 3) characterising the MN9a (Atz + Vö) assemblages in the Vienna Basin: i.e. *Muscardinus hispanicus, Megacricetodon minutus, Anomalomys rudabanyensis, Democricetodon* sp., *Schizogalerix voesendorfensis, Amphilagus*. In association with *Hipparion* s.l., which first occurs in these assemblages, they indicate the lower part of the lower Vallesian. In addition, the last occurrence of *Steneofiber* sp. is typical (as a singleton, it does not appear in the cluster analysis).

5.2. Assemblages of the Lower Vallesian (upper part): MN9b

In the assemblages RH (Richardhof-Golfplatz), Gö (Götzendorf) and Stix (Stixneusiedl) the diversity of small mammals increases rapidly, with highest origination values in Richardhof-Golfplatz but low extinction rates in Götzendorf and Stixneusiedl. The percentage of residents decreases to 15%. The first appearance of numerous species is defining the clusters II-IV (Fig. 3).

Characteristic and common taxa of these MN9b assemblages are *Pliopetaurista kollmanni*, *Keramidomys ermannorum*, *Eomyops catalaunicus*, *Muscardinus hispanicus*, *Muscardinus vallesiensis*, *Eumyarion leemanni*, *Kowalskia* sp. A., *Democricetodon* sp., *Microtocricetus molassicus*, *Anomalomys rudabanyensis*, *Eozapus intermedius*, *Euroxenomys minutus*, *Archaeodesmana vinea*, *Lantanotherium sanmigueli*, *Plesiodimylus* aff. *chantrei*.

5.3. Assemblages of the Upper Vallesian (lower part): MN10a

In Rh (Richardhof-Wald) and NS (Neusiedl am See), the diversity of small mammals is high, and composition of the assemblages is similar to MN9b (Fig. 2). The main differences from faunas of MN9b are: the originations of *Progonomys hispanicus* (first occurrence of Murinae in Austria), *Kowalskia* sp. B and *Collimys primus*, and the extinctions of typical MN9 species, e.g., *Albanensia grimmi*, *Pliopetaurista kollmanni*, *Muscardinus vallesiensis*, *Muscardinus hispanicus*, *Paraglirulus werenfelsi*, *Eumyarion leemanni*, *Democricetodon*, *Microtocricetus molassicus*, *Anomalomys rudabanyensis*. This turnover is also indicated in clusters I–II (Fig. 3). Characteristic taxa

restricted to the MN10a are *Progonomys hispanicus*, *Kowalskia* sp. B., and *Prolagus* aff. *crusafonti*.

5.4. Assemblages of the Upper Vallesian (upper part): MN10b

In Schernham (Sch) the origination- and extinction numbers are almost balanced, and the diversity of small mammals is unchanged (Fig. 2). New small mammal species (*Parapodemus lugdunensis*, *Pliopetes hungaricus*, *Pliopetaurista bressana*, *Pseudocollimys steiningeri*, *Prospalax* aff. *petteri*) initiate the trend toward the Turolian type of fauna.

The high number of residents and the considerable amount of species bridging the Vallesian/Turolian boundary prevent a clear grouping; the species from Schernham are spread in all clusters except for cluster VI (Fig. 3). Nevertheless, some species are known so far exclusively from this locality: *Paraglirulus schultzi*, *Kowalskia* sp. C, *Pseudocollimys steiningeri*, *Prospalax* aff. *petteri*, *Postpalerinaceus vireti*, *Proscapanus austriacus* and *Kervoula murinoides*. Although not restricted to MN10b, several species are at least quantitatively of great importance: *Parapodemus lugdunensis*, *Pliopetes hungaricus*, *Pliopetaurista bressana*, *Muscardinus pliocaenicus austriacus*, *Euroxenomys minutum*, *Archaeodesmana* aff. *vinea*, *Storchia biradicata*, *Proscapanus austriacus*, *Plesiosorex evolutus*, *Plesiodimylus* aff. *chantrei*, *Prolagus* sp.

