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Badenian and Sarmatian s.str. from the Carpathian area: Overview and ongoing research on Hungarian and Romanian small vertebrate evolution

Badénien et Sarmatien s.str. de la région des Carpates : présentation générale et recherches en cours concernant l'évolution des petits vertébrés hongrois et roumains

János Hír[a], Márton Venczel[b], Vlad Codrea[c,i], Chiara Angelone[d], Lars W. van den Hoek Ostende[e], Uwe Kirscher[f], Jérôme Prieto[g,h,*]

[a] *Pásztói Múzeum, 5, Múzeum tér, 3060 Pásztó, Hungary*
[b] *Țării Crișurilor Museum, 1-3, B-dul Dacia, 410464 Oradea, Romania*
[c] *Babeș-Bolyai University, 1, Kogălniceanu Street, 400084 Cluj-Napoca, Romania*
[d] *Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA-ICP, Carrer de les Columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain*
[e] *Naturalis Biodiversity Center, 2, Darwinweg, 2333 CR Leiden, The Netherlands*
[f] *ARC Centre of Excellence for Core to Crust Fluid Systems (CCFS) and The Institute for Geoscience Research (TIGeR), Department of Applied Geology, WASM, Curtin University, 6845 Perth, Australia*
[g] *SNSB–Bayerische Staatssammlung für Paläontologie und Geologie, 10, Richard-Wagner-Street, 80333 Munich, Germany*
[h] *Department of Earth- and Environmental Science, paleontology, Ludwig-Maximilians-University Munich, 10, Richard-Wagner-Street, 80333 Munich, Germany*
[i] *Dipartimento di Scienze, Largo S.L. Murialdo 1, 00146 Roma, Italy*

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ABSTRACT

The fossil record from the Carpathian area plays a key role for the understanding of the processes leading to the faunal interchanges between western Europe and Asia Minor during the late part of the Middle Miocene. Important mammal successions are now available from the Central Paratethys, especially Hungary and Romania. Here, we present the current state-of-the-art of the ongoing research concerning these faunas, especially small mammals and herpetofauna. We underscore the relevance of the Middle to earliest Late Miocene fossil record from these countries for chrono(bio)stratigraphic and palaeoenvironmental studies at the Eurasian scale.

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* Corresponding author. Department of Earth- and Environmental Science, paleontology, Ludwig-Maximilians-University Munich, 10, Richard-Wagner-Street, 80333 Munich, Germany.

E-mail addresses: hirjanos@gmail.com (J. Hír), mvenczel@gmail.com (M. Venczel), codrea_vlad@yahoo.fr (V. Codrea), chiara.angelone@icp.cat (C. Angelone), lars.vandenhoekostende@naturalis.nl (L.W. van den Hoek Ostende), uwe.kirscher@curtin.edu.au (U. Kirscher), j.prieto@lrz.uni-muenchen.de (J. Prieto).

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RÉSUMÉ

Mots clés :
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Reptiles

L'enregistrement fossile de la région des Carpates joue un rôle clé dans la compréhension des processus responsables des échanges fauniques entre l'Europe de l'Ouest et l'Asie mineure au cours de la fin du Miocène moyen. D'importantes successions de faunes mammaliennes sont maintenant connues pour la Paratéthys centrale, spécialement en Hongrie et en Roumanie. Nous présentons ici les derniers résultats des recherches en cours concernant ces faunes, en particulier les petits mammifères et les herpétofaunes. Nous soulignons l'importance de l'enregistrement fossile Miocène moyen/supérieur basal de ces pays pour les études chrono(bio)stratigraphiques et paléo-environnementales à l'échelle eurasienne.

1. Introduction

The late Middle Miocene presents a drastic reorganization of the continental vertebrate communities at the Eurasian scale, as a result of climatic changes due to the extension of the Antarctic ice sheet during the Middle Miocene climate transition, at around 14 My (e.g., Knorr and Lohmann, 2014). Because of its geographic position, as well as its complex geologic context, the fossil record from the Carpathian area (Fig. 1) plays a key role for the understanding of the processes leading to the faunal interchanges between western Europe and Asia Minor. The complicated regional tectonics of the central Paratethys, as well as glacio-eustatic sea-level changes influenced mammal evolution.

Intensive fieldwork during the last decades has yielded an important small mammal collection from Hungary and Romania. Based on integrated stratigraphic considerations, the record of the Carpathian area can be correlated to other European basins and allows for the study of the paleobiogeography during a time ranging from the Early/Middle Badenian transition to most probably the earliest part of the Pannonian.

The general aim of this work is to provide an overview of the vertebrate assemblages from this period in Hungary and Romania, to underscore the importance of the area for continental faunal evolution, and to give the latest results of ongoing research. Compared to other European basins, such as the Calatayud-Teurel (García-Paredes et al., 2016) and the Vallès-Penedès (Casanovas-Vilar et al., 2016) basins in Spain and the North Alpine Foreland Basin in Switzerland and Germany (Prieto and Rummel, 2016), the study of the small mammals from the Middle Miocene of Hungary and Romania is at an early stage. Pre-Pannonian localities were not known before the presentation of Hasznos in 1986. The taxonomy is therefore not yet as settled as in other areas, particularly since we are studying the counterparts of species and genera that have been defined elsewhere. A critical review of the taxonomy of the published small mammals, as well as the most recent data with regard to their stratigraphic context will be published separately (Hír et al., submitted), further developing our knowledge on the accompanying bird and herpetofauna and the first data on the ruminants from Mátraszőlős and Felsőtárkány.

In the present contribution, we provide some preliminary discussions on the biochronostratigraphic importance of the area, as well as some notes on the palaeobiogeography and paleoenvironments.

2. Geological context and small mammal localities

The geographic position of the localities is provided in Fig. 1. The proposed chronostratigraphic positions, except for those of Váralja and Sámsonháza 0-2, are presented in Fig. 2.