5.5. Assemblages of the Lower Turolian: MN11

In Kohfidisch (Ko) and Eichkogel (Eich) the diversity of small mammal faunas decreases (Fig. 2). The statistical analysis reveals a homogenous cluster VI (Fig. 3) comprising *Progonomys woelferi*, *Prospalax petteri*, *Kowalskia skofleki*, *Epimeriones austriacus*, *Myomimus dehmi*, *Vasseuromys pannonicus* and *Crusafontina kormosi* as stratigraphically characteristic taxa for this zone occurring at both localities. Other typical MN11 species are *Megaderma vireti*, *Rhinolophus delphinensis*, *Hystrix parvae*, *Ischymomys* sp., *Schizogalerix zapfei* and *Kowalskia fahlbuschi* (only known from Kohfidisch) and *Schizogalerix moedlingensis* (only from Eichogel). Cluster V (Fig. 3) yields also several species, which are frequently found in the MN11 sections but already appear in MN10b assemblages, e.g. *Apodemus lugdunensis*, *Muscardinus pliocaenicus austriacus*, *Spermophilinus* aff. *bredai*, *Pliopetes hungaricus* and *Pliopetaurista bressana*.

6. Palaeoecological aspects

The suprageneric composition of small mammal communities within the various localities of the study area is rather homogeneous except for the Atzelsdorf and Vösendorf complexes. These assemblages of the Lower and Middle Pannonian (MN9a) show incomparably low species and specimen numbers (Tables 1–3), and therefore will be excluded from further analyses.

All considered assemblages of the Upper Pannonian (MN9b to MN11b) show highest species numbers of Rodentia (20–24 taxa) followed by Eulipotyphla (12–21 taxa). Chiroptera and Lagomorpha are present in low numbers or are absent. Only in Schernham numbers of Eulipotyphla (21 taxa) and Rodentia (20 taxa) are almost equal (Table 1).

Table 1
Number of small mammal species per order and stratigraphic unit (MN9b to MN11).
Tableau 1
Nombre d'espèces de micromammifères par ordre et par unité stratigraphique (MN9b à MN11).

	MN9b RH	MN9b Gö + Stix	MN10a Rh + NS	MN10b Sch	MN11 Ko	MN11 Eich
Rodentia	24	20	22	20	23	21
Eulipotyphla	15	12	12	21	12	13
Chiroptera	3	1	4	2	5	1
Lagomorpha	0	1	1	2	1	0

Table 2
Number of rodent species per family and stratigraphic unit (MN9b to MN11).
Tableau 2
Nombre d'espèces de rongeurs par famille et par unité stratigraphique (MN9b à MN11).

Rodentia	MN9b RH	MN9b Gö + Stix	MN10a Rh + NS	MN10b Sch	MN11 Ko	MN11 Eich
Sciuridae	5	6	5	7	5	5
Eomyidae	3	2	2	2	2	1
Gliridae	8	5	8	5	6	5
Cricetidae	6	5	6	3	5	5
Muridae	0	0	1	1	2	2
Dipodidae	1	1	0	1	1	1
Hystricidae	0	0	0	0	1	0
Castoridae	1	2	0	1	1	2

The analysis of the Rodentia (Table 2) documents high diversities of Gliridae, Sciuridae (tree-squirrels), Cricetidae (Paracricetodontinae, Cricetodontinae and Cricetinae) in all assemblages of the Upper Pannonian. Many of these taxa can be traced back to the Middle Miocene or to Middle Miocene ancestor groups. Gliridae and Cricetidae reach the highest species numbers in the two Richardhof localities (RH/MN9b and Rh/MN10a), Sciuridae in Schernham (MN10b), followed by Götzendorf (MN9b). The species numbers of Eomyidae and Castoridae are comparatively low. The immigrants *Microtocricetus* and *Eozapus* reached the Vienna Basin in MN9, Murinae in MN10, *Hystrix*, *Epimeriones* and *Ischymomys* in MN11. These immigrants retain low species numbers, but – except *Ischymomys* – developed high individual numbers.

Eulipotyphla (Table 3) are represented by Erinaceidae, Plesiosoricidae, Talpidae, Dimylidae and Soricidae families, with the Talpidae being most diverse followed by the Soricidae. Most striking is the high number of Talpidae from Schernham followed by Richardhof-Wald and Eichkogel. The diversity of Soricidae is rather uniform in all assemblages. Low species numbers of Erinaceidae and Dimylidae are known from all assemblages, and occurrences of Plesiosoricidae are restricted to Götzendorf and Schernham.