The studied area is created by the inter-arc Carpathian basin s. l. (Pannonian + Transylvanian basins) enclosed by the Carpathian Mountain arc, the eastern Alps and the northern Dinarids, as a result of Oligo-Miocene plate collision of the African/Arabian continent with Eurasia. This tectonic activity divided the Tethys Ocean into the Paratethys, a large epicontinental sea ranging from the Rhône basin (France) to Lake Aral in central Asia, and the Mediterranean. In response to complex regional tectonics and sea-level lowering, the Paratethys retreated and was fragmented (e.g., Rögl, 1999; Steininger and Wessely, 2000). As such, it was subdivided into three bioprovinces characterized by very peculiar fossil assemblages (mainly mollusks, foraminifera and ostracods) that led to the introduction of separate regional chronostratigraphic scales for the western/central Paratethys and eastern Paratethys (e.g., Piller et al., 2007). The fossil localities taken into consideration belong to the central Paratethyan part (e.g., Steininger and Wessely, 2000) and the majority of the data are derived from deposits of the Pannonian Basin. These deposits started accumulating from around 20 Ma onwards, with a peak of fault activity during the Badenian-Sarmatian syn-rift phase. The small mammal associations considered here cover basically the latter period, ranging from the Middle Badenian (sensu Hohenegger et al., 2014) to the Earliest Pannonian. Traditionally, the terrestrial faunas of the area are correlated with the marine stages. The Sarmatian is considered herein using the central Paratethys concept (see for instance Krijgsman and Piller in Hilgen et al., 2012). The equivalent eastern Paratethyan stages are indeed most often poorly dated, but for our purpose, it is important to notice that the bases of the Volhynian and Sarmatian s. str. are identical (e.g., Harzhauser and Piller, 2007). The equivalent global stages are Langhian and Serravallian, while the youngest localities considered herein are most probably Earliest Tortonian. In terms of mammalian stages, they span the

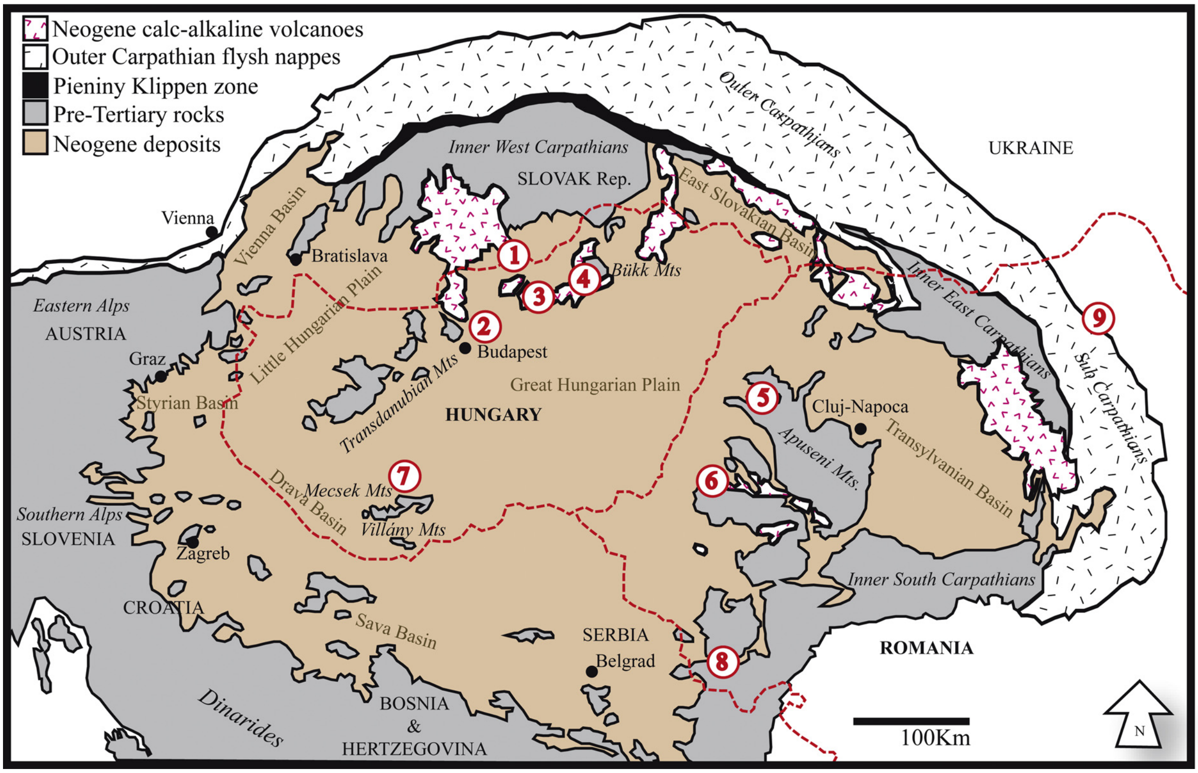


Fig. 1. Position of the Hungarian and Romanian small mammal localities in the Carpathian area. Map simplified after Haas (2012) (fig. 3.1) and Filipescu et al. (2014) (fig. 1). 1. Egerszólát, Felsőtárkány 1, Litke 1 + 2. 2. Szentendre. 3. Sámsonháza, Hasznos, Mátraszőlős, Kozárd. 4. Egerszólát, Felsőtárkány. 5. Subpiatră, Vârciorog, Tăşad. 6. Comănesti 1, Tauţ. 7. Váralja. 8. Bozovici. 9. Bogata.

Fig. 1. Position des localités à petits mammifères hongroises et roumaines. Carte simplifiée d'après Haas (2012) (fig. 3.1) et Filipescu et al. (2014) (fig. 1). 1. Egerszólát, Felsőtárkány 1, Litke 1 + 2. 2: Szentendre. 3: Sámsonháza, Hasznos, Mátraszőlős, Kozárd. 4: Egerszólát, Felsőtárkány. 5: Subpiatră, Vârciorog, Tăşad. 6: Comănesti 1, Tauţ. 7: Váralja. 8: Bozovici. 9: Bogata.

Aragonian/Astaracian, or MN 5/6 to MN 9 (depending on which taxon is used to define the base of the MN 9; see Prieto and Rummel, 2016).