Our study confirms that the majority of mammals of the Late Pannonian inhabited forested wetland environments. This observation is evidenced by the high variability of climbing and gliding Sciuridae, Eomyidae

Table 3
Number of insectivore species per family and stratigraphic unit (MN9b to MN11).
Tableau 3
Nombre des espèces d'insectivores par famille et par unité stratigraphique (MN9b à MN11).

Eulipotyphla	MN9b RH	MN9b Gö + Stix	MN10a Rh + NS	MN10b Sch	MN11 Ko	MN11 Eich
Erinaceidae	3	2	1	3	2	2
Plesiosoricidae	0	2	0	1	0	0
Talpidae	5	5	6	10	5	6
Dimylidae	2	1	1	2	0	1
Soricidae	5	3	5	5	4	4

and Gliridae species, by the frequency of Castoridae, Dimylidae and Talpidae – most of them are known to live close to waterbodies, in floodplains and wet forests. Although the diversity of small mammal species slowly decreased from the Late Vallesian towards the Early Turolian (Fig. 2), many forest dwellers (*Pliopetaurista*, *Pliopetes*, *Neopetes*, *Blackia*, *Miopetaurista*, *Glirulus*, *Keramidomys* and *Eomyops*) persisted to the Turolian in low individual numbers per fauna. Simultaneously, ground dwelling Rodentia (*Spermophilinus* aff. *bredai*, *Kowalskia fahlbuschi*, *Kowalskia skofleki*, *Prospalax petteri*, *Muscardinus pliocaenicus austriacus*, *Vasseuromys pannonicus*, *Myomimus dehmi*, *Progonomys woelferi*, *Apodemus lugdunensis* and *Hystrix*) originated and developed significantly higher specimen numbers per fauna than the specialists adapted to humid forested environments (Daxner-Höck, 2004a; Daxner-Höck and Höck, 2009, 2015).

7. Conclusions

Our data suggest a major diversification of small mammal communities after the retreat of Lake Pannon from the Austrian part of the Vienna Basin beginning with the Late Pannonian. This pattern is partly explained by the establishment of forested wetland environments in the entire Vienna Basin, resulting in an increase of available habitats and thus is a regional signal. Nevertheless, the apparent increase in diversity (RH; MN9b) may partly be overemphasised due to the comparatively poor record from the Early and Middle Pannonian (MN9a), when Lake Pannon attained its maximal size and covered large parts of the Vienna Basin. Generally, the associations of mainly forest dwelling small mammals underwent minor diversity changes throughout the Vallesian. Apart from numerous extinctions at the beginning of the Late Vallesian (Fig. 3; clusters I–II; MN10a) no clear indication of a Vallesian Crisis (in the sense of Agusti and Moyà-Solà, 1990) can be deduced from our data (compare also Casanovas-Vilar et al., 2014).

A slight shift in communities is observed with the onset of the Turolian, when the small mammal diversities slowly decreased, and some xerophylic species originated and predominated the mammal spectra by very high individual numbers. This seems to reflect the beginning changing of closed forest environments toward patches of open landscape, as a result of less humid conditions at the Vallesian–Turolian transition.

Acknowledgments

The research on small mammals from the Late Miocene of Austria was funded by the Austrian Science Funds (FWF): P-15724-N06. We gratefully acknowledge the support of all our contributors of fieldwork and scientific input. We very much thank reviewers J. Klietmann and W. Wessels for useful comments.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.crpv.2015.06.008.