The oldest locality considered herein is a borehole in the Szászvár Formation at Váralja (Hungary, Tolna County). The finding of a tooth of *Anomalomys minor* lead Kordos (1989) to tentatively correlate the fossil to the Ottnangian or Karpatian. Litke 1 + 2 (Hungary, Nógrád County) contains *Cricetodon meini* (Hír, 2013) and is thus correlated to the Early to Middle Badenian transition. The Middle Badenian is better documented in the Hungarian Nógrád (Sámsonháza and Hasznos) and Pest Counties (Szentendre; e.g., Hír et al., 1998; Hír and Mészáros, 2002; Kordos, 1986). The transition to Late Badenian is recorded through the three small mammal-bearing layers of the Subpiatră section (Romania, Bihor County; Hír and Venczel, 2005; see also discussion in Hír et al., submitted). Additionally, the small mammals obtained from the Bozovici borehole #1266 (Romania, Caraş-Severin County; Codrea, 2001) allow a correlation to the late Middle/earliest Late Badenian. The end of the Badenian, in contrast, is only known from Mátraszőlős (Hungary, Nógrád County), especially thanks to the uppermost fauna from the layer number 3 (Hír and Kókay, 2004, 2011). Note that the find of *Forsythia gaudryi* in Egerbocs (Hungary, Heves County; Hír, 2001) does not rule out a correlation to the Late Badenian. Tăşad (Romania, Bihor County; Hír et al., 2001) is placed in the *Mohrensternia* Zone of the Early Sarmatian s. str. Similarly, the microfossil assemblages from Vârciorog (or Vércsorog, Romania, Bihor County; Filipescu et al., 2014) are characteristic for the *Elphidium reginum* Zone and *Mohrensternia* Zone. These new superposed small mammal layers are under study (see discussion in Hír et al., submitted). The palaeomagnetic data of the layers overlying the vertebrate-enriched deposits indicate an inverse polarity possibly correlated to chron C5Ar.1r. Similarly, the new locality Kozárd (Hungary, Nógrád County; Tóth and Csoma, 2015) has delivered the foraminifer *Elphidium reginum*. Finally, the Late Sarmatian s. str. is well represented with three localities from Romania, namely Comăneşti 1 (Arad County; end Volhynian/base Bessarabian; Feru et al., 1980), Tauţ (Arad County; most probably Early Bessarabian; Feru et al., 1979, Hír et al., 2011) and Bogata (Suceava County; Upper Volhynian; single find of *Dinosorex*; Codrea and Ţibuleac, 1999). The Hungarian record is even richer, especially in the Felsőtárkány basin (Heves County), where two sections (Felsőtárkány – Güdör-kert and Felsőtárkány – Felnémet) provided seven fossiliferous layers (e.g., Andreánszky and Kovács, 1955; Éhik, 1926; Hír, 2006; Hír and Kókay, 2009, 2010; Kretzoi, 1982; Schréter, 1913; Sümeghy, 1923). Felsőtárkány 3/8 and 3/10 are the highest layers in the section and they cover a time interval including the Late Sarmatian and

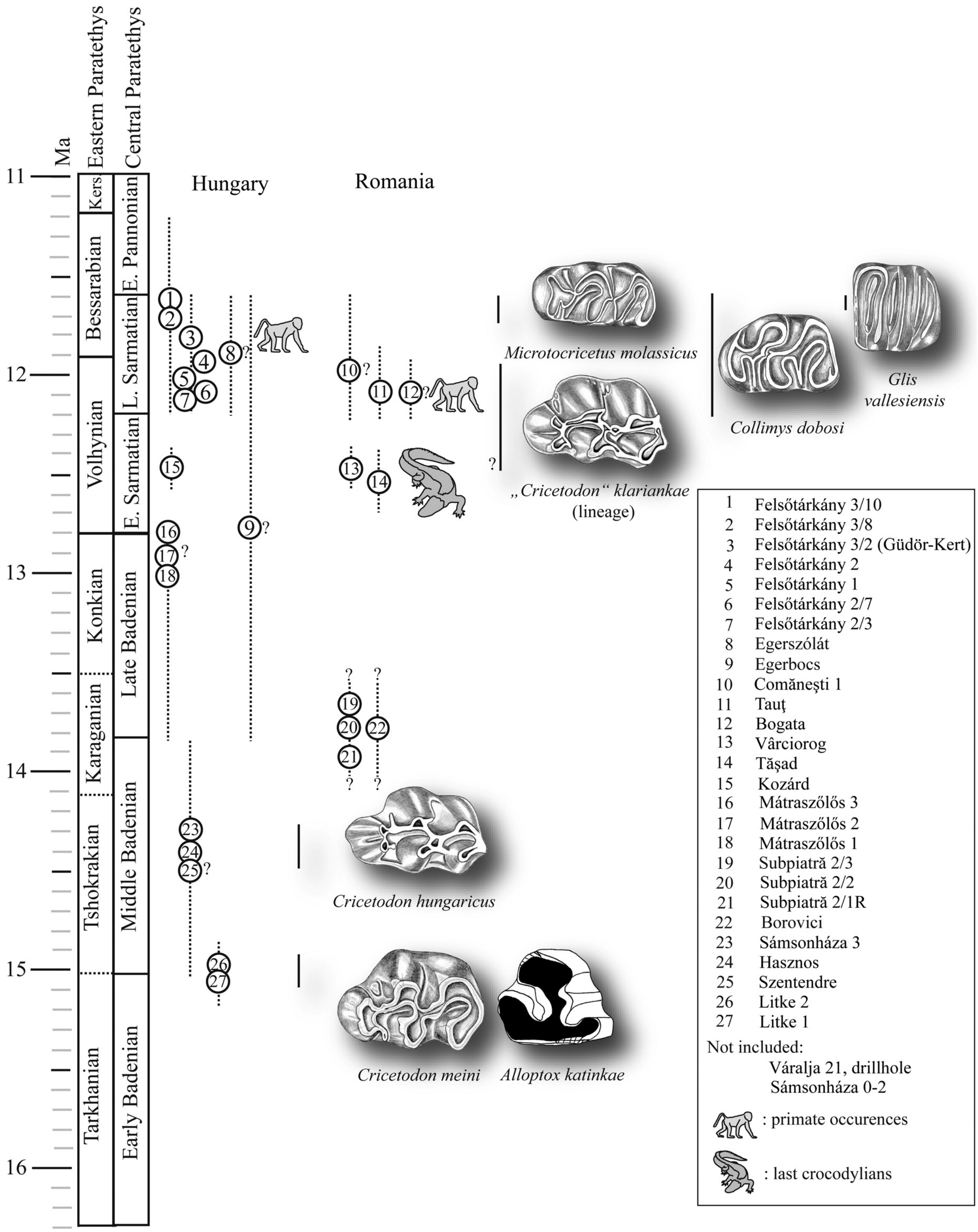


Fig. 2. Chronostratigraphic position of the Hungarian and Romanian small mammal localities. The division and limits of the Badenian follow the proposal of Hohenegger et al. (2014). The figured small mammals indicate some biostratigraphically important taxa, and are not to scale. Ranges of taxa are indicated by continuous lines, while dotted lines indicate age uncertainty of the considered sites.

Fig. 2. Position chronostratigraphique des localités à petits mammifères hongroises et roumaines. La division, ainsi que les limites du Badénien, suivent la proposition de Hohenegger et al. (2014). Les petits mammifères figurés illustrent quelques taxons à caractère biostratigraphique important et ne sont pas à l'échelle. Le domaine stratigraphique de ces taxons est indiqué par une ligne continue, alors que les lignes pointillées indiquent les incertitudes concernant l'âge des sites.

Pannonian A/B. The fauna from Egerszólát (Heves County) is also correlated to the Late Sarmatian s. str. (Hír, 2011).

3. The Miocene vertebrate succession

As shown in Hír et al. (submitted), the small mammal fossil localities yield also important collections of other vertebrates. Small mammals are summarized in Figs. 3 and 4, with reptiles (chelonians excluded) and amphibians in Fig. 5. Finally, the birds are based on Kessler (2014).