References

Agusti, J., Moyà-Solà, S., 1990. Mammal extinctions in the Vallesian (Upper Miocene). Lect. Notes Earth Sci. 30/1990, 425–432.
Agusti, J., Cabrera, L., Garcés, M., Parés, J.M., 1997. The Vallesian mammal succession in the Valles-Penedes basin (Northeast Spain): paleomagnetic calibration and correlation with global events. Palaeogeogr. Palaeoclimatol. Palaeoecol. 133, 149–180.
Angelone, C., 2009. The Early Vallesian vertebrates of Atzelsdorf (Late Miocene, Austria). 6. Lagomorpha. Ann. Nat. Hist. Mus. Wien. 111/A, 515–518.
Angelone, C., Veitschegger, K., 2015. MN10 *Prolagus* (Ochotonidae, Lagomorpha) from Austria: a new tile for the central European palaeobiogeography of the genus. N. Jb. Geol. Paläont. Abh. 275, 1–10.
Bachmayer, F., Wilson, R.W., 1970. Die Fauna der altpliozänen Höhlen- und Spaltenfüllungen bei Kohfidisch, Burgenland (Österreich). Ann. Nat. Hist. Mus. Wien 74, 533–587.
Bachmayer, F., Wilson, R.W., 1978. A second contribution to the Small Mammal Fauna of Kohfidisch, Austria. Ann. Nat. Hist. Mus. Wien 81/A, 129–161.
Bachmayer, F., Wilson, R.W., 1980. A third contribution to the fossil Small Mammal Fauna of Kohfidisch (Burgenland), Austria. Ann. Nat. Hist. Mus. Wien 83/A, 351–386.
Bachmayer, F., Zapfe, H., 1969. Die Fauna der altpliozänen Höhlen- und Spaltenfüllungen bei Kohfidisch, Burgenland (Österreich). Geologische und biostratigraphische Verhältnisse der Fundstelle, Ausgrabungen. Ann. Nat. Hist. Mus. Wien. 73, 123–139.
Bernor, R.L., Mittmann, H.-W., Rögl, F., 1993. Systematic and chronology of the Götzendorf « Hipparion » (Late Miocene, Pannonian F, Vienna Basin). Ann. Nat. Hist. Mus. Wien. 95/A, 101–120.
Casanovas-Vilar, I., van den Hoek Ostende, L.W., Furió, M., Madern, P.A., 2014. The range and extent of the Vallesian Crisis (Late Miocene): new prospects based on the micromammal record from the Vallès-Penedès (Catalonia, Spain). J. Iber. Geol. 40 (1), 29–48.
Daxner, G., 1967. Ein neuer Cricetodontide (Rodentia, Mammalia) aus dem Pannon des Wiener Beckens. Ann. Nat. Hist. Mus. Wien 71, 27–36.
Daxner-Höck, G., 1972a. Die Wirbeltierfauna aus dem Alt-Pliozän (Pont) vom Eichkogel bei Mödling (Niederösterreich). IV. Gerbillinae (Rodentia, Mammalia). Ann. Nat. Hist. Mus. Wien 76, 143–150.
Daxner-Höck, G., 1972b. Cricetidae aus dem Alt-Pliozän vom Eichkogel bei Mödling (Niederösterreich) und von Vösendorf bei Wien. Paläont. Z. 46 (3/4), 133–150.
Daxner-Höck, G., 1977. Muridae, Zapodidae and Eomyidae (Rodentia, Mammalia) des Eichkogels bei Mödling (Niederösterreich). Paläont. Z. 51 (1/2), 19–31.
Daxner-Höck, G., 1980. Rodentia (Mammalia) des Eichkogels bei Mödling (Niederösterreich). 1. Spalacinae und Castoridae. 2. Übersicht über die gesamte Nagetierfauna. Ann. Nat. Hist. Mus. Wien. 83, 135–152.
Daxner-Höck, G., 1996. Faunenwandel im Obermiozän und Korrelation der MN-"Zonen" mit den Biozonen des Pannons der Zentralen Paratethys. Beitr. Paläont. 21, 1–9.
Daxner-Höck, G., 2004a. Flying Squirrels (Pteromyinae, Mammalia) from the Upper Miocene of Austria. Ann. Nat. Hist. Mus. Wien 106A, 387–423.
Daxner-Höck, G., 2004b. *Pseudocollimys steiningeri* nov. gen. nov. spec. (Cricetinae, Rodentia, Mammalia) aus dem Ober-Miozän der Molassezone Oberösterreichs. In: Plodowski, G. (Ed.), Festschrift zu Ehren von Prof. Dr. Fritz F. Steininger. Cour. Forschungsinst. Senckenberg 246, 1–13.

Daxner-Höck, G., Bernor, R.L., 2009. The Early Vallesian vertebrates of Atzelsdorf (Late Miocene, Austria). 8. Anchitherium, Suidae and Castoridae (Mammalia). Ann. Nat. Hist. Mus. Wien. 111A, 575–584.
Daxner-Höck, G., Höck, E., 2009. New data on Eomyidae and Gliridae (Rodentia, Mammalia) from the Late Miocene of Austria. Ann. Nat. Hist. Mus. Wien 111A, 375–444.
Daxner-Höck, G., Höck, E., 2015. Catalogus Fossilium Austriae. Band 4: Rodentia neogenica. Osterr. Acad. Wiss. Wien. (in press, Verlag Österreichische Akademie der Wissenschaften).
Garces, M., Agusti, J., Cabrera, L., Parés, J.M., 1996. Magnetostratigraphy of the Vallesian (Late Miocene) in the Vallès Penédes Basin (NE Spain). Earth Planet. Sci. Lett. 142, 381–396.
Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: Palaeontological Statistics Software package for education and data analysis. Palaeont. Electron. 4, 9 pp.
Harzhauser, M., 2009. The Early Vallesian vertebrates from Atzelsdorf (Austria, Late Miocene). 2. Geology. Ann. Nat. Hist. Mus. Wien 111A, 479–488.
Harzhauser, M., Binder, H., 2004. Synopsis of the Late Miocene mollusc fauna of the classical sections Richardhof and Eichkogel in the Vienna Basin. Arch. Molluskenkd. 133 (1/2), 109–165.
Harzhauser, M., Mandic, O., 2004. The muddy bottom of Lake Pannon – a challenge for dreissenid settlement (Late Miocene; Bivalvia). Palaeogeogr. Palaeoclimatol. Palaeoecol. 204, 331–352.
Harzhauser, M., Mandic, O., 2008. Neogene lake systems of central and South-Eastern Europe: faunal diversity, gradients and interrelations. Palaeogeogr. Palaeoclimatol. Palaeoecol. 260, 417–434.
Harzhauser, M., Tempfer, P.M., 2004. Late Pannonian Wetland Ecology of the Vienna Basin based on Molluscs and Lower Vertebrate Assemblages (Late Miocene, MN9, Austria). Cour. Forschungsinst. Senckenberg 246, 55–68.
Harzhauser, M., Daxner-Höck, G., Piller, W.E., 2004. An integrated stratigraphy of the Pannonian (Late Miocene) in the Vienna Basin. Austr. J. Earth Sci. 95/96, 6–19.
Harzhauser, M., Daxner-Höck, G., Göhlich, U.B., Nagel, D., 2011. Complex faunal mixing in the early Pannonian palaeo-Danube Delta (Late Miocene, Gaweinstal, Lower Austria). Ann. Nat. Hist. Mus. Wien 113, 167–208.
Harzhauser, M., Kovar-Eder, J., Nehyba, S., Ströbitzer-Hermann, M., Schwarz, J., Wójcicki, J., Zorn, I., 2003. An Early Pannonian (Late Miocene) transgression in the Northern Vienna Basin. The paleoecological feedback. Geol. Carpathica 54 (1), 41–52.
Kern, A.K., Harzhauser, M., Piller, W.E., Mandic, O., Soliman, A., 2012. Strong evidence for the influence of solar cycles on a Late Miocene lake system revealed by biotic and abiotic proxies. Palaeogeogr. Palaeoclimatol. Palaeoecol. 329-330, 124–136.
Kern, A.K., Harzhauser, M., Soliman, A., Piller, W.E., Mandic, O., 2013. High-resolution analysis of Upper Miocene lake deposits: evidence for the influence of Gleissberg-band solar forcing. Palaeogeogr. Palaeoclimatol. Palaeoecol. 370, 176–183.
Lirer, F., Harzhauser, M., Pelosi, N., Piller, W.E., Schmid, H.P., Sprovieri, M., 2009. Astronomically forced teleconnection between Paratethyan and Mediterranean sediments during the Middle and Late Miocene. Palaeogeogr. Palaeoclimatol. Palaeoecol. 275, 1–13.