3.1. Chronostratigraphic importance of the Hungarian and Romanian records

At the central/eastern European scale, the studied area fills an important stratigraphic gap in the small mammal record. Fig. 6 shows the number of micromammalian localities through the Ottnangian-earliest Pannonian in the Carpathian area. The Serbian record (Marković and Milivojević, 2010) has not been added because of correlation problems, but is discussed below. While a small mammal record ranging from Ottnangian to Early Badenian is almost missing in Hungary and Romania, important and rich localities from this time span, especially in Austria (Daxner-Höck and Höck, 2015, and references therein), provide valuable data. In Serbia and Poland, the period is also documented (Snegotin, Sibnica 1, Bełchatów C; Garapich, 2002 Marković and Milivojević, 2010), and numerous localities are known from the North Alpine Foreland basin (e.g., Seehuber, 2015; Ziegler and Fahlbusch, 1986). Similarly, the earliest part of the Pannonian, scarcely represented in Hungary, is best documented in Austria (Daxner-Höck et al., 2016) and important localities are reported from Switzerland, Germany, Slovak Republic, Poland and Ukraine (e.g., Nebelbergweg, Hammerschmiede, Borský Svätý Jur, Bełchatów A, Gritsiv; Garapich, 2002; Joniak, 2005; Kälin and Kempf, 2009; Mayr and Fahlbusch, 1975). In sharp contrast, the Late Badenian–Sarmatian from Hungary and Romania gives a rare insight into the micromammal assemblages. Elsewhere, only a few good localities are known, such as Gratkorn in Austria (Böhme et al., 2014; Gross et al., 2011) or Devínská Nová Ves–Bonanza in the Slovak Republic (Sabol and Kovàč, 2006). Even in the North Alpine Foreland basin, only a few Late Badenian localities are available (e.g., Anwil, Giggenhausen; Engesser, 1972; Fahlbusch, 1964). Marković and Milivojević (2010) correlate the Serbian site Vračevići to MN 7 + 8, and report *Byzantinia bayraktenpensis* in the fauna, a species known from Anatolia in the biozone H (Ünay et al., 2003). Fine correlations of our scheme with Anatolian and eastern Anatolian records are even much more difficult because of the near-absence of independent dating of the Turkish localities, the succession of which is mostly based on biostratigraphic evidence and their presumed relation to the MN system (Ünay et al., 2003). Some rare radiometric or paleomagnetic results indicate that localities correlate to Early (Thymiana, Greece; Koufos, 2006) or Late Badenian (Yenieskihisar, Turkey; Ünay et al., 2003).

3.2. Biostratigraphic notes

As shown above and in Figs. 2 and 6, the Hungarian and Romanian localities basically cover the Middle Badenian through the Sarmatian s. str. with a plausible correlation to the oldest Pannonian for the youngest sites. Thus, it is not surprising that several members of the cricetid tribe Cricetodontini are present in most of the localities discussed in this work, as they first occur in central Europe at around 15 Ma. Their diversity makes of them an important group for biostratigraphic correlation in the area. Other taxa, such as for instance *Megacricetodon*, are widely used for accurate relative dating in other regions such as the North Alpine Foreland Basin (e.g., Abdul Aziz et al., 2008, 2010; Reichenbacher et al., 2013), but the *Megacricetodon* lineages present in our study area are currently not well characterized or do not show much change through time. On the whole, only a single cricetodontine species occurs in each locality. Hír (2004) documents the relative abundance of the tribe in the Felsőtárkány Basin and comes to the conclusion that a decrease in “*Cricetodon*” *klariankae* abundance is observed between Felsőtárkány 2/7 and 2/3, ultimately leading to the disappearance of the species in the younger deposits (see also Fig. 3). Before this extinction, Early and Late Sarmatian sites contain species that can be attributed to the “*C.*” *klariankae* lineage. This suggests that, with the help of sufficient (new) material, a lineage spanning this period might adequately be characterized. Only the species (one or several) from Comăneşti 1 do(es) not seem to fit such a model. During the Middle Badenian, the Cricetodontini record consists of brachydont species that are related to *Cricetodon hungaricus*. Unfortunately, the key molar assemblage from Mátraszőlős at the latest part of the Badenian is too poor to be attributed to a given species. In addition, the two fossil sites from Subpiatră, which are a bit younger than Hasznos and Sámsonháza 3, lack cricetodontines (Hír and Venczel, 2005), making any interpretation even more hazardous. The oldest localities from the mid-Badenian contain *Cricetodon meini*, a widespread species (López-Guerrero et al., 2015).

The cricetid rodent *Collimys* is, at present, and in our studied area, characteristic for the Late Sarmatian–Earliest Pannonian faunas. Older finds of the genus are reported from the Middle and Late Badenian of the North Alpine Foreland basin and the surrounding Alps, but a relationship with the Hungarian species cannot be demonstrated (Prieto and Rummel, 2009a, 2009b, 2016). Only the species occurring around the Sarmatian/Pannonian transition show clear morphological similarities with the Hungarian one.

The presence of the microtoid rodent *Microtocricetus molassicus* in the youngest localities from the Felsőtárkány Basin documents a large-scale migration wave at the Middle to Late Miocene transition in central Europe, as shown by the presence of the species for instance in Hammerschmiede and Marktl (Germany; Fahlbusch and Mayr, 1975), Nebelberg TGL II (Switzerland; Kälin and Kempf, 2009), Bełchátow A (Poland; Kowalski, 1993) and Gritsiv (Ukraine; Kowalski, 1993). A new single molar of the genus discovered in Mörgen (Germany; see Seehuber, 2009 for other taxa) suggests a more complicated story for *Microtocricetus* (Prieto and Rummel, 2016).

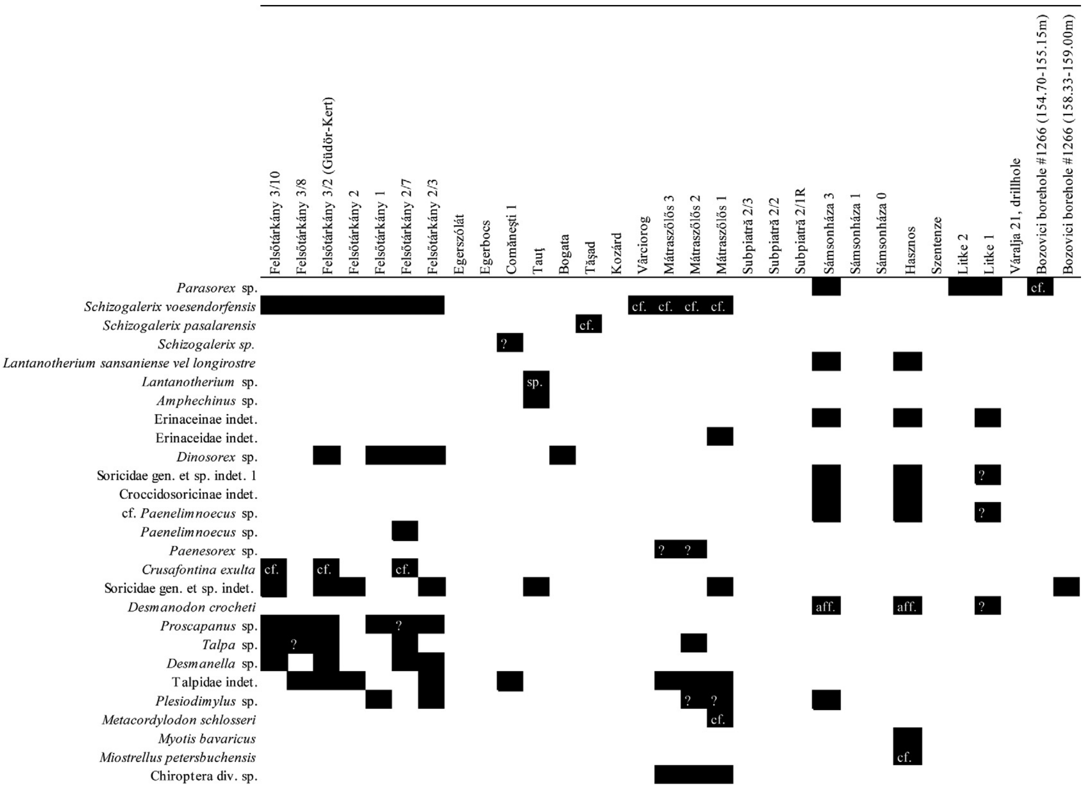
	Felsőtárkány 3/10	Felsőtárkány 3/8	Felsőtárkány 3/2 (Güdör-Kert)	Felsőtárkány 2	Felsőtárkány 1	Felsőtárkány 2/7	Felsőtárkány 2/3	Egerszólát	Egerbocs	Comănești 1	Tauț	Bogata	Tășad	Vârciorog	Kozárd	Mátraszőlős 3	Mátraszőlős 2	Mátraszőlős 1	Subpiatră 2/3	Subpiatră 2/2	Subpiatră 2/1R
Cricetodon meini																					
Cricetodon hungaricus																					
"Cricetodon" klariankae (lineage)						■	■						?	cf.	cf.						
cf. *Byzantinia* sp./div. sp.										■											
Cricetodon sp.																■	■	■			
Megacricetodon minor						■	■								x		cf.	cf.			
Megacricetodon similis																			■		cf.
Megacricetodon minutus	■		■	■	■			■		cf.			cf.								
Megacricetodon sp.														■							
Democricetodon mutilus																					
Democricetodon hasznosensis																					
Democricetodon brevis																cf.	cf.			?	?
Democricetodon cf. sp. nov.				cf.	cf.	cf.	cf.						■	■							
Democricetodon zarandicus											■										
Democricetodon gaillardi																			■		
Democricetodon freisingensis										cf.							cf.				
Democricetodon sp.									■					x	■						
Collimys dobosis	■		■	■	■	■	■														
Collimys sp.								■													
Microtocricetus mollassicus	■	■																			
Anomalomys minor																					
Anomalomys gaudryi	■	■	■		■	■	■	■								■		■			
Eumyarion bifidus																					
Eumyarion medius	■	■	■			■	■						■				■	■		■	
Eumyarion sp.											■			■		■					
Spermophilinus besana																					
Spermophilinus bredai			■		■	■	■				■		■	■	■	■		■	■	■	
Spermophilinus sp.																					
Palaeosciurus sutteri																					
Palaeosciurus ultimus																					
Palaeosciurus sp.																				■	
Blackia miocaenica			■			■	■				■			■		■				■	
Neopetes hoeckarum											■										
Neopetes sp.	■		■																■		
Forsythia gaudryi									■												
Miopetaurista dehmi																					
Miopetaurista gaillardi			■																	■	
Miopetaurista sp.											■				■						
Albanensia albanensis																					
Albanensia grimmi			■																		
Albanensia sp.							■				?				■	?			■		
Sciuridae indet.				■					■											■	
Keramidomys thaleri																					
Keramidomys mohleri			■	cf.	cf.												■				
Keramidomys sp.						■	■	■													
Eomyops oppligeri	■	■	■		■		■				■						■				
Microdyromys koenigswaldi																					
Microdyromys complicatus					■	■															
Microdyromys sp.																					
Glirulus lissiensis		cf.						■			■									■	
Paraglirulus werenfelsi	■	■	■		■															■	■
Miodyromys aegercii																					
Miodyromys hamadryas							■														
Miodyromys grycivensis										aff.											
Miodyromys sp.														sp.							
Muscardinus thaleri																			aff.	aff.	aff.
Muscardinus sansaniensis			aff.											aff.	aff.		aff.				
Muscardinus hispanicus											■										
Muscardinus sp.	■		■			■	■														
Paraglis astarensis																	■				
Myoglis meini	■		■		■	■	■							■	■				■	■	■
Myoglis ucrainicus											■										
Glis vallesiensis	■																				
Gliridae indet.													■								
Euroxenomys minutus	■		■			■	■														
Rooted Ochotonid	■	■		■				■						■			■	■	■		■
Alloptox katinkae																					
Prolagus oeningensis						■	■			sp.											

Fig. 3. Faunal list of the studied localities. Rodentia and Lagomorpha.

Fig. 3. Liste faunique des localités étudiées. Rodentia et Lagomorpha.