Magyar, I., Geary, D.H., Sütö-Szentai, M., Müller, M.L.P., 1999. Integrated biostratigraphic, magnetostratigraphic and chronostratigraphic correlation of the Late Miocene Lake Pannon deposits. Acta Geolog. Hung. 42, 5–31.
Nehyba, S., Roetzel, R., 2004. The Hollabrunn-Mistelbach Formation (Upper Miocene, Pannonian) in the Alpine-Carpathian Foredeep and the Vienna Basin in Lower Austria – An example of a Coarse-grained Fluvial System. Jb. Geol. Bundesanst. 144 (2), 191–221.
Papp, A., 1951. Das Pannon des Wiener Beckens. Mitt. Geol. Ges. Wien 1946-1948, 39–41, and 99–193.
Papp, A., Thenius, E., 1954. Vösendorf – ein Lebensbild aus dem Pannon des Wiener Beckens. Mitt. Geol. Ges. Wien Sonderband 46 (1953), 1–109.
Paulissen, E., Luthi, S.M., Grunert, P., Ćorić, S., Harzhauser, M., 2011. Integrated high-resolution stratigraphy of a Middle to Late Miocene sedimentary sequence in the central part of the Vienna Basin. Geol. Carpathica 62, 155–169.
Rabeder, G., 1973. *Galerix* und *Lanthanotherium* (Erinaceidae, Insectivora) aus dem Pannon des Wiener Beckens. N. Jb. Geol. Paläont. Monatshefte 1973 (7), 429–446.
Rabeder, G., 1985. Die Säugetiere des Pannonien. In: Papp, A., Jambor, A., Steininger, F.F., (Eds.), M6, Pannonien (Slavonien und Serbien). Chronostrat. Neostratotypen 6, 440–463.
Rabeder, G., 1998. *Dinosorex* (Insectivora, Mammalia) aus dem Miozän von Österreich. Geol. Palaont. Mitt. Innsbruck 23, 117–126.
Rögl, F., Zapfe, H., Bernor, R.L., Brzobohaty, R., Daxner-Höck, G., Draxler, I., Fejfar, O., Gaudant, J., Herrmann, P., Rabeder, G., Schultz, O., Zetter, R., 1993. Die Primatenfundstelle Götzendorf an der Leitha, Niederösterreich (Obermiozän des Wiener Beckens). Jb. Geol. Bundesanst. 136 (2), 503–526.
Steininger, F.F., 1999. The Continental European Miocene. Chronostratigraphy, Geochronology and Biochronology of the Miocene "European Land Mammal Mega-Zones" (ELMMZ) and the Miocene "Mammal-Zones (MN-Zones)". In: Rössner, G.E., Heissig, K. (Eds.), The Miocene Land Mammals of Europe. Dr. Friedrich Pfeil, München, pp. 9–38.
Van Dam, J., 1997. The small mammals from the Upper Miocene of the Teruel-Alfambra Region (Spain): paleobiology and paleoclimatic reconstructions. Geol. Ultraiectina 156, 1–204.
Van der Meulen, A.J., Peláez-Campomanes, P., Levin, S.A., 2005. Age structure, residents, and transients of Miocene Rodent communities. Am. Nat. 165 (4), Online article.
Van Weers, D.J., Montoya, P., 1996. Taxonomy and stratigraphic record of the oldest European porcupine *Hystrix parvae* (Kretzoi, 1951). Proc. Nederlandse Akad. Wetenschappen 99(B), 131–141.
Ziegler, R., 2006. Insectivores (Lipotyphla) and bats (Chiroptera) from the Late Miocene of Austria. Ann. Nat. Hist. Mus. Wien 107A, 93–196.
Ziegler, R., Daxner-Höck, G., 2005. Austria. In: Hoek Ostende, L.W., van den Doukas, C.S., Reumer, J.W.F., (Eds.), The Fossil Record of the Eurasian Neogene insectivores (Erinaceomorpha, Soricomorpha, Mammalia). Part. 1. Scr. Geol. Sp. Issue 5, 11–29.