	Sámsonháza 3	Sámsonháza 1	Sámsonháza 0	Hasznos	Szentendre	Litke 2	Litke 1	Váralja 21, drillhole	Bozovici borehole #1266 (154.70-155.15m)	Bozovici borehole #1266 (158.33-159.00m)
Cricetodon meini						●	●			
Cricetodon hungaricus	cf.	sp.	cf.	●	●					
"Cricetodon" klariankae (lineage)										
cf. *Byzantinia* sp./div. sp.										
Cricetodon sp.										
Megacricetodon minor	?			●		●	●			
Megacricetodon similis										
Megacricetodon minutus										
Megacricetodon sp.										
Democricetodon mutilus						●	●			
Democricetodon hasznosensis				●	●					
Democricetodon brevis										
Democricetodon cf. sp. nov.										
Democricetodon zarandicus										
Democricetodon gaillardi										
Democricetodon freisingensis	●									
Democricetodon sp.										
Collimys dobosis										
Collimys sp.										
Microtocricetus mollassicus										
Anomalomys minor								●		
Anomalomys gaudryi				●	●					
Eumyarion bifidus				aff.						
Eumyarion medius										
Eumyarion sp.	●			●						
Spermophilinus besana						●	●			
Spermophilinus bredai	●									
Spermophilinus sp.				●						
Palaeosciurus sutteri						●				
Palaeosciurus ultimus				●						
Palaeosciurus sp.										
Blackia miocaenica										
Neopetes hoeckarum										
Neopetes sp.										
Forsythia gaudryi										
Miopetaurista dehmi							●			
Miopetaurista gaillardi										
Miopetaurista sp.										
Albanensia albanensis										
Albanensia grimmi										
Albanensia sp.										
Sciuridae indet.										
Keramidomys thaleri							cf.			
Keramidomys mohleri										
Keramidomys sp.										
Eomyops oppligeri										
Microdyromys koenigswaldi	●									
Microdyromys complicatus										
Microdyromys sp.				?						
Glirulus lissiensis										
Paraglirulus werenfelsi										
Miodyromys aegercii	2 sp.		●							
Miodyromys hamadryas										
Miodyromys grycivensis										
Miodyromys sp.			●			●	●			
Muscardinus thaleri										
Muscardinus sansaniensis	●									
Muscardinus hispanicus										
Muscardinus sp.										
Paraglis astarensis							●			
Myoglis meini										
Myoglis ucrainicus										
Glis vallesiensis										
Gliridae indet.										●
Euroxenomys minutus										
Rooted Ochotonid										
Alloptox katinkae						●				
Prolagus oeningensis						sp.				

Fig. 3. (*Continued*)



	Felsőtárkány 3/10	Felsőtárkány 3/8	Felsőtárkány 3/2 (Güdör-Kert)	Felsőtárkány 2	Felsőtárkány 1	Felsőtárkány 2/7	Felsőtárkány 2/3	Egerszólát	Egerbocs	Comăneşti 1	Tauţ	Bogata	Tăşad	Kozárd	Várciorog	Mátraszőlős 3	Mátraszőlős 2	Mátraszőlős 1	Subpiatră 2/3	Subpiatră 2/2	Subpiatră 2/1R	Sámsonháza 3	Sámsonháza 1	Sámsonháza 0	Hasznos	Szentenze	Litke 2	Litke 1	Váralja 21, drillhole	Bozovici borehole #1266 (154.70-155.15m)	Bozovici borehole #1266 (158.33-159.00m)
Parasorex sp.																						■					■	■		cf.	
Schizogalerix voesendorfensis	■	■	■	■	■	■	■								cf.	cf.	cf.	cf.													
Schizogalerix pasalarensis													cf.																		
Schizogalerix sp.										?																					
Lantanotherium sansaniense vel longirostre																						■			■						
Lantanotherium sp.											sp.																				
Amphechinus sp.											■																				
Erinaceinae indet.																						■			■			■			
Erinaceidae indet.																		■													
Dinosorex sp.			■		■	■	■					■																			
Soricidae gen. et sp. indet. 1																						■			■			?			
Croccidosoricinae indet.																						■			■						
cf. *Paenelimnoecus* sp.																						■			■			?			
Paenelimnoecus sp.						■																									
Paenesorex sp.																?	?														
Crusafontina exulta	cf.		cf.			cf.																									
Soricidae gen. et sp. indet.	■		■	■			■				■							■													■
Desmanodon crocheti																						aff.			aff.			?			
Proscapanus sp.	■	■	■		■	?	■																								
Talpa sp.	■	?	■			■											■														
Desmanella sp.	■		■			■	■																								
Talpidae indet.		■	■	■			■			■						■	■	■													
Plesiodimylus sp.					■		■										?	?				■									
Metacordylodon schlosseri																		cf.													
Myotis bavaricus																									■						
Miostrellus petersbuchensis																									cf.						
Chiroptera div. sp.																■	■	■													

Fig. 4. Faunal list of the studied localities. Eulipotyphla and Chiroptera.

Fig. 4. Liste faunique des localités étudiées. Eulipotyphla and Chiroptera.

Figs. 3 and 4 show that an "abrupt" faunal change occurs around the latest part of the Badenian. This is especially clear for the insectivore record. These fossils are currently under study, and will provide important data for the understanding of the processes leading to this restructuring of the ecosystems. Interestingly, the published data, available only for Hasznos and Sámsonháza 3, show that *Desmanodon* is the only talpid present during the Middle Badenian. This genus is also dominant in Litke, but apparently disappears in Hungary in the Late Badenian/Sarmatian.

3.3. Paleobiogeographical notes

The lagomorphs of the Middle Miocene of the Carpathian area, though often lacking a taxonomic revision, reveal very interesting details (see Hír et al., submitted). *Prolagus* from the Middle Miocene of the Carpathian area did not undergo a taxonomic revision, however ongoing research provides indication of a longitudinal gradient in the dental morphology of western and central European populations of *Prolagus oeningensis* at the end of Middle Miocene (Angelone et al., 2014; Prieto et al., 2012a). The differences become even more marked in the Late Miocene, when a remarkably high *Prolagus* palaeobiodiversity has been reported from the Paratethyan area (Angelone and Čermák, 2015; Angelone and Veitschegger, 2015). The same can be said for rooted lagomorphs, unusually frequent and abundant compared to western Europe (Hír et al., submitted). While the faunal assemblages are not endemic, *Prolagus* shows endemic traits, probably because it could not override geographical and/or ecological barriers. This phenomenon can be observed in some other taxa as well, as for example the endemic ochotonid *Alloptox katinkae*, found in the non-endemic assemblage of Litke 2 (Angelone and Hír, 2012), which contains *Cricetodon meini*, a widespread species in Europe. In contrast, *Parasorex* sp. from the same locality is not recognized in the Late Miocene in the North Alpine Foreland Basin, where members of the genus *Galerix* are common. Interestingly, Prieto et al. (2015) recognize, especially based on the mole *Desmanodon* aff. *crocheti*, clearer similarities with the insectivore compositions of German localities correlated to the Late Badenian. This would indicate a westward shifting of the ecosystems at this time. This is also suggested by the presence in Hasznos of two bat species previously defined in the Frankian Alb (southern Germany, Latest Badenian; Rosina and Rummel, 2012; Rosina et al., 2015). *Megacricetodon similis* in Subpiatră (as *Megacriceton* sp. in Hír and Venczel, 2005; see discussion in Hír et al., submitted) also supports this assumption, as well as the presence of the squirrel *palaeosciurus ultimus* in Hasznos, a species only known from the younger fissure fillings from La Grive in France (Mein and Ginsburg, 2002). Unfortunately, no data are available at present for the insectivores from Subpiatră.

The Sarmatian faunas are, in this respect, even more remarkable in their composition. This is, with the exception of the Spanish record, evidently due to the lack of sufficient localities of this time interval in Europe (see above). Indeed,

	Felsőtárkány 3/10	Felsőtárkány 3/2	Felsőtárkány 2	Felsőtárkány 1	Felsőtárkány 2/3, 2/7	Tauţ	Tăşad	Vârciorog	Mátraszőlős 2	Mátraszőlős 1	Subpiatră 2/2	Subpiatră 2/1	Sámsonháza 3	Litke 1, 2
Albanerpetontidae indet.	■													
Parahynobius sp.	■													
Mertensiella caucasica	■													
Salamandra cf. *sansaniensis*														■
Salamandra cf. *salamandra*	■													
Chelotriton paradoxus						■								
Chelotriton sp.													■	■
Salamandrina sp.				■										
Carpathotriton matraensis									■	■				
Carpathotriton sp.						■								
Lissotriton vulgaris												■		
Lissotriton cf. *rohrsi*	■	■	■	■					■					
Lissotriton sp.						■		■		■	■			■
Triturus cf. *marmoratus*	■					■								
Latonia gigantea	■	■	■	■	■	■		■	■	■	■	■	■	■
Discoglossus sp.									■	■				
Palaeobatrachus hiri	■				■	■			■	■			■	
Palaeobatrachus sp.								■			■			
Pelodytes cf. *caucasicus*					■									
Pelobates sanchizi	■	■	■	■	■				■	■			■	■
Pelobates sp.						■						■		
Bufotes cf. *viridis*	■		■			■			■	■		■	■	■
Hyla cf. *arborea*	■		■	■	■	■		■	■	■	■			
Hyla sp.														■
Pelophylax esculenta synkl.									■	■			■	
Pelophylax sp.	■	■	■		■	■						■		■
Geckonidae indet.			■	■		■		■			■			
Agama sp. (s.l.)							■							■
Anguis cf. *fragilis*		■	■	■	■								■	
Ophisaurus cf. *spinari*	■	■	■	■	■									
Ophisaurus sp. (s.l.)						■	■	■	■	■	■	■		■
Pseudopus sp.	■	■			■		■	■						
Miolacerta sp.														■
Lacerta sp.		■		■	■	■	■	■					■	
Lacertidae indet.	■	■	■	■	■	■					■	■		■
Blanus cf. *gracilis*						■								
Chalcides cf. *ocellatus*	■				■									
Chalcides sp.				■										
Scincidae indet.			■					■						
Varanus sp.								■				■		■
Scolecophidia indet.	■		■	■	■	■			■	■		■		
Albaneryx volynicus			■											
Eryx sp.														■
Texasophis sp.										■			■	■
Neonatrix cf. *crassa*														■
Natrix cf. *rudabanyaensis*	■	■	■			■								
Natrix sp.				■				■	■	■		■	■	
"Coluber" poucheti	■	■												
Coluber cf. *caspioides*														■
Coluber sp.										■			■	
Hierophis cf. *hungaricus*					■	■		■		■				
Coronella miocaenica						■								
Zamenis sp.				■					■	■				
Colubrinae indet.	■		■	■			■				■	■		■
Micrurus cf. *gallicus*										■			■	
Elapidae indet.		■	■											
Macrovipera sp.						■		■						
Vipera sp. (gr. *berus*)	■		■	■										
Vipera sp. (gr. *aspis*)	■				■							■		
Viperidae indet.		■	■	■	■				■					
Diplocynodon sp.							■	■			■	■	■	

Fig. 5. The fossil record of Lissamphibia, Squamata and Crocodylia of several Badenian – early Pannonian localities from the Pannonian region.

Fig. 5. Enregistrement fossile des Lissamphibia, Squamata and Crocodylia de quelques localités badéniennes – pannoniennes précoces de la région pannonienne.

the Latest Sarmatian-Earliest Pannonian faunas share common or closely related elements with, for instance, the German localities Hammerschmiede and Hillenloh which range in age between 11.6 and 11.3 Ma (Kirscher et al., 2016), or Bełchatów A and Opole in Poland. This indicates that the ecosystem structure was most probably relatively homogeneous at this time in central and Eastern Europe. In contrast, the early Late Sarmatian locality of Gratkorn (Austria), although geographically close, shows distinct differences in its small mammal composition. The explanation for this pattern is currently unclear. Remarkable differences are also observed with some Romanian localities (Tauţ, Comănesti 1), which deserve further analysis. Finally, the small mammal communities indicate an influence of southeastern ecosystems (Anatolia) throughout the studied period, as shown, for instance, by *Desmanodon*, *Schizogalerix*, *Alloptox* and the "high-crowned" Cricetodontini. An Asiatic origin can also be assumed for some snakes and amphibians (Venczel and Hír, 2015, and references therein). Such a relationship has been noted by De Bruijn et al. (2013) who recognized up to 40% shared species of Cricetidae and Dipodidae between Europe and Anatolia during the considered time span.

3.4. Palaeoenvironmental notes

The end of the long and warm period of the Middle Miocene climate optimum (MMO) is documented in our work especially by the Early and Middle Badenian faunas. At around 15 Ma, the start of the global cooling with obliquity modulation of the climate is proposed by Böhme et al. (2011). More precisely, the palaeofaunas of central to western Europe show mean daily precipitation comparable to present-day values, but the absolute precipitation values for central Europe were lower than today. At this time, Litke 1 and 2 contain the widespread *Cricetodon meini* that geographically ranges from France to Greece, probably indicating relatively homogenous conditions across Europe. In addition, the lissamphibian and squamate reptile faunas characterized by numerous thermophilous taxa indicate moderately warm conditions with considerably low mean annual precipitation (Venczel and Hír, 2015), but typical groups present during the MMO (e.g., crocodilians) are missing. Notably, crocodiles are known from the lagoonal environment of Sámsonháza 3 (Middle Badenian; Hír and Mészáros, 2002), but we do not notice significant differences with Litke in the small mammal composition, especially the insectivores (Prieto et al., 2012b, 2015, Fig. 4).

The Middle Miocene cooling (MMC) is a stepwise global event between ca. 14 and 13.2 Ma. The first phase between 14 and 13.8 Ma is an abrupt drop in temperature (Lewis et al., 2008). This cooling is accompanied by an increase in aridity leading to the replacement of evergreen forest by deciduous and mesothermic vegetation in Hungary (Jiménez-Moreno, 2006). Just following the glacial event Mi-3b, the onset of the Badenian salinity crisis at 13.8 Ma (De Leeuw et al., 2010) also marks substantial environmental changes. This critical period is recorded in the Subpiatră section, and strong differences in the small mammal composition occur between the different layers, suggesting a dry scrub environment for the layer 2/1, while the fauna

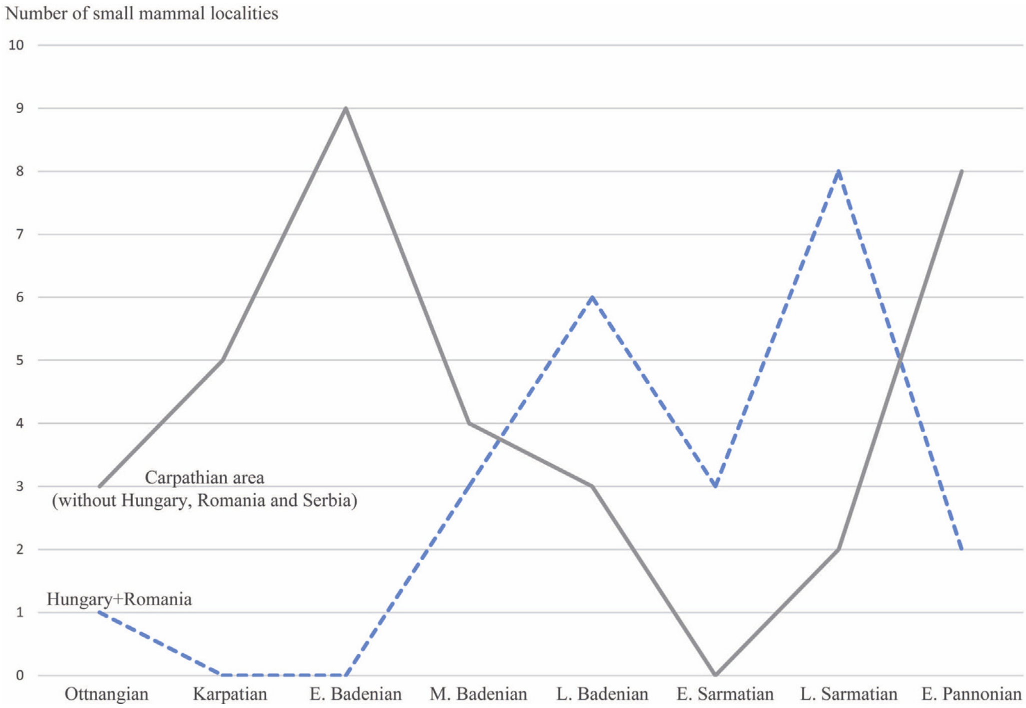


Fig. 6. Numbers of small mammal localities in the Carpathian area from the Ottnangian to the earliest part of the Pannonian showing the importance of the Hungarian and Romanian records particularly for the Sarmatian stage.

Fig. 6. Nombre de localités à petits mammifères dans la région des Carpates depuis l'Ottnangien jusqu'à la base du Pannonien montrant l'importance des enregistrements hongrois et roumains, pour l'étage Sarmatien en particulier.

from 2/2 points to a forested cover because of the high percentage of squirrels and dormice (Hír and Venczel, 2005). Typical groups present in the MMO are still present.

The central Paratethys is the theater of a major extinction event at the Badenian-Sarmatian transition with brutal and full loss of corals and echinoids for instance (Harzhauser and Piller, 2007; Ser3 low stand). The chronology of this event is debated, and the age used in this paper (12.83 Ma after Hohenneger et al., 2014) could be a bit too old (12.65 Ma after Palcu et al., 2015 and see references therein). Also in terrestrial environments, drastic changes are observed in small mammal composition, especially among the insectivores (Fig. 4), as shown in Mátraszőlős 3. Unfortunately, the correlation of the locality is rather tentative, but may be correlated near the Late Badenian/Sarmatian s. str. transition as the assemblage resembles in many points the small mammal faunas of the Sarmatian s. str. Böhme and Vasilyan (2014) compare the rich lower vertebrate collection from Gratkorn (Austria, early Late Sarmatian s. str.; Böhme et al., 2014; Gross et al., 2011) to the Sarmatian record from Hungary and Romania and come to the conclusion that the entire regional stage shows annual precipitation well below to near the present days values, which considering the much warmer temperature, would implicate a lack of perennial freshwater bodies. However, crocodiles, thought to be completely absent in the Sarmatian deposits (Böhme, 2003), are indeed recorded in the early part of the stage (Fig. 5; Venczel and Hír, 2015). In addition, the presence of *Varanus* in Vârciorog implies a mean annual temperature not below 14.8 °C (Böhme, 2003). Based on the small mammal composition and the paleoflora, increasing humidity and decreasing temperatures are proposed for the Felsőtárkány basin (Erdei, 1999; Hír, 2004; Venczel and Hír, 2015).

The isolation of the Pannonian Basin caused by the uplift of the Carpathian mountains, possibly coupled with eustatic sea-level fluctuation, occurs at the end of the Middle Miocene, more precisely at 11.63 Ma. It resulted in major paleoenvironmental changes from marine to freshwater conditions and the regional Sarmatian-Pannonian extinction event (Ser4/Tor1 Low stand; Borgh et al., 2013 and references therein). From a terrestrial point of view, newcomers (*Microtocricetus molassicus*, *Glis vallesiensis*) document also notable changes in the small mammal communities. In the western Paratethys, synchronous faunas (e.g., Hammerschmiede) might represent the last faunas with a Middle Miocene character (Fuss et al., 2015; Kirscher et al., 2016).

4. Conclusions

Thanks to the intensive fieldwork of the last decades, a representative vertebrate collection from the Hungarian and Romanian Middle/early Late Miocene is now available to science. Whereas large mammals are mostly rare in the studied localities, rodents, eulipotyphlans, lagomorphs and chiropterans are well-represented. These are accompanied by diverse faunas of reptiles, amphibians and birds, whose richness in some localities of the middle and late Miocene is especially impressive for the Pannonian basin.

The chronostratigraphic range of the localities (basically Middle Badenian-?Earliest Pannonian) covers a period marked by strong, even catastrophic events that greatly influenced the marine fauna in the Carpathian Basin s. l. (Badenian-Sarmatian and Sarmatian-Pannonian extinction events), in relation with global events such as the middle Miocene cooling. The Hungarian and Romanian records are thus a unique window into the terrestrial impact of these changes. Most importantly, the Late Sarmatian, abundant in the studied area, is extremely poorly documented elsewhere. The geographic position of the studied area is of primary importance to document the faunal exchange between Europe and Asia Minor. As such, the Carpathian area is of the utmost importance for understanding the faunal dynamics of western Eurasia during the Middle Miocene, and for helping to develop long-distance correlations that will allow us to develop a full picture of the ecosystem development of this period.

